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Forest Ecosystems

More than Just Trees

Edited by Juan A. Blanco and Yueh-Hsin Lo

FOREST ECOSYSTEMS – MORE THAN JUST TREES

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Meet the editors

After graduating in Agricultural Engineering, Dr Blanco obtained a PhD in Forest Ecology from the Public University of Navarre, Spain, and is currently a Research Associate at the Department of Forest Sciences, University of British Columbia, Canada. His work is focused on the development and evaluation of ecological models to simulate the influences of management, climate and other ecological factors on tree growth. Dr Blanco is currently collaborating with research teams from several countries on using ecological models to explore the effects of climate change, atmospheric pollution and alternative forest practices in natural and planted forest in boreal, temperate and tropical forests. He has published more than 70 scientific papers on forest ecology topics, and his research has been applied in various fields. Dr Blanco has co-authored "Forecasting Forest Futures" (Earthscan, London), the first book dedicated exclusively to the use of hybrid ecological models in forest management, and has edited three books on Climate Change published by InTech.

Dr Lo graduated in Forest and Natural Resource Management at the National Taiwan University, and obtained a PhD in Forest Ecology from the University of British Columbia (Canada). She is currently working as a Research Fellow at the Department of Geography, National Taiwan University. During her research, Dr Lo has studied the influence of climate on tree growth and productivity, and developed and tested models to simulate the effects of climate change on tree productivity, combining the use of tree-ring records with field data on biogeochemical factors and tree distribution. She has numerous scientific papers on forest ecology and environmental sciences and is is involved in several research lines studying the long-term influence of environmental factors on tree growth and forest development. In a more short-term perspective, Dr Lo is developing new algorithms to complete the records of eddy covariance to study forest respiration and productivity.

Contents

Preface

The common idea for many people is that forests are just a collection of trees. However, forests are much more than just that. They are complex, functional systems of interacting and often interdependent biological, physical, and chemical components, the biological part of which has evolved to perpetuate itself through the production of new organic matter created by consecutive generations of plants and animals (Kimmins 2004). This complexity produces combinations of climate, soil, and animal and plant species unique to each site, resulting in hundreds of different forest types around the world. Logically, trees are an important component and focus of any forest research program, but the wide variety of other life forms and abiotic components in most forests means that other elements, such as wildlife or soil nutrients, are often out of the focal point, even if they are of great importance for the composition and function of the ecosystem. Thus, the study of forest ecosystems is a highly diverse and important branch of the field of ecological studies. In this book, the readers can find the latest research related to forest ecosystems but with a different twist. The chapters in this book are not just on trees and are focused on the other components, structures and functions that are usually overshadowed by the focus on trees, but that are equally important in order to maintain the ecological services provided by forests.

Forests around the globe share common traits that allow us to develop general theoretical frameworks. Such common features obviously include the presence of trees, but also the presence of other plant and animal communities that are usually less noticeable but also play important roles. However, the presence of trees as large, non-mobile and long-lived individuals allows forests to be highly heterogeneous environments compared to other terrestrial plant communities. The infinite number of possible spatial arrangements of trees of various sizes and species produces a highly intricate and diverse microenvironment in which environmental variables such as solar radiation, air and soil temperature, relative humidity, soil moisture, nutrient availability, wind speed and others can vary considerably over large and small distances. In addition, an important proportion of forest biomass is often underground, where soil structure, water quality and quantity, and levels of various soil nutrients and gases can vary greatly. This heterogeneity in turn can enable great biodiversity of species of both plants and animals. This is why it is estimated that forests contain roughly 90% of the world terrestrial biodiversity (WWF 2004).

A number of factors within the forest ecosystem affect biodiversity; primary factors enhancing wildlife abundance and biodiversity are the presence of diverse tree species within the forest and the absence of timber management (Burton et al. 2003). In addition, the abiotic factors, such as climate, geology or topography are also important in determining which type of forest can or cannot grow in different areas. As a consequence, forests can be studied at a number of organizational levels, from the individual organism to the ecosystem. The first section of this book is focused on the structure of forest ecosystems. Merganic et al. discuss the importance of not just trees but also plant diversity in forests, whereas Roversi and Nannelli focus their work on the diversity of microfauna in forest ecosystems (arthropods and nematodes). Additionally, Patreze et al. describe the latest methodological advances to estimate the diversity of another important component of forests: the fungi. Both microfauna and fungi can be found at different levels in the forest ecosystem, but deadwood is probably where they play a more important role. However, deadwood itself is also an important part of the structure of any forest, and Merganicova et al. provide a review of the different types of deadwood, their structure and importance in forest ecosystems. Biodiversity and complexity varies among forest types, and tropical forests are usually considered to be among the most complex ones. Integral studies are needed to analyse the forest ecosystem as a whole and not just as competition among different tree species. To provide an example of such research, the section includes the analysis of two such forests: one in India, described by Mishra et al., and another one in Cameroon described by Assi-Kaudjhis. This section ends with the review by Martínez Morales on the current techniques and applications of remote sensing to study the forest structure, an important tool when working with large areas of landscape or in areas with restricted or difficult access, a common situation in tropical, alpine and boreal forests.

The study of the structure of the ecosystem lets us know how the forest is composed. However, knowing who is in the forest does not show us what they are doing in the system. To learn this, it is necessary to study the functioning of the forest ecosystem. The importance of the knowledge on ecosystem functioning (meaning fluxes of energy, water, carbon and nutrients) is increasing under the current global change that our planet is experiencing. These fluxes maintain the stability and the link among the structural components of ecosystems. It follows that if we want to understand and predict the change in a forest ecosystem and its influence on other ecosystems, it is crucial to know how forests function (Kimmins 2004). Long-term sustainability of forest ecosystems depends on maintaining natural nutrient, water and energy cycles. However, resource exploitation disturbs nutrient, water and energy fluxes in forests, and sometimes the effects can be irreversible, affecting productivity and other functions. Therefore, forest managers should be interested in understanding energy and resource cycling in their forest sites to anticipate ecosystem changes, assess if certain forest practices are sustainable, and finally to adapt and implement forest management techniques that preserve the ecosystem in the best possible way (Imbert et al. 2008). Because of the importance of viewing any renewable resource as a system, and because of the preoccupation for renewable-resource management that respects ecosystem function, in this section, these cycles are considered from the point of view of the non-tree components of the ecosystem. First, Kim et al. examine the links between ecohydrology and biogeochemistry in temperate forests. Takahashi et al. study the cycle of carbon in teak plantations, whereas Pinheiro Ruivo et al. analyze the relationship between site fertility and soil microbial and microfauna biomass. Augustyniuk-Kram and Kram explore the relationship between fungi and insects, and their roles as major disturbance agents in forest ecosystems. Rahman and Motiur review the chemistry of litter and its implication for nutrient cycling, and Nkongolo et al. study the sustainability of genetic diversity in polluted and altered forest ecosystems.

Forest ecosystems provide a wide range of supporting, provisioning, regulating and cultural services (the so-called ecosystem services: FAO 2011). Forests are essential to all humans because they provide a diverse range of resources (timber, fibre, fruits, energy, etc.); they store carbon, aid in regulating our climate, purify water and mitigate natural hazards such as floods. The complexity and diversity of ecosystems mentioned before has an important consequence: future events and conditions in forest ecosystems are difficult to predict. A detailed knowledge of ecosystem structure and function (Sections 1 and 2) greatly improves our ability to make accurate predictions, but this knowledge on its own is not always sufficient. Many ecological phenomena and resource management problems involve so many interacting factors that predictions are difficult despite our best knowledge. Therefore, site-specific research is always needed before designing forest management plans, either for productive objectives or for conservation. However, forest management must be a holistic activity in which the human intervention is planned taking into account the whole ecosystem, and not just the trees. Section 3 provides some examples of such type of research. Lo et al. describe a study in tropical plantations to move from passive conservation to active restoration of original forests, in which the role of forest fauna can be decisive. In the same line, Likhanova and Archegova describe the efforts of restoring disturbed boreal forests near the treeline. Moravcik et al. discuss the new approach to manage forest ecosystems simulating natural disturbance events in mountain ecosystems. Demir reviews the interactions between forest roads (a vital part of any forest management system) and the ecosystem. This topic is further discussed by Pentek and Porsinsky, who examine the transportation systems as a key factor in designing sustainable forest management plans.

All things considered, these 18 chapters provide a good overview of the “other” parts of the forest ecosystem that are usually less represented in research and usually not taken into account in forest management. These chapters show the importance of the non-tree component on the structure and function of forests that can be applied to all the regions of the world. They are an introduction to the research being done around the globe related to this topic. We hope the readers from academia, management, conservation and any other stakeholders will enjoy reading this book and regard it as an initial source of information and study cases on what is in a forest ecosystem apart from trees.

The Editors want to finish this preface acknowledging the collaboration and hard work of all the authors. We are also thankful to the Publishing Team of InTech for their continuous support and assistance during the creation of this book. Special thanks are due to Ms. Adriana Pecar for inviting us to lead this exciting project and helping us during the first stages of the process, and to Mr. Dejan Grgur for coordinating the different editorial tasks.

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Part 1

Forest Structure and Biodiversity

1

Plant Diversity of Forests

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1. Introduction

Changes in biological diversity of natural ecosystems have in the second half of 20th century become a global problem due to intensive human activities. Therefore, higher attention has been paid to these problems. The year 1992 can be considered as the pivotal year in this field since in this year the Convention on Biological Diversity was approved on the United Nations Conference on Environment and Development in Rio de Janeiro. This document defines biological diversity - biodiversity as „the variety and variability among living organisms from all sources including inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part". This definition covers three fundamental components of diversity: genetic, species, and ecosystem diversity (Duelli, 1997, as cited in Larsson, 2001; Merganič & Šmelko, 2004). However, also this widely accepted definition like many others fails to mention ecological processes, such as natural disturbances, and nutrient cycles, etc., that are crucial to maintaining biodiversity (Noss, 1990). The complexity of the understanding of the term biodiversity was well documented by Kaennel (1998). Therefore, Noss (1990) suggested that for the assessment of the overall status of biodiversity more useful than a definition would be its characterisation that identifies its major components at several levels of organisation. Franklin et al. (1981 as cited in Noss, 1990) recognised three primary attributes of ecosystems: composition, structure, and function.

1.1 Species diversity

Strictly speaking, species diversity is the number of different species in a particular area (species richness) weighted by some measure of abundance such as number of individuals or biomass. However, conservation biologists often use the term species diversity even when they are actually referring to species richness, i.e. to number of present species (Harrison et al., 2004). Noss (1990) defines species diversity as a composition that refers to the identity and variety of elements in a population, includes species lists and measures of species diversity and genetic diversity.

1.2 Structural diversity

"Structural diversity refers to the physical organisation or pattern of a system, including the spatial patchwork of different physical conditions in a landscape, habitat mosaics, species assemblages of different plant and animal communities, and genetic composition of subpopulations" (Stokland et al., 2003). The main structural indicators that are used to describe the conditions for forest biodiversity include stand vertical structure, age class distribution and the amount of dead wood (Christensen et al., 2004). They represent an indirect approach „as they show, typically on a rather gross scale, how the house is built, but give no information on whether the inhabitants have moved in" (Christensen et al., 2004).

1.3 Functional diversity

According to Noss (1990), function involves all ecological and evolutionary processes, including gene flow, disturbances, and nutrient cycling. "Functional diversity involves processes of temporal change, including disturbance events and subsequent succession, nutrient recycling, population dynamics within species, various forms of species interactions, and gene flow" (Stokland et al., 2003).

2. Factors influencing plant diversity in forest ecosystems

Within certain time and space, diversity is determined by the combination of abiotic constraints, biotic interactions, and disturbances (Frelich et al., 1998; Misir et al., 2007; Nagaraja et al., 2005; Spies & Turnier, 1999; Ucler et al., 2007). Abiotic factors, such as elevation, slope, aspect, soil texture, climate etc., specify the conditions of physical environment and thus the primary species distribution. The relations were already regarded and studied in 19th century (Hansen & Rotella, 1999). The parameters affecting the plant growth and nutrient availability, e.g. climate, are considered as primary factors (Terradas et al., 2004), while terrain characteristics, e.g. elevation, are regarded as indirect factors, because they do not influence the plant growth directly, but are correlated to primary factors (Pausas et al., 2003; Bhattarai et al., 2004).

Primary climate and site conditions have influenced and determined biodiversity on a specific site in the long-term development of forest ecosystems (Stolina, 1996). Hence, the actual biodiversity is the result of the adaptation process of species. In the current conditions of climate change the species will have to respond to faster changes. Although the effect of climate change will vary from site to site, it is likely that its impacts on ecosystems will be adverse, as species will have to deal with a variety of new competitors, and biotic factors (diseases, predators), to which they have no natural defense so far (IUCN, 2001).

Indirect factors are often used in the analyses, when the information about the primary factors is not available (Pausas & Saez, 2000). Most often, the relationship between the diversity and elevation is examined (Bachman et al., 2004; Bhattarai & Vetaas, 2003; Grytnes & Vetaas, 2002), while the influence of other topography characteristics is tested only seldom (Johnson, 1986; Palmer et al., 2000). Although modern ecologists focus mainly on other influencing factors, e.g. natural disturbances, the influence of abiotic conditions on species diversity has recently begun to gain attention of researchers (Austin et al., 1996; Burns, 1995; Hansen & Rotella, 1999; Ohmann & Spies, 1998; Rosenzweig, 1995). However, most of these works analyse the environmental factors only with regard to the number of tree species representing just one part of species diversity.

Abiotic factors, such as elevation, slope, aspect, terrain type etc., create together a unique complex of environmental conditions specifying forest communities (Spies & Turner, 1999). The relation between elevation and species diversity is generally accepted and was documented by several authors, not only for tree species but also regarding the diversity of plants and animals (Rosenzweig, 1995). Very often hump-shaped curves with maximum species diversity at mid-elevations were reported (Bhattarai & Vetaas, 2003; Bachman et al., 2004; Ozcelik et al., 2008). In Merganič et al. (2004), elevation was also found to have a significant influence on tree species diversity, but at mid-elevations the lowest values of tree species diversity were observed. This performance can most probably be explained by the fact that in the Slovak Republic at about 600 m above sea level, beech has its optimum growing conditions, which causes that at these altitudes beech is so vital and competitive that other species become rare. Johnson (1986) and Ozcelik et al. (2008) detected the significant correlation between tree species diversity and aspect.

2.1 Forest management

In Europe forests have played an important role since their establishment after the last ice age that ended 12,000 years ago. In the human thoughts, the forest was an unknown and untouched place with secrets and dangers. It provided a man with a shelter, fuel wood, and cosntruction material (Reinchholf, 1999). A man started to have a stronger influence on a forest ecosystem around the year 4,000 B.C. The impact was first low; he cut trees to obtain space for settlements and for grazing of his animals. With the increasing demands on space, forest ecosystems were more and more utilised, which led to the significant decrease of forest area in the whole Europe. In 16th century, the first attempts to grow introduced tree species, namely Castanea sativa, occurred. However, the most significant changes of forest ecosystems started in 19th century with the beginning of a so-called "spruce and pine mania". In this period, the majority of forestland was afforested with spruce, even in completely unsuitable conditions. The main reason of this boom was to maximise wood production. Nowadays, it is known that such an approach has had a negative impact on stand stability, as well as on forest biodiversity. The look of the forests today particularly in the densely inhabited areas is related to management intensity and methods (Hédl & Kopecký, 2006). The absence of suitable management is another cause of decreasing forest biodiversity (Hédl, 2006).

Although currently biodiversity has become a key component of Central European forests, there is only a limited number of studies, which examine the influence of forest management on biodiversity of e.g. plants (Prevosto, 2011). In addition, the results are often contradictory. On one side, some works present that forest management has a negative effect on biodiversity (Gilliam & Roberts, 1995; Sepp & Liira, 2009). Other works (e.g. Battles, 2001; Newmaster, 2007; Ramovs & Roberts, 2005; Ravindranath, 2006; Wang & Chen, 2010) show that a well-chosen management can influence biodiversity positively. The compatibility of suitable management activities with biodiversity conservation is critical to ensure wood harvesting and other ecologically valuable aspects in forested land (Eriksson & Hammer, 2006). Sustainable forest management represents how high biodiversity can be achieved together with high wood production. This type of management maintains forests and forest soil in order to secure biodiversity, productivity, regeneration capacity, vitality, and abilities to fulfil all ecological, economic, and social functions today and in future on any spatial scale (local, regional, national) without the drawback on other ecosystems (Poleno, 1997). Sustainability means the ability to provide current and future generations with permanent and optimal wood yield and other forest ecosystem products (Smola, 2008).

3. Diversity assessment

Due to the complexity of biodiversity and of forest ecosystems, complete assessments of biodiversity are not practically achievable (Humphrey & Watts, 2004) because of the impossibility to monitor all taxa or features (Lindenmayer, 1999). Therefore, means to reduce complexity are necessary (Christensen et al., 2004). In this context, reliable indicators or short-cut measures of biodiversity are searched for (Ferris & Humphrey, 1999; Jonsson & Jonsell, 1999; Noss, 1999; Simberloff, 1998 as cited in Humphrey & Watts, 2004). From the long-term perspective, the basic criterion for any biodiversity assessment system is that it is based on an enduring set of compositional, structural and functional characteristics (Allen et al., 2003). In addition, a complete long-term biodiversity strategy must take into account both interactions between the different geographical levels and the fact that different elements of biodiversity are dependent on different geographical scales, in different time perspectives (Larsson, 2001).

3.1 Species diversity

Species diversity can be evaluated by a great number of different methods (e.g. see Krebs, 1989; Ludwig & Reynolds, 1988). All of the proposed methods are usually based on at least one of the following three characteristics (Bruciamacchie, 1996):

- species richness – the oldest and the simplest understanding of species diversity expressed as a number of species in the community (Krebs, 1989);
- species evenness – a measure of the equality in species composition in a community;
- species heterogeneity – a characteristic encompassing both species abundance and evenness.

The most popular methods for measurement and quantification of species diversity are species diversity indices. During the historical development, the indices have been split into three categories: indices of species richness, species evenness and species diversity (Krebs, 1989; Ludwig & Reynolds, 1988). The indices of each group explain only one of the above-mentioned components of species diversity (Merganič & Šmelko, 2004).

3.1.1 Species richness

The term species richness was introduced by McIntosh (1967) to describe the number of species in the community (Krebs, 1989). Surely, the number of species S in the community is the basic measure of species richness, defined by Hill (1973) as diversity number of 0th order, i.e. N0. The basic measurement problem of N0 is that it is often not possible to enumerate all species in a population (Krebs, 1989). In addition, S depends on the sample size and the time spent searching, due to which its use as a comparative index is limited

(Yapp, 1979). Hence, a number of other indices independent of the sample size have been proposed to measure species richness. These indices are usually based on the relationship between S and the total number of individuals observed (Ludwig & Reynolds, 1988). Two such well-known indices are R1 and R2 proposed by Margalef (1958) and Menhinick (1964), respectively. Hubálek (2000), who examined the behaviour of 24 measures of species diversity in a data from bird censuses, assigned to the category of species richness-like indices also the index α (Fischer et al., 1943; Pielou, 1969), Q (Kempton & Taylor, 1976, 1978), and R500 (Sanders, 1968; Hurlbert, 1971).

3.1.2 Species evenness

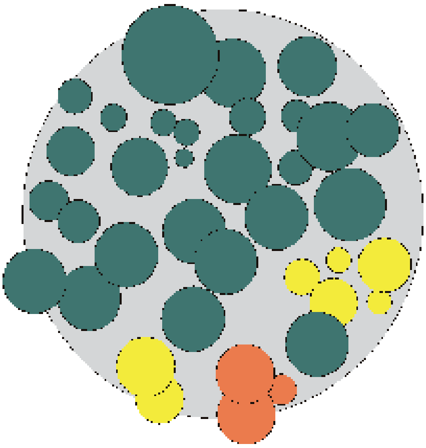
Lloyd & Ghelardi (1964) were the first who came with idea to measure the evenness component of diversity separately (Krebs, 1989). The principle of the evenness measures is to quantify the unequal representation of species against a hypothetical community in which all species are equally common. Ludwig & Reynolds (1988) present five evenness indices E1 (Pielou, 1975, 1977), E2 (Sheldon, 1969), E3 (Heip, 1974), E4 (Hill, 1973), and E5 (Alatalo, 1981), each of which may be expressed as a ratio of Hill´s numbers. The most common index E1, also known as J′ suggested by Pielou (1975, 1977) expresses H′ relative to maximum value of H′ (= log S). Index E2 is an exponentiated form of E1. Based on the analysis of Hubálek (2000), McIntosh`s diversity D (McIntosh, 1967; Pielou, 1969), McIntosh`s evenness DE (Pielou, 1969), index J of Pielou (1969) and G of Molinari (1989), are also evenness measures.

3.1.3 Species heterogeneity

This concept of diversity was introduced by Simpson (1949) and combines species richness and evenness. The term heterogeneity was first applied to this concept by Good (1953). Many ecologists consider this concept to be synonymous with diversity (Hurlbert, 1971, as cited in Krebs, 1989). According to Peet (1974, as cited in Ludwig & Reynolds, 1988), an infinite number of diversity indices exist. Simpson proposed the first heterogeneity index λ, which gives the probability that two individuals picked at random from the community belong to the same species. This means that if the calculated probability is high, the diversity of the community is low (Ludwig & Reynolds, 1988). To convert this probability to a diversity measure, the complement of Simpson´s original measure, i.e. 1-λ, is used (Krebs, 1989).

Probably the most widely used heterogeneity index is the Shannon index H′ (or Shannon-Wiener function), which is based on information theory (Shannon & Weaver, 1949). It is a measure of the average degree of "uncertainty" in predicting to what species an individual chosen at random from a community will belong (Ludwig & Reynolds, 1988). Hence, if H´ = 0, the community consists of only one species, whereas H´ is maximum (= log(S)) if all species present in the community are represented by the same number of individuals. Shannon index places most weight on the rare species in the sample, while Simpson index on the common species (Krebs, 1989).

From other heterogeneity measures we mention Brillouin Index H (Brillouin, 1956), which was first proposed by Margalef (1958) as a measure of diversity. This index is preferred being applied to data in a finite collection rather than H´. However, if the number of individuals is large, H and H´ are nearly identical (Krebs, 1989). The indices N1 and N2 from Hill`s family of diversity numbers (Hill, 1973), which characterise the number of “abundant”, and “very abundant” species, respectively, also belong to diversity measures. The McIntosh index is based on the representation of a sample in an S-dimensional hyperspace, where each dimension refers to the abundancy of a particular species (Bruciamacchie, 1996). According to the evaluation performed by Hubálek (2000), NMS “number of moves per specimen” proposed by (Fager, 1972), H´adj, which is an adjusted H´ by the d(H) correction (Hutcheson, 1970), and R100 (Sanders, 1968; Hurlbert, 1971) can also be regarded as heterogeneity indices.



Legend:
🟢 Fagus sylvatica, 🟡 Picea abies, 🟠 Abies alba
Species richness: 3, Species evenness: Low, Species heterogeneity: Low.

Fig. 1. Assessment of tree species diversity.

3.2 Structural diversity

Structural diversity is defined as the composition of biotic and abiotic components in forest ecosystems (Lexer et al., 2000), specific arrangement of the components in the system (Gadow, 1999) or as their positioning and mixture (Heupler, 1982 as cited in Lübbers, 1999). According to Zenner (1999) the structure can be characterised horizontally, i.e. the spatial distribution of the individuals, and vertically in their height differentiation. Gadow & Hui (1999) define the structure as spatial distribution, mixture and differentiation of the trees in a forest ecosystem.

There exist a number of different methods to describe the structure and its components. The classical stand description is based on qualitative description of stand closure, mixture, density, etc. Graphical methods presenting diameter distribution, stand height distribution curves, tree maps, etc. are also useful. However, both verbal and graphical methods may not be sufficient to reveal subtle differences (Kint et al., 2000). Therefore, a number of quantitative methods have been proposed that should overcome these shortages. Partial reviews can be found in Pielou (1977), Gleichmar & Gerold (1998), Kint et al. (2000), Füldner (1995), Lübbers (1999), Gadow & Hui (1999), Neumann & Starlinger (2001), Pommerening (2002) etc.

3.2.1 Horizontal diversity

The indices characterising forest horizontal structure usually compare a hypothetical spatial distribution with the real situation (Neumann & Starlinger, 2001). Probably the most well-known index is the aggregation index R proposed by Clark & Evans (1954) that describes the horizontal tree distribution pattern (or spacing as named by Clark & Evans (1954), or positioning as defined by Gadow & Hui (1999)). It is a measure of the degree to which a forest stand deviates from the Poisson forest, where all individuals are distributed randomly (Tomppo, 1986). It is the ratio of the observed mean distance to the expected mean distance if individuals were randomly distributed.

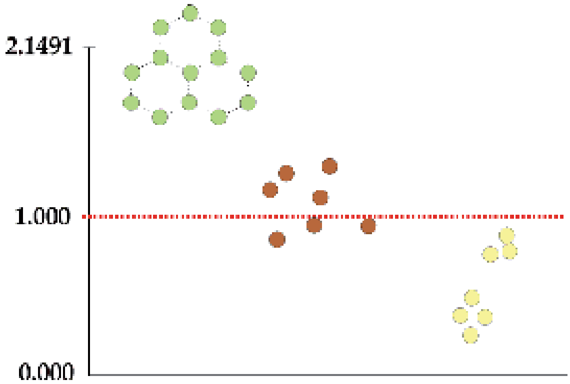


Fig. 2. Schematic visualisation of the assessment of forest horizontal structure using R index by Clark & Evans (1954).

A similar measure is the Pielou index of nonrandomness (Pielou, 1959), which quantifies the spatial distribution of trees by the average minimum distance from random points to the nearest tree (Neumann & Starlinger, 2001). The Cox index of clumping (Strand, 1953; Cox, 1971) is the ratio of variance to mean stem number on sub-plots. Gadow et al. (1998) proposed an index of neighbourhood pattern based on the heading angle to four next trees. Another commonly used measures of horizontal structure are methods proposed by Hopkins (1954), Prodan (1961), Köhler (1951) and Kotar (1993 as cited in Lübbers, 1999).

According to Gadow & Hui (1999), mixture is another component of structure. For the quantification of mixing of two tree species, Pielou (1977) proposed the segregation index based on the nearest neighbour method like the index A of Clark & Evans, while the calculated ratio is between the observed and expected number of mixed pairs under random conditions. Another commonly used index is the index DM (from German Durchmischung) of Gadow (1993) adjusted by Füldner (1995). On the contrary to the segregation index, DM accounts for multiple neighbours (Gadow, 1993 used 3 neighbours) and is not restricted to the mixture of two species (Kint et al., 2000).

Differentation is the third component of structure (Gadow & Hui, 1999), which describes the relative changes of dimensions between the neighbouring individuals (Kint et al., 2000). Gadow (1993) and Füldner (1995) proposed the differentiation index T, which is an average of the ratios of the smallest over the largest circumference calculated for each tree and its n nearest neighbours. Instead of the circumference, diameter at breast height can be used in this index to describe the horizontal differentiation as presented by Pommerening (2002). Values of the index T close to 0 indicate stands with low differentiation, since neighbouring trees are of similar size. Aguirre et al. (1998) and Pommerening (2002) suggested the scales of five or four categories of differentiation, respectively.

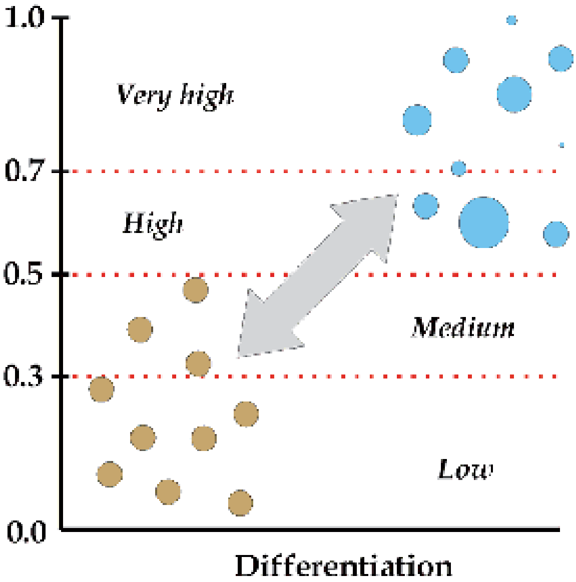


Fig. 3. Schematic visualisation of the assessment of stand differentiation according to Füldner (1995) with categories proposed by Aguirre et al. (1998).

3.2.2 Vertical diversity

While there are many indices that measure horizontal structure, there are only few for vertical structure (Neumann & Starlinger, 2001). Simple measures such as the number of vegetation layers within a plot can be used as an index of vertical differentiation (Ferris-Kaan & Patterson, 1992 as cited in Kint et al., 2000). The index A developed by Pretzsch (1996, 1998) for the vertical species profile is based on the Shannon index H'. In comparison with H' the index A considers species portions separatelly for a predefined number of height layers (Pretzsch distinguished 3 layers). The index proposed by Ferris-Kaan et al. (1998) takes the cover per layer into account, but needs special field assessments (Neumann & Starlinger, 2001). Therefore, using the same principles as Pretzsch (1996), i.e. Shannon index and stratification into height layers, Neumann & Starlinger (2001) suggested an index of vertical evenness VE that characterises the vertical distribution of coverage within a stand. The differentiation index T of Gadow (1993) is also applicable for the description of vertical differentiation, if the index is calculated from tree heights.

3.2.3 Complex diversity

Complex indices combine several biodiversity components in one measure. These indices are usually based on an aditive approach, i.e. the final value is obtained as a sum of the values of individual biodiversity components. Usually, two ways of quantification individual biodiversity components are applied: (1) by assigning the value on the base of a pre-defined scale, or (2) to use the real measurement units. In addition, if required individual biodiversity components can be assigned different weights according to their importance for the whole biodiversity.

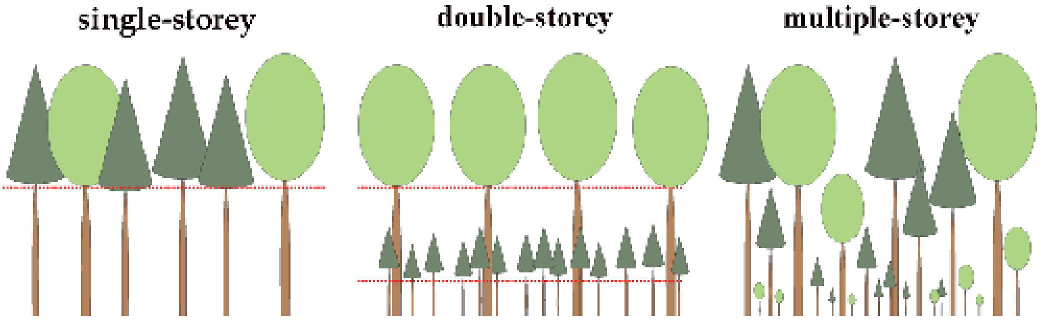


Fig. 4. Quantification of vertical diversity.

The first system of biodiversity assessment using scores is simple and easy to use (Meersschaut & Vandekerkhove, 1998). Such quantification was already used in 1969 by Randwell to assess the need for the protection of seashore sites on the base of Comparative Biological Value Index (Nunes et al., 2000). Meersschaut & Vandekerkhove (1998) developed a stand-scale forest biodiversity index based on available data from forest inventory. The index combines four major aspects of a forest ecosystem biodiversity: forest structure, woody and herbaceous layer composition, and deadwood. Each aspect consists of a set of indicators, e.g. forest structure is defined by canopy closure, stand age, number of stories, and spatial tree species mixture. The indicators are given a score determined on the basis of a common agreement. The biodiversity index is calculated as the sum of all scores, while its maximum value is set to 100. Another complex index named Habitat Index HI was developed by Rautjärvi et al. (2005). The authors also use the name habitat index model as it was produced as a spatial oriented model. The inputs in the model come from thematic maps from Finnish Multi-source national forest inventory (predicted volume of growing stock, predicted stand age, and predicted potential productivity) and kriging interpolation maps from national forest inventory plot data (volume of dead wood, and a measure for naturalness of a stand). The input variables were selected based on the forest biodiversity studies in Scandinavia. The index is of additive form where all input layers contribute to the result layer. All input variables (layers) are reclassified and enter the model as discreet variables, while each input layer is assigned a different weight according to its importance to biodiversity.

The second quantification method was used in the model BIODIVERSS proposed by Merganič & Šmelko (2004) that estimates tree species diversity degree of a forest stand by summing up the values of 5 diversity indices (R1, R2, λ, H′ and E1). The fundamental method of the model BIODIVERSS is a predictive discriminant analysis (StatSoft Inc., 2004; Huberty, 1994; Cooley & Lohnes, 1971), which means that each species diversity degree is represented by one discriminant equation. For each examined forest stand, four discriminant scores are calculated, and the stand is assigned a species diversity degree with maximum discriminant score.

LLNS index proposed by Lähde et al. (1999) is a complex index for calculating within-stand diversity using the following indicator variables: stem distribution of live trees by tree species, basal area of growing stock, volume of standing and fallen dead trees by tree species, occurrence of special trees (number and significance), relative density of undergrowth, and volume of charred wood. The LLNS index is calculated as the sum of diversity indices describing particular components (i.e. living trees, dead standing trees etc.). However, the authors also developed a scoring table for the indicator variables. The final value of LLNS is then obtained by adding all the scores together. The evaluation of this index using Finnish NFI data revealed, that the LLNS index differentiates even-sized and uneven-sized stand structures, the development classes of forest stands and site-types fairly well (Lähde et al., 1999).

A special category of complex indices covers complex structural indices that encompass several components of structural diversity. For example, Jaehne & Dohrenbusch (1997) proposed the Stand Diversity Index that combines the variation of species composition, vertical structure, spatial distribution of individuals and crown differentiations. The Complexity Index by Holdridge (1967) is calculated by multiplying four traditional measures of stand description: dominant height, basal area, number of trees and number of species. Hence, this index contains no information on spatial distribution nor accounts for within stand variation (Neumann & Starlinger, 2000). Zenner (1999), and Zenner & Hibbs (2000) developed the Structural Complexity Index (SCI) based on the vertical gradient differences between the tree attributes and the distances between the neighbouring trees. When all trees in a stand have the same height, the value for SCI is equal to one, which is the lower limit of SCI (Zenner & Hibbs, 2000).

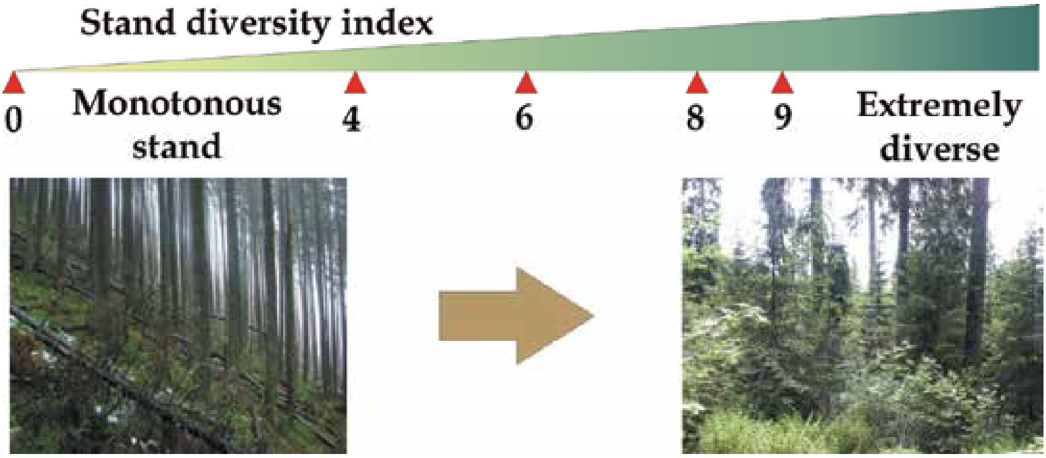


Fig. 5. Complex assessment of stand diversity according to Jaehne & Dohrenbusch (1997).

3.3 Functional diversity

From a functional point of view, species can be subdivided into categories like primary producers, herbivores, predators, and decomposers (Stokland et al., 2003). Belaoussoff et al. (2003) defined a functional group as a group of species, which do not necessarily have to be related, but which exploit a common resource base in a similar fashion. Hence, there is an overlap in resource requirements between species in a functional group (Belaoussoff et al., 2003).

The BEAR-project strongly recommends including functional indicators in any Biodiversity Evaluation Tool. Within the framework of the BEAR project, fire, wind and snow, and biological disturbance have been identified as the most important functional key factors in the group of "natural influences", while the area affected by a particular factor are suggested as possible indicators with high ecological significance (BEAR Newsletter 3). Although in reality the ecosystem function might be more important than species diversity (Sobek & Zak, 2003), structural and compositional indicators are considered to be more tractable for end-users (Angelstam et al., 2001 as cited in Humphrey & Watts, 2004).

3.4 Diversity inventory in forest ecosystems

To get an overview, forest inventory data can be a cost effective source of information for large areas (Söderberg & Fridman, 1998), because forest inventories represent a major source of data concerning forests (Estreguil et al., 2004). The original aim of forest inventories was to describe the main features of forests in terms of size, condition, and change, particularly from the production perspective (Rego et al., 2004). An increasing demand for information on non-productive functions of forests caused that recently variables more related to biodiversity have been introduced to forest inventories (Söderberg & Fridman, 1998). For example, the recognition of the ecological importance of decaying wood has led to the incorporation of quantitative measures of deadwood in forest inventories (Humphrey et al., 2004). Hence, national forest inventories are becoming more comprehensive natural resources surveys (Corona & Marchetti, 2007) .

Basically, forest inventories provide us with the information about: 1) forest area and land cover, 2) resource management (growing stock), 3) forestry methods and land use (felling systems, regeneration methods, road network density), 4) forest dynamics with regard to different disturbance factors (fire, storm, insect, browsing), 5) forest state (tree species composition, age distribution, dimension of living trees, tree mortality and deadwood), and partly also about 6) conservation measures, i.e. protected forest areas (Stokland et al., 2003). Hence, data from forest inventories are also useful for biodiversity assessment. For example, these data can be used for the quantification of several biodiversity indicators related to species composition, mainly in terms of species richness and the presence of species of high conservation value (threatened or endemic species, Corona & Marchetti, 2007).

However, data from forest inventories may not be suitable for every analysis. For example, national forest inventory field plots are inadequate for measuring landscape patterns of structural ecosystem diversity because of the small plot size (Stokland et al. 2003). In addition, in many cases precision guidelines for the estimates of many variables cannot be satisfied due to budgetary constraints and natural variability among plots (McRoberts et al. 2005). In neither of the cases, it is efficient to increase the plot size or their number. Instead, other data sources that enable rapid data generation, e.g. digital photogrammetry; geographical information systems (GIS), digital elevation model (DEM), global positioning system (GPS) or remote sensing (Gallaun et al., 2004; Kias et al., 2004 as cited in Wezyk et al., 2005) can be used more efficiently. Fieldwork itself has been enhanced by satellite positioning systems (GPS), automatic measuring devices, field computers and wireless data transfer (Holopainen et al., 2005).

For special purposes, specific monitoring programmes are needed. These programmes attempt to investigate particular features of a forest ecosystem that are of specific interest and their monitoring is not included within national forest inventories. Many of such surveys have been performed by non-governmental organisations and within the frame of specific forest monitoring programmes (Heer et al., 2004). Although this kind of information can be of high value at a local or national scale, its applicability at a higher level (region, Europe) is restricted and requires pre-processing of data with regard to their quality, and biases and gaps in time and space (Heer et al., 2004). Therefore, many international projects dealing with biodiversity have been solved in the last decade (e.g. BioAssess, BEAR, ForestBIOTA, ALTER-Net, SEBI, DIVERSITAS).

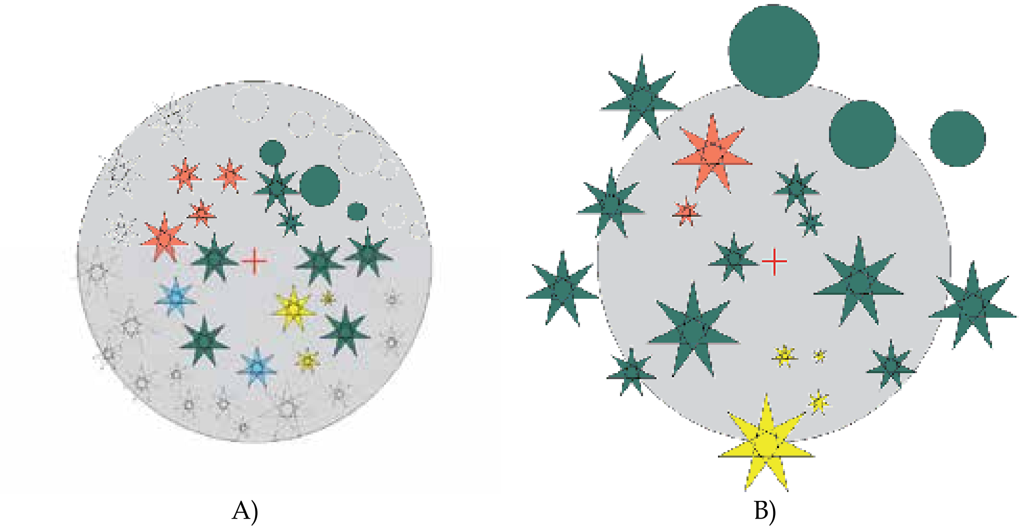
The quantification of biodiversity indicators can be performed in two ways, which affect the calculation of their confidence intervals. One method is that the indicator is calculated from the summary data about the whole population. In this case, there are several possibilities how to obtain the summary data:

- by accurate measurement of all individuals in population, i.e. complete survey;
- by visual estimation during the inspection of the examined population;
- by sampling methods in such a way, that the summary information is obtained by summing up the data collected on several places in a forest stand.

We call this approach the "method of sum". Biodiversity indicator determined with this method refers to the area that is larger than the minimum area. Hence, the comparison of the results of different populations is usually correct. In other cases, it is possible to use various standardisation methods given in e.g. Ludwig & Reynolds (1988) or Krebs (1989).

The second approach is called the "method of mean", because in this case biodiversity indicators are determined on several locations distributed over the whole community, and from them the average value typical for the whole population is derived. An important condition of this method is to assess biodiversity indicators on the samples of equal size, because in this case area has a significant effect on the value of biodiversity indicator. The final value of the biodiversity indicator refers to the area of the samples. Another alternative of this method is to determine indicator on the same number of individuals, e.g. 20 trees (Merganič & Šmelko, 2004).

At the ecosystem and landscape level, remote sensing represents a powerful and useful tool for biodiversity assessment (Ghayyas-Ahmad, 2001; Innes & Koch, 1998; Foody & Cutler, 2003). This method can provide cost efficient spatial digital data which is both spatially and spectrally more accurate than before (Holopainen et al., 2005). Moreover, remote sensing technology can provide the kind of information that was previously not available to forestry at all or was not available on an appropriate scale (Schardt et al., 2005). According to Innes & Koch (1998), "remote sensing provides the most efficient tool available for determining landscape-scale elements of forest biodiversity, such as the relative proportion of matrix and patches and their physical arrangement. At intermediate scales, remote sensing provides an ideal tool for evaluating the presence of corridors and the nature of edges. At the stand scale, remote sensing technologies are likely to deliver an increasing amount of information about the structural attributes of forest stands, such as the nature of the canopy surface, the presence of layering within the canopy and presence of coarse woody debris on the forest floor."



A) B)

Fig. 6. Assessment and quantification of tree species diversity on a set of 20 trees in case of a dense (A) and released (B) stand. In contrast to sampling on the plots with constant area, the sampled area varies.

Literature survey revealed that remote sensing data have been successfully used for:

1. habitat categorisation and estimation of their changes over large areas (Brotherton, 1983; Cushman & Wallin, 2000 as cited in Humphrey & Watts, 2004)
2. estimation of forest characteristics, e.g. basal area, stand volume, stem density, (Ingram et al., 2005; Maltamo et al., 2006 ; Reese et al., 2003; Tuominen & Haakana, 2005)
3. measuring vegetation (forest) structure (Ingram et al., 2005; Maltamo et al., 2005; Prasad et al., 1998; Wack & Oliveira, 2005)
4. analysis of canopy surface and canopy gaps (Nuske & Nieschulze, 2005)
5. identification of dead standing trees (Butler & Schlaepfer, 2004) and estimation of their amount (Uuttera & Hyppanen, 1998)
6. stratification for ground inventory (Roy & Sanjay-Tomar, 2000; Ghayyas-Ahmad, 2001; Jha et al., 1997) or to increase the precision of estimates (McRoberts et al., 2003, 2005; Olsson et al., 2005)

Nagendra (2001) who evaluated the potential of remote sensing for assessing species diversity distinguished three types of studies:

1. direct mapping of individuals and associations of single species,
2. habitat mapping using remotely sensed data, and prediction of species distribution based on habitat requirements,
3. establishment of direct relationships between spectral radiance values recorded from remote sensors and species distribution patterns recorded from field observations.

Direct mapping is applicable over smaller areas to obtain detailed information on the distribution of certain canopy tree species or associations. Habitat maps appear most capable of providing information on the distributions of large numbers of species in a wider variety of habitat types (Nagendra, 2001).

Turner et al. (2003) recognise two general approaches to the remote sensing of biodiversity. „One is the direct remote sensing of individual organisms, species assemblages, or ecological communities from airborne or satellite sensors. The other approach is the indirect remote sensing of biodiversity through reliance on environmental parameters as proxies“(Turner et al., 2003), that can be clearly identified remotely.

4. Importance of diversity

4.1 Productivity

Experimental relationship between site productivity and biodiversity of community is a widely discussed question in scientific literature. This problem was studied in detail at the end of 1980s (Rozenzweig & Abramsky, 1993). In many cases, this relationship has a humped shape with maximum species diversity at average productivity and minimum at both extremes, i.e. at low and high productivity. This shape was observed both in plant and animal communities. However, no general model that would explain this relationship has been derived yet. The humped shape can be linked with the theory of the limiting factor. On every site each species has a specific productivity threshold. Site factors are limiting for the survival of the species. As the site productivity increases, more and more species exceed their threshold value and hence, can survive in the environment. The decline of diversity with increasing productivity after the peak of the curve is a mystery that has been in the centre of interests of many scientists, who presented several explanations and hypotheses. However, none of them was sufficiently satisfactory. As an example we present two of them.

In the first hypothesis, species diversity is related to micro-site diversity (Rozenzweig & Abramsky, 1993). In theoretical ecology it is a well-known fact that one ecological niche can carry only one species. This theory, also called as "niche theory" says that average sites have more niches than very poor or very rich sites. Hence, we can conclude that they also have higher species diversity. This can be illustrated using three basic site factors: temperature, moisture, nutrients. On poor sites (cold, dry, and nutrient poor), all factors have low values, which results in a unique combination of factors that represent a specific site with very low productivity. Similarly, rich sites (warm, moist, and nutrient rich) are also the result of a unique combination of factors leading to one specific site. However, on average sites, a great number of combinations of site factors exist, while each combination represents a specific niche, which can carry a specific community. According to this theory, site diversity is maximum on average sites, and therefore, species diversity is maximum on average sites.

The second hypothesis is based on the theory of the „right of the limiting factor" (Rozenzweig & Abramsky, 1993). When the site productivity is high, all species have the potential to survive. However, a large number of species on the site leads to a strong competition resulting in the reductions in species number. Hence, low diversity can be caused by the strong competition of the most vital species, which suppress other species.

In forestry applications, this issue is closely related to the production in mixed forest stands, which is becoming an up-to-date theme due to accepting the principles of sustainable and close-to-nature forestry and consequently the transformation of forest management. This management results in greater area of uneven-aged and heterogenous forest stands, which complicates the use of traditional dendrometric models. Some efforts have been made to create models that would enable to determine the volume of several mixture types and forms. From this point of view, tree growth simulators are promising tools that are able to predict the development of mixed forests (Fabrika, 2005; Hasenauer, 1994; Kahn & Pretzsch, 1997; Nagel, 1995; Sterba et al., 1995).

4.2 Stability

Most ecologists agree that species diversity is a good basis for long-term existence of communities, i.e. communities that are composed of only a small number of species are more susceptible to extinction than species-rich communities. Due to this fact, diversity is implicitly linked to stability. However, this theory was disapproved, when May (1973) using Lotka - Volter systems presented that stability decreases with increasing complexity of iterations, i.e. with the increasing value of Simpson diversity index. May´s argument was based on the analysis of system stability through the linearisation of the surrounding balance. In other words, random Lotka-Volter system is stable if it consists of several interconnected species, or if the intensity of connections is low. A lot of important connections lead to system instability. It is still questionable if this is generally valid for all systems. This statement caused wide discussions. Anti-arguments say that in the ecosystem the interconnections are not randomly distributed, but consistently structured, which should cause the increase of stability. A short review of the progress in this field since the work of May (1973) can be found in Sigmund (1995).

In forestry field, stand stability is one of the main principles of sustainable forest management, which was approved in Helsinki Ministerial Conference on the Protection of Forests in Europe. Its importance increases particularly in the last time, which is characterised by more frequent occurrence of large-scale disturbances. Concerning the relationship of stability to biodiversity, Stolina (1996) stated that:

- natural forest ecosystems that are not influenced by anthropogenic activities are characterised by specific species diversity which is adequate to conditions of abiotic environment, because it has resulted from the long-term adaptation process.
- species diversity can be taken as an indicator of forest ecosystem stability;
- not every increase of species diversity measures indicate the increase of stability.

4.3 Naturalness – Diversity indicators of forest naturalness

Both biodiversity and naturalness are frequently used in conservation (Schnitzler et al., 2008), as the criteria for assessing the conservation status of forest ecosystems. Their significance was approved in many international schemes, e.g. both concepts were included in the list of pan-European indicators of sustainable forest management (MCPFE, 2002). The concepts are closely interlinked. For example, the degrees of forest naturalness distinguished within the scope of MCPFE are characterised with regard to biodiversity and its components. In forests undisturbed by man, processes and species composition remain natural to a considerable extent or have been restored. Semi-natural forests can keep certain natural characteristics allowing natural dynamics and biodiversity closer to the original ecosystem. Plantations represent man-made (artificial) forest communities, which are completely distinct from the original ecosystem (MCPFE, 2002).

The objective assessment of forest naturalness presented by several authors (e.g. Bartha et al., 2006; Machado, 2004; Moravčík et al., 2010; Winter et al., 2010) is based on a number of compositional, structural, and functional attributes of biodiversity, such as species composition and structure of different forest layers, occurrence of deadwood, etc. Tree species composition is the most common attribute used for the assessment of forest naturalness (Glončák, 2007; Guarino et al., 2008; Šmídt, 2002; Vladovič, 2003), but recently the amount of deadwood has also gained attention due to the large differences between managed and unmanaged stands. From other structural characteristics, horizontal structure characterised by diameter distribution (Pasierbek et al., 2007), differentiation of vertical and age structure are biodiversity indicators used in the assessment of forest naturalness (Moravčík et al., 2010).

5. Conclusion

Biodiversity is a keystone of ecosystem functioning. Its actual state determines if the ecosystem is sustainable, and hence, if it can fulfil particular functions, or ecosystem services. Since nowadays biodiversity has been receiving much attention worldwide, it is of great importance to understand this term thoroughly and to be able to quantify it mathematically. Various assessment methods and evaluation procedures have been used for the quantification of partial components of biodiversity, which allow users to evaluate and compare ecosystems objectively. In the presented chapter, we reviewed the current state-of-art of plant diversity assessment and examined the relationship of plant diversity to main forestry issues, namely forest management, productivity, stability and naturalness. The review of the available knowledge indicates that for the proper utilisation of biodiversity measures, their values should always refer to the area they represent. The questions about the relationships between biodiversity and forest productivity, stability and consequently management remain open for future research.

6. Acknowledgments

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2

Arthropods and Nematodes: Functional Biodiversity in Forest Ecosystems

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1. Introduction

Despite the great diversity of habitats grouped under a single name, forests are ecosystems characterized by the dominance of trees, which condition not only the epigeal environment but also life in the soil. Unlike other ecosystems such as grasslands or annual agricultural crops, forests are well characterized by precise spatial structures. In fact, we can identify three main layers in all forests: a canopy layer of tree crowns, including not only green photosynthesizing organs but also branches of various sizes; a layer formed by the tree trunks; a layer including bushes and grasses, which can sometimes be missing when not enough light filters through the canopy. To these layers must be added the litter and soil, which houses the root systems. Other characteristic features of forests, in addition to their structural complexity, are the longevity of the plants, the peculiar microclimates and the presence of particular habitats not found outside of these biocoenoses, such as fallen trunks and tree hollows. Even in the case of woods managed with relatively rapid cycles to produce firewood, forests are particularly good examples of ecosystems organized into superimposed layers that allow the maximum use of the solar energy.

The biomass of forests is largely stored in the trees, with the following general distribution: ca. 2% in the leaves and almost 98% in trunks, branches and roots. In conditions of equilibrium between the arboreal vegetation and animal populations, saprophages, which use parts of plants and remains of organisms ending up in the litter, play a very important role. Indeed, the consumption of living tissues by other organisms included in the second trophic level is minimal, ranging between 0.1% and 2.5% of the net primary production. Any interruption of the mechanisms of demolition and degradation of organic substances would quickly lead to an accumulation of organic matter harmful to the operation of the forest system. For example, in Italian Apennine beech woods, the mean production of leaves reaching the litter is ca. 2.7 t/ha (Gregori & Miclaus, 1985), while for beech woods in southern Sweden it has been estimated at 5.7 t/ha. This mass of organic material reaching the ground would submerge the beech woods within several decades. In truth, however, the functioning of these woods would decline much earlier due to the lack of recycling of immobilized elements. If we turn our attention from temperate woods to tropical forests, we can see that the process would soon lead to the rapid collapse of the system. In fact, rapid decay of material reaching the ground (an estimated mean value of 20 t/ha is considered reliable) (Rodin & Bazilevich, 1967) is a *conditio sine qua non* for a system with great luxuriance of vegetation but rather poor and fragile soils.

The oldest inhabitants of this planet are for the most part trees. Yet, even without discussing the great patriarchs of the Earth, we must consider that growth cycles of over a century are the norm for many European forests. These rhythms were used for the oak forests that furnished the wood for the ships of the Most Serene Republic of Venice and even earlier for the Roman galleys. Vikings ships were constructed in Scandinavia with wood obtained from large old growth trees, especially oaks. The earliest forests can be identified on the basis of fossilized trees and forest soils from the mid-Devonian, between 400 and 350 million years ago. Starting from this period, we see an increasing number of remains of trees as well as a parallel exponential increase of the biodiversity of terrestrial zoocoenoses, with particular reference to the increased numbers of arthropod species (Retallack, 1997).

Forests are relatively stable ecosystems in which the tree component mediates the flows of organic matter by means of its long-term cycles. They support complex plant and microbial communities and represent, even in temperate climates, the largest storehouses of animal biodiversity, largely belonging to the Phyla Arthropoda and Nematoda. In table 1 are reported the values estimated in abundance of arthropod fauna living in a tropical forest (Seram rain forest).

Biotopes	**N (millions/ha)**
soil	23.7
leaf litter	6.0
ground vegetation	0.1
tree trunks	0.5
canopy	12.0
Total	42.3

Table 1. Abundance of arthropod fauna estimated in a tropical forest (Stork,1988).

Present-day forests host a diversified and largely specific fauna able to use not only the trees but also bushes and grasses. Trees are also more or less covered by microalgae, epiphytic lichens and mosses which can serve as food for phytophages, estimated to make up 20% of the total number of species in Danish beech woods (Nielsen, 1975). The primary production of epiphytes in many temperate forests is comparable to the production of the herbaceous layer, and some groups of arthropods specifically associated with these food substrates, such as Psocidae, can reach a density of 4,000 individuals per square metre of bark (Turner, 1975).

Moreover, the levels of biodiversity can vary enormously among different types of woods and within the same forest according to the age of the tree populations or the spatial heterogeneity characterizing woods of different ages. There are also trees with an extremely reduced arthropod fauna due to the production of phytoecdysones similar to moulting hormones, which act as repellents. In contrast, other trees host a much higher number of primary consumers due to the presence in their tissues of salicylic acid derivates, which act as attractants.

It is important to underline that when we speak of biodiversity we are often referring to three principal components:

- genetic diversity;
- diversity of species;
- diversity of habitats or ecosystems.

However, a fourth component was recently proposed, namely "FUNCTIONAL DIVERSITY", based on the trophic role of the species and the interactions among organisms and between them and their environment.

In forest ecosystems, the animal component is distributed differently in the various layers, playing a fundamental role in terms of the following functional groups:

- primary consumers or herbivores;
- demolishers;
- degraders (often associated with symbiotic micro-organisms).

Arthropods in the different functional groups can be further divided into ecological-nutritional subgroups or categories based on their feeding behaviour:

- leaf suckers - species that puncture plant organs or tissues and suck the cell contents or substances circulating in the trees;
- defoliators - species that feed on green parts of the trees (leaves, buds and unlignified bark) throughout the life cycle or only in some stages;
- xylophagous - species able to feed throughout their life cycle or for part of it on lignified tree structures Xylophagous are further subdivided into:
  - corticolous,
  - corticolous-lignicolous,
  - lignicolous.

2. Tree crown

Arthropods that live in tree crowns present a great variety of biological aspects. They are represented mainly by insects, spiders and mites, and to a lesser extent by representatives of other groups such as Apterygota, Chilopoda and Diplopoda. Not all of these animals live stably in the canopy, with various species using the crown only for part of their biological cycle (various lepidopterans feed on leaves but when their larval development is completed they move into the soil to undergo metamorphosis, e.g. *Lycia hirtaria* (Clerck) in European temperate forest and *Erannis tiliaria* (Harris) in Canadian mixedwood boreal forest. In contrast, other arthropods, such as coleopterans of the genus *Polydrusus,* only feed on leaves and needles as adults after living in the soil as larvae and feeding on roots.

Crown arthropods can be grouped as follows:

- phyllophages, which feed on leaves or needles, eroding them from the outside (mainly lepidopterans plus some hymenopterans and coleopterans);
- leaf and bud miners (above all lepidopterans plus some coleopterans);
- floricolous arthropods:
  - anthophages,
  - pollenophages;

- arthropods that develop by eating fruits (carpophages) and seeds (spermophages);
- arthropods that induce the formation of galls, with shapes that vary according to the species involved (cinipid hymenopterans, dipterans and mites);
- suckers of cell contents and sap (mainly but not exclusively elaborated sap – above all Rhyncota insects of the suborder Homoptera);
- herbivores that feed on algae (algophages), fungi (mycetophages) and lichens (lichenophages) (mainly psocopterans);
- detritivores (including dermapterans, psocopterans,…);
- predators (many coleopterans but also some arboricolous orthopterans, Heteroptera Miridae, etc.);
- parasitoids (primarily hymenopterans but also many dipterans).

Primary consumers prevail in the canopy layer, especially phytophages in the ecological-nutritional categories of defoliators (with a masticatory buccal apparatus for feeding on leaves and green buds) and leaf suckers (provided with a puncturing-sucking buccal apparatus). A study conducted on oaks, black locusts and birches in England and South Africa showed substantial similarity of the crown arthropod communities between the two areas, with phytophages representing ca. one quarter of all species, half of the biomass and two thirds of all individuals (Moran & Southwood, 1982).

Defoliator insects are common in all coniferous and broadleaf forest ecosystems. They are an integral part of the forests and they can be useful to the ecosystem or harmful to the conservation and productivity of these habitats according to the quantity of photosynthesizing material removed and the possible repetition of severe attacks. In many forest formations, a primary role is played by various families of defoliator lepidopterans. Formations purely or prevalently of oaks provide a particularly important example. In Italy, there is a wide variety of biogeographical contexts within a relatively small surface area, and this is reflected in the number of *Quercus* species. The middle European oaks, often distributed in a fragmentary manner on plain and hilly terrains now largely dominated by agriculture, are joined by the larger contingent of Mediterranean species, the most important being the cork oak and holm oak. These oaks are very important in helping to form some of the most complex forest ecosystems in Italy, with an extremely various phytophagous arthropod fauna able to utilize the different ecological niches available in relation to seasonal conditions, composition, age and silviculture treatments. This heterogeneous complex of wooded formations, where human activities have profoundly modified the phytocoenoses, supports a rich and diversified lepidopteran fauna. Over 200 lepidopteran species belonging to 32 families feed on the green parts of the crowns of these Fagaceae, eroding buds, leaves and shoots from the outside or mining into them (Luciano and Roversi, 2001; Cao and Luciano, 2007). They constitute the most numerous group of phytophagous insects. The pre-eminence of this group is related to bio-ethological characteristics common to most of the species:

- the more or less strong polyphagy, which allows them to best utilize the occasionally available food;
- the possibility of laying eggs on different substrates without being bound to the trees that will serve as food for the larvae;
- the great variability of biological cycles, with species that pass the winter in different developmental stages;
- the absence of diapause (with rare exceptions), allowing the species to express the maximum potential for numerical increase in each generation;

- amphigonic reproduction, which provides the species with greater adaptability;
- the ability to carry out migrations or at least medium- and long-term movements, favouring rapid diffusion into suitable territories;
- possibilities for passive diffusion by some species, particularly in the first larval stages.

Lepidoptera are also cited as major defoliators of tropical forest trees and there are actually an increasing number of publications dedicated to the attack in neotropical forest environments (Nair, 2007; Haugaasen, 2009).

Thanks to these characteristics, a small group of oak-defoliating lepidopterans can give rise to spectacular numerical explosions or "outbreaks" with the sudden defoliation of whole stands, as in the case of mass *Lymantria dispar* (L.) infestations (Fig. 1). From an ecological point of view, outbreaks present characteristic phases of population abundance.

Fig. 1. *Lymantria dispar* larvae on *Quercus pubescens*.

After remaining at low numerical levels for years, becoming almost impossible to observe (latency phase), the phytophage populations show rapid density increases (progradation phase) which in several years lead to true numerical explosions or mass infestations (peak phase), followed by a more or less rapid decline (retrogradation phase) toward a new latency phase. In some defoliator lepidopterans, these mass changes are fairly common and are regulated by various biotic and abiotic factors that strongly affect the vitality and survival of the individuals. The main factors include climate (able to influence populations directly, e.g. allowing a higher or lower number of individuals to survive winter, and indirectly, by modifying the phenology of the host trees and thus the quantity and quality of food available for species that feed on the trees at the beginning of spring) and the set of natural antagonists (predators, parasitoids, pathogens) (Fig.2).

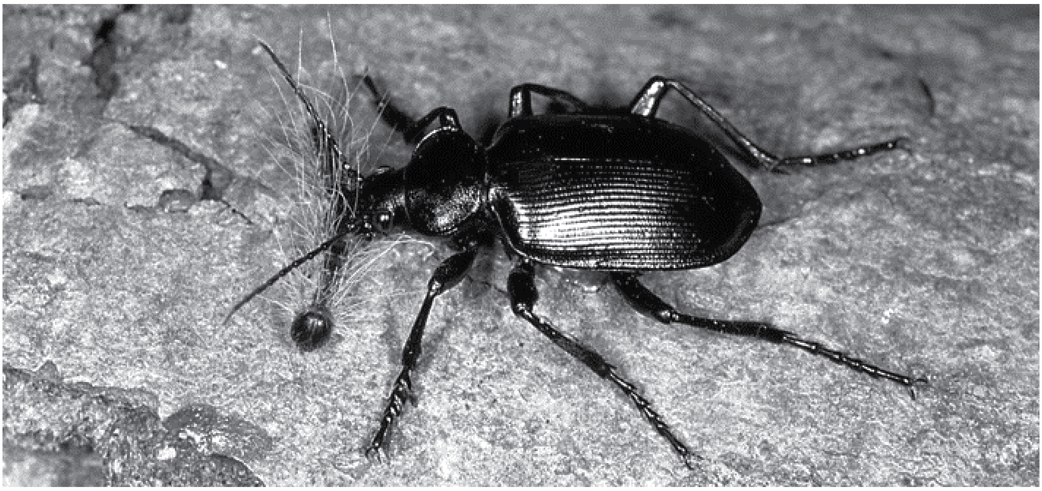

Fig. 2. *Calosoma sycophanta* a voracious Carabid consumer of caterpillars.

The different combinations of these factors produce more or less intense demographic variations, which allow species with a high biotic potential to reach high enough densities to cause the complete removal of the leaf mass of entire forests, even extending over hundreds of thousands of hectares. These mass appearances can occur at regular intervals or give rise to attacks irregularly distributed in space and time.

Very dramatic outbreaks often occur in degraded forest ecosystems or in marginal zones of the distribution area of the tree species where the appearances of defoliators are more frequent. This aggravates existing ecological imbalances, leading to very severe situations of widespread tree weakening, predisposing them to subsequent attacks by aggressors able to cause an irreversible decline. During such outbreaks, a large part of the organic matter produced by the trees can be diverted from the normal circuit. A good example is the activity of *Operophthera brumata* (L.), a geometrid able to defoliate entire stands in Swedish forests, whereas in the latency period the larvae remove no more than 0.004÷0.006 of the net primary production (Axelsson et al., 1975).

Leaf sucking insects have a puncturing-sucking buccal apparatus in which the mandibles and maxillae are profoundly modified to form an efficient tool similar to a hypodermic needle. They use it to suck sap and cell contents from the trees, becoming the first factor of deviation of part of the organic matter otherwise destined for the production of photosynthesizing and reproductive organs, the constitution of reserves and the accumulation of wood mass.

Three large groups of leaf sucking insects can be identified: species that feed by directly puncturing cells or groups of cells in superficial tissues (as in the case of thysanopterans) or deep tissues (as for some Homoptera Rhyncota); species that feed on elaborated sap, which stick their buccal stylets directly into the phloem conducting system (including Homoptera Rhyncota, mainly Aphidoidea, Coccoidea, Psylloidea and Aleyrodoidea); species that reach the xylem transport pathways, feeding on crude sap (including a small group of homopterans such as some Cercopidae). In these last species, also known as "spit bugs", the larval stages are found inside large foamy masses formed by the insects to eliminate the excess of water they are forced to ingest: indeed, the low concentration of nitrogen compounds in crude sap compels the Cercopidae to ingest large quantities of food in order to extract the necessary amounts of nutrients (Thompson, 1994). Adults of Cercopidae, including species that complete their larval development in the soil, also withdraw food and liquids by tapping into the xylem circuit of the leaves of host plants by means of refined behavioural adaptations: for instance, adults of *Haematoloma dorsatum* (Ahrens) puncture the needles of pines and other conifers by introducing their buccal stylets through the stomata to reach the feeding sites without an excessive energy expenditure (Roversi et al., 1990).

Leaf suckers that feed on elaborated sap consume large quantities of sugars which are not completely used and thus are expelled as drops of honeydew, highly attractive to ants, bees, wasps and adults of predators and parasitoids of aphids. Hence, these animals consume a part of the products of photosynthesis by trees that are otherwise unavailable to them. Therefore, in conditions of general equilibrium of forests, leaf suckers (particularly those that produce honeydew) are integral parts of the system, allowing an intensification of the network of interrelationships within the ecosystem and between it and other biocoenoses.

With the changing of the seasons, trees are subjected to strong variability in the transfer of nutrients and mineral salts. This is extremely important for leaf suckers, which gain their nutriment from the host tree's vascular system. In Italian environments, there can be strong differences between deciduous and evergreen trees, since the former are subjected not only to a marked translocation of crude and elaborated materials during growth resumption in spring but also to an autumn re-allocation of nitrogen substances and others when the leaves fall.

Tree crowns also host arthropods with such close associations with trees that they modify the host's local physiological processes and morphology, forcing them to create particular structures, called galls, in which the arthropods develop and shelter. There is a great morphological variety of galls, with forms and colours characteristic of each insect species. This is particularly true for structures formed by Hymenoptera Cynipidae and Diptera Cecidomyiidae, which have long attracted the attention of students of nature, starting with Francesco Redi who in the 17th century dedicated three manuscripts to them, including tempera drawings of the insects and their larvae (Bernardi et al., 1997). In some habitats such as beech woods, the unmistakable reddish leaf galls of the cecidomyiid *Mikiola fagi*, with their larval contents, are a food supplement for micromammals in an ecosystem in which food reserves for these vertebrates are particularly scarce.

On the crowns of both coniferous (various *Pinus* spp.) and broadleaf trees (oaks), we find insects that carry out most of their life cycle elsewhere, usually in subcortical and woody tissues, but which require a relatively brief period of feeding on vigorous shoots for maturation of their reproductive apparatus. They include Coleoptera Scolytidae of the genera *Tomicus* and *Scolytus*, which burrow galleries in the shoots, and Cerambycidae of the genus *Monochamus*, which erode young bark, all widely distributed in temperate forests. The alternation of feeding sites between woody tissues of trees often weakened by pathogenic infections and peripheral parts of the crown introduces another peculiar aspect into the relationships among very different groups of animals. Scolytidae and Cerambycidae with this behaviour can act as vectors, not only carrying fungal spores directly into contact with living tissues of new host trees but also becoming efficient vehicles of inoculation of healthy plants with phytopathogenic nematodes, which benefit from the damage caused by the xylophages to reach the conductor system of the host trees. Among the various relationships between nematodes and arthropods, especially insects, the associations established by the phoretic entomophilous nematodes of the genus *Bursaphelenchus* can have very severe consequences. In favourable conditions, they can allow the nematodes, transported by beetles under their elytra or in the trachea, to multiply with extreme rapidity in the conducting tissues of the trees (Covassi & Palmisano, 1997).

Acari living in the forest canopy (on leaves and small and main branches) are represented by various groups with different densities. Phytophagous mites belonging to the Tetranychidae, Tenuipalpidae and Eriophyidae, feed on the tree sap or cell contents. Their behaviour and densities are influenced by the environmental conditions and by the cohort of their predators, mainly Acari Mesostigmata and Prostigmata (Figs. 3 and 4) of the families Phytoseiidae, Stigmaeidae, Cheyletidae, Anystidae, Cunaxidae, Bdellidae and Trombidiidae. Their behaviour is also influenced by the type of plant, i.e. broadleaf or evergreen. Phytophagous species living on deciduous trees in unfavourable periods tend to move onto the branches and trunk to find micro-environments suitable for overwintering. On coniferous and evergreen trees, which keep their leaves even in winter, phytophagous mites tend to shelter at the base of the leaf nervation or in cracks in small branches.

Fig. 3. A predatory mesostigmatid mite living in the forest canopy (SEM x 40).

Fig. 4. A predatory prostigmatid mite living on bark of tree trunks.

Tree crowns host a wide variety of Acari: fungivores, algophages or those associated with mosses and lichens. These Acari belong to different groups, including Oribatida or Cryptostigmata, Astigmata and Prostigmata Tydeidae and Tarsonemidae, in fine equilibrium with their predators, generally Acari Mesostigmata and other Prostigmata, which habitually frequent leaves and small branches.

3. Tree trunks

The bark of tree trunks is an important element of forest ecosystems. It creates particular microclimates and provides micro-habitats that differ greatly according to the rugosity and irregularity of the surface, particularly in terms of the presence of deep fissures. In this spatial sector, which hosts phytophages as well as various predators and detritivores, the dominant groups are spiders, mites and insects, mainly springtails, psocids and some coleopterans and dipterans (Funke & Summer, 1980).

The trunk can contain mites associated with mosses and lichens but also strictly corticolous species, which find food and protection there. Galleries burrowed under the bark by scolytid, cerambycid and buprestid beetles host Acari belonging to Astigmata, Mesostigmata and particularly Prostigmata Tarsonemidae, which feed on the fungi typical of this environment. Other mites live in rifts in the bark caused by cortical cancers, feeding on fungal mycelia and fruiting bodies or on the associated microflora.

Also active on trunks are leaf suckers able to reach the tree's lymphatic system with long buccal stylets, e.g. the highly mimetic Heteroptera Rhyncota of the genus *Aradus* and cochineals of the genus *Matsucoccus*. Trunk-living insects with a puncturing-sucking buccal apparatus also include predators with a high degree of adaptation; this is observed especially in species of the genus *Elatophilus*, whose body is very flattened and admirably adapted to working its way between bark scales (Covassi & Poggesi, 1986).

Bark and especially wood constitute the main reserves of organic matter and mineral elements, with values that can vary enormously according to the vegetational composition, age of the woods and their conservation state. A beech wood of the Fontainbleau Forest in France had an estimated total tree biomass of over 280 t/ha, of which 195 represented by trunks, 48 by branches, 41 by roots, 3.2 by leaves and sprigs, and 0.9 by reproductive organs (Dajoz, 2000). In the so-called "Old Forests" of the western United States, consisting of coniferous associations with a mean age of 450 years, the epigeal biomass varied from 492 to 976 t/ha, with woody residues varying between 143 and 215 t/ha (Spies et al., 1988).

However, bark and wood tissues are degraded much more slowly than leaves. Arthropods, and xylophages in particular, play a primary role in accelerating the processes of decomposition and mineralization, often acting simultaneously with various fungi. In a transverse section of a trunk with, from external to internal, bark or rhytidome, phloem, cambium and xylem or real wood (separated into sapwood and heartwood), we can see a progressive change in the composition in terms of cellulose, hemicellulose, lignin, pectin, suberin, starch, nitrogen compounds, lipids and minerals, with a clear prevalence of the first three compounds. Cellulose, a polymer formed by the association of a high number of carbohydrate molecules in both the amorphous form and crystalline form, constitutes from 40 to over 60% of the dry weight of wood and can be hydrolyzed only by fungi, bacteria and some isopods, diplopods and insects provided with cellulase.

Only a few insect species can completely degrade cellulose since many xylophages that feed on bark, subcortical tissues or wood have only one of the three enzymes necessary for the final conversion into glucose. Among the few arthropods able to totally degrade cellulose are Thysanura (Lasker & Giese, 1956), Dermaptera (Cleveland, 1934), Isoptera, Hymenoptera Siricidae, Coleoptera Anobiidae, Buprestidae, Cerambycidae and Scarabeidae. However, occasionally in the wild, some xylophagous species can ingest bacteria, fungi and protozoa, using them as a source of enzymes to increase their ability to digest cellulose, hemicellulose and lignin. In the case of Hymenoptera Siricidae that develop in the wood of coniferous trees, their ability to utilize this food depends on the fact that the larvae ingest wood invaded by fungi of the genus *Amylostereum* and establish a mutualistic symbiosis with them, which provides the digestive enzymes necessary to use the pabulum on which the larvae develop (Kukor & Martin, 1983).

Lignin forms 18-38% of the durable tissues of trees. However, this term groups very different complex substances into a single category and these substances make the degradation of wood even more difficult since no animals, including insects, produce enzymes able to degrade them. Micro-organisms that can decompose lignin include fungi, bacteria and protozoa, many of which live in the digestive apparatus of arthropods, establishing mutualistic symbioses that allow the hosts to degrade lignin.

The bark of tree trunks also constitute "highways" for the daily (ants of the genus *Rufa*) or seasonal movements of species that migrate from the soil or litter to the tree crown during their cycles. Many species use the bark of the trunk as mating, egg-laying or wintering sites. In some cases, the bark becomes a summer refuge for species that live on the crown but abandon it when the temperatures reach their summer peak, as in the case of the woolly oak aphid (Binazzi & Roversi, 1990).

The subcortical layers are the site of development of various species, mainly insects and especially scolytid and cerambycid beetles. The Scolytidae are one of the most important groups of phytophagous insects, linked mainly to forest habitats and particularly coniferous woods (Figs. 5 and 6). There they express their maximal diversity of cycles and modes of development, behaviours and abilities to settle on trees in different vegetative conditions, often becoming dominant elements in the mechanism regulating ecological successions (Chararas, 1962; Pennacchio et al., 2006). In Europe, 39 species have been recorded on *Pinus* alone. The family Scolytidae numbers over 6,000 species of small insects, usually of more or less cylindrical shape and less than 2 mm long, with mandibles that move horizontally and the initial part of the intestine provided with sclerified denticles that act as a filter preventing the ingestion of excessively large wood fragments. The family includes polygamous species, such as those in the genera *Ips*, *Orthotomicus*, *Pityophthorus*, *Pityogenes* and *Pityokteines,* or monogamous ones such as those in the genera *Tomicus* and *Cryphalus*, which burrow characteristic systems of breeding galleries where they lay their eggs. The galleries of adults and those dug by the larvae to complete their development are well determined for each species; indeed, it is possible to make an *a posteriori* identification of scolytid species that have developed on a given tree merely by examination of the damage.

Very many other insects, mites and non-hexapod invertebrates with diversified alimentary regimes are found in the subcortical galleries burrowed by Scolytidae. They contribute substantially to the maintenance of high levels of biodiversity of the animal communities living under tree bark.

Fig. 5. Galleries on Pine produced by *Tomicus minor*.

Fig. 6. Galleries in Spruce produced by *Ips typographus*.

Most scolytids attack trees with integral phloem and cambium tissues. However, these trees are often weakened for various reasons, including drought and attacks by other phytophages, primarily defoliators but also a small number of species that colonize trees in more or less advanced stages of decay with active fermentation processes in the subcortical tissues and with low levels of starch and protein contents, e.g. species in the genera *Dryocoetes* and *Hylurgops*.

It is important to underline that, even in scolytid species that attack only a single host, not all the trees are equally attractive. These small hexapods are refined aggressors able to perceive with their sensory organs changes in the spectrum of substances emitted by each individual tree as a result of biotic and abiotic stresses. The manner in which thousands of individuals of a given scolytid species swarm onto single trees among thousands of other unaffected trees illustrates the precision of these beetles' stimulus perception mechanism.

The relationships among trees, semiochemicals and xylophagous insects constitute one of the most interesting research fields in forest entomology, not only for an understanding of the subtle mechanisms that allow their correct functioning but also for their practical implications. The use of semiochemicals for the monitoring and mass capture of these phytophages is a current strategy for the management of biotic adversities in many forest areas because of the possibility of limiting beetle population increases via agents with low environmental impact and without the use of synthetic biocides.

Examples of species well known for their ability to modify the structure and species composition of wooded formations are various *Dendroctonus* in North America and *Ips typographus* in Europe. The latter species caused the loss of over 5 million cubic metres of timber in Norway in the period 1970-1982 alone. In the Palaearctic Region, *Scolytus* species on elms have been responsible, in association with the fungal agent of Dutch elm disease *Ophiostoma novo-ulmi* Brasier, for the devastation of elm trees, while *Tomicus* species have been a constant threat to pine woods along coastlines and on hills and mountains.

The Cerambycidae are medium to large-sized beetles with a lengthened body and generally long antennae, very common in forests since the larvae of most species develop under bark or in wood. They are important both for conservation and for maintenance of the functionality of the woods; although some species cause damage, others actively contribute to the degradation of dead wood, intervening effectively in the first phase of demolition of durable tree structures. Species of the genus *Monochamus*, particularly *Monochamus galloprovincialis galloprovincialis* (Olivier) in Mediterranean pine woods, are able to rapidly kill trees that are only momentarily weakened (Francardi & Pennacchio, 1996). The harmfulness of these and other beetles of the family is also due to their role as vectors of phytopathogenic nematodes of the genus *Bursaphelenchus* (Fig.7).

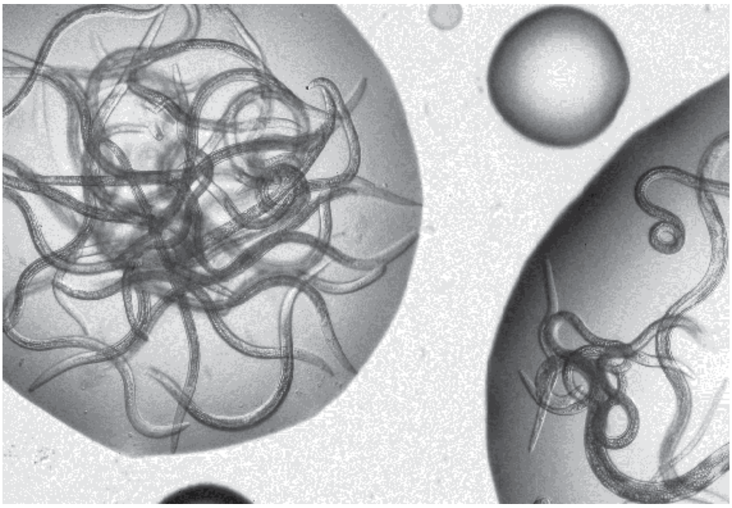

Fig. 7. *Bursaphelenchus eremus*: a phytoparasitic nematode living on *Quercus* spp.

Some lepidopterans develop by feeding on durable tree tissues, such as species of the genus *Dioryctria*. They are known as "pine resin moths", even though they can also live on cedars and red firs. Their larvae dig subcortical galleries exclusively on conifers thanks to their ability to isolate themselves from the abundant resin emitted by the trees in an attempt to defend themselves. To do so, they create tunnels lined with sericeous tissue.

Isopterans, various coleopteran families (including Scolytidae, Cerambycidae and Buprestidae), Lepidoptera Cossidae and Sesiidae, Hymenoptera Siricidae and some dipterans contain xylophagous species able to develop for part of their life or for the entire larval period by feeding on living wood or wood at various stages of decay. In the first case, we are referring to species included in the corticolous-lignicolous group whose larvae feed first on the phloem and later on the xylem, moving deep inside trunks and branches to complete their development and undergo metamorphosis. The second case involves xylophagous species *sensu stretto* or lignicolous ones that feed exclusively on woody tissues. They are fundamental in accelerating the decay of tree branches and trunks, and the group includes some of the largest of all arthropods. For instance, among Cerambycidae, the larvae of *Ergates faber* found on pines, oaks, chestnuts, elms, cherries and other hosts in Italy reach 8 cm in length, while the larvae of *Acrocinus longimanus,* distributed from Mexico to South America, are up to 13 cm long. The larval activity of these true burrowers can demolish age-old trees, even reaching the most resistant portions of the heartwood. Some xylophages *s.s.* are found on only one host species, although many develop by feeding on different trees; some species, mainly linked to decayed wood already invaded by fungi, are able to accept hundreds of coniferous and broadleaf species. On account of the poor pabulum, many species in this group, particularly those in relatively dry habitats, require several years to complete their larval development, even up to six years. Examples are the cerambycid *Hylotrupes bajulus* L. and a scarabaeid that lives in dead wood and is one of the best known and most characteristic of insects, the stag beetle (*Lucanus cervus* L.), whose adult males are provided with unmistakable long but absolutely harmless mandibles. Some xylophages found in dead wood in humid tree hollows are among the rarest of protected insects worldwide, e.g. the Scarabaeidae Dynastinae *Osmoderma eremita*. Various other coleopteran families include important xylophagous species, e.g. Buprestidae, Melandryidae (*Serropalpus barbatus*), Anthribidae and Tenebrionidae. The Diptera families Tipulidae, Cecidomyiidae and Asilidae contain species often found in dead wood.

Therefore, many xylophagous insects are important components of forest ecosystems, and, in conditions of equilibrium with the host trees, help maintain the vigour of the system, assuring the dynamism of the biocoenosis. In fact, forest insects and pathogens:

1. colonize trees suitable for their development, modifying the structure and composition of the woods and modelling the tree population to the conditions offered by the site.
2. participate in tree turnover via elimination of the less fit trees, accelerating the availability of elements and other substances to the healthier trees. Indeed, the action of corticolous, corticolous-lignicolous and lignicolous insects contributes to the decay of the durable tree parts, thus favouring the action of nitrogen-fixing bacteria and saprophytic micro-organisms which mineralize and liberate elements for roots and mycorrhizae.
3. create peculiar habitats, via deformations of the crown, the death of some trees and the opening of clearings, and make available nutrients for other species that play a critical role in the maintenance of forest stability and productivity. A good example is the formation of suitable habitats and refuges for insectivorous birds.

Hence, the action of xylophagous insects and associated pathogenic agents plays a primary role in the maintenance of productivity and biodiversity levels in forest environments.

Fig. 8. Adult of *Ergates faber*.

4. Litter and soil

Although leaf-sucking and defoliator arthropods prevail in the crown layer, demolishers are of great importance in the lower layers and especially the litter, which receives not only leaves but also large amounts of organic matter in the form of fallen trunks and branches. Indeed, their role becomes essential in the phase of breakdown and decay of organic substances (Fig.9). To underline the complexity of the trophic networks, we should also mention that nematodes form an important part of all the functional groups in the soil, from phytoparasites active on root organs to bacteriophages with densities that can reach 30 million individuals/m^2 in forests.

The forest litter and soil are the environment with the greatest animal biodiversity and the site of recycling of materials and nutrients. The dominant groups of soil organisms, in terms of number and biomass, are micro-organisms such as bacteria, fungi and yeasts, representing ca. 85% of the biomass. However, other extremely important and complex components are represented by animals with sometimes very diverse dietary regimes, such as protozoa (amoebas, flagellates, ciliates), nematodes (bacteriophages, fungivores, omnivores, predators), Enchytraeidae, Lumbricidae and micro-arthropods, mainly mites (bacteriophages, fungivores, predators), springtails (fungivores and predators), and dipteran and coleopteran larvae, which make up the remaining 15% of the biomass. Nevertheless, the systematic spectrum of large taxonomic groups is limited with respect to the specific variety found within the same groups (Fig.10).

Table 2 summarize the soil fauna living in a temperate forest.

Fig. 9. *Abies alba* windfall in the Vallombrosa Forest (Central Italy).

Zoological groups	Number of individuals/m^2	Weight in g
Protozoa	100 to 1000 x 10^6	2 to 20
Nematoda	1 to 30 x 10^6	1 to 30
Lumbricidae	50 to 400	20 to 250
Enchytraeidae	10 to 50 x 10^3	1 to 6
Acari	20 to 500 x 10^3	0.2 to 5
Pseudoscorpionida+ Araneidae+Opilionidae	60	0.06
Collembola	20 to 500 x 10^3	0.5 to 5
Protura	200	insignificant
Diplura	150	insignificant
Thysanura	few individuals	insignificant
Formicidae	variable according to site	-
Coleoptera larvae	100	1
Diptera larvae	400	3.5
Symphyla	1000	0.1
Chilopoda	50	1
Diplopoda	1 - 200	8
Isopoda	100	4

Table 2. Division of the forest soil fauna in temperate regions (values estimated from data of different authors). (From Bachelier, 1971).

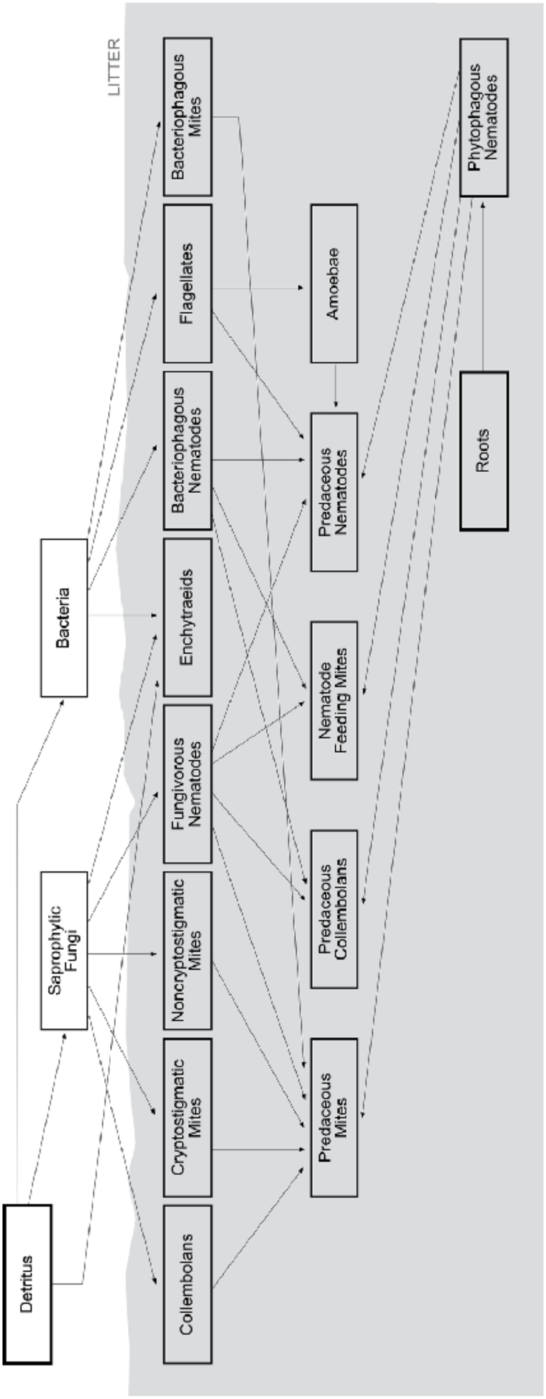

Fig. 10. Diagram of the food web in the forest floor and soil.

An important subdivision of soil-living animals is based on their size. This parameter is of primary importance in the edaphic environment since the organisms must move through the soil to search for food, breed and avoid natural antagonists and momentarily adverse conditions, as occur during periods of drought. The classification of soil animals based on size allows us to distinguish the macrofauna and microfauna from the mesofauna, which includes the major part of soil organisms and whole groups such as Diplura, Collembola and Protura as well as the majority of species of Tardigrada, Rotifera, Isopoda and especially Nematoda (Wallwork, 1976). The biological population of the soil has a dual origin: on the one hand a contingent of species living in capillary and gravitational water that fills or covers the soil cavities (protozoa, nematodes, most oligochaetes); on the other hand a different group originating from the epigeal part, which has adapted to life in the soil (almost all arthropods with the exception of small groups such as copepods). However, there is a third contingent, whose origin has been directly identified in Palaeozoic deposits, containing forms strongly adapted to hypogeal life (Insecta Symphyla, Collembola and Pauropoda, Protura and Diplura). The abundance and composition of these groups depend on the type of soil and overlying vegetation. Coniferous needles have a high C/N ratio and high polyphenol contents, which make this material more resistant to decomposition than the leaves in broadleaf litter, where the C/N is lower and decomposition is more rapid. In this type of litter, the mineral soil is much less acidic and the more active decomposer groups are favoured (lumbricids, millipedes and isopods). Soil arthropods are generally not uniformly distributed and often show aggregative behaviour, being distributed in horizontal aggregates in the same profile or in different profiles. Their densities are closely correlated to the organic matter, which is mainly concentrated in the most superficial layer of the forest soil, i.e. the litter.

The abundance of animals in the soil is negatively correlated with soil depth, since it depends on the availability of nutrient substances and oxygen. In forest soils, more than 60% of the ground fauna is typically concentrated in the first 10 cm of the superficial horizon (Peterson & Luxton, 1982). Soil arthropods make an enormous contribution to organic matter decomposition, breaking down and transforming all the material coming from the epigeal part of the forest. In fact, arthropods:

1. disintegrate the dead plant or animal tissues, transforming them into a substratum more easily attacked by micro-organisms,
2. selectively decompose and chemically modify part of the organic residues,
3. transform the plant residues into humic substances,
4. increase the surface area attacked by fungi and bacteria,
5. form complex aggregates of organic matter with mineral parts of the soil,
6. transport and mix the organic substances among the different layers,
7. disseminate propagules of fungi and stimulate their growth through symbiotic, commensal or phoretic relationships.

In temperate forests, the soil fauna remains active even in winter, under the snow cover and in the layers underlying the frozen litter. In these conditions, the breakdown and mineralization of organic matter is reduced to minimal levels.

Forest management practices can increase or reduce the ecological niches of the soil and thus influence the range of species. In environments less impacted by human activities, the diversity and stability of animal populations are correlated via interactions among the different functional groups, which tend to bring the system toward equilibrium and stability. Soil arthropods and nematodes are notoriously flexible in terms of their diet and it is not easy to assign a single trophic level to each group. According to the available resources, Acari Oribatida and Collembola can behave as detritivores but can also feed on fungi, algae and amorphous detritus. Among Acari Mesostigmata, some Uropodina species are detritivores, while others behave as specialized predators. Likewise some soil-living nematodes are phytophages, feeding on tree roots, while others are generalists and others still are preyed upon by Acari Parasitidae, Macrochelidae and fungi (Marinari Palmisano & Irdani, 1996). Acari, particularly the Oribatida (Figs. 11 and 12), are very important for the maintenance of soil productivity, actively participating in the breakdown of plant detritus, the vertical transport of organic matter and the formation of humus. Studies conducted in beech and pine woods of central Italy revealed the presence of 90 species belonging to 64 genera and 42 families (Nannelli, 1972, 1980): 72 species were recorded in a single temperate beech stand (Nannelli, 1990).

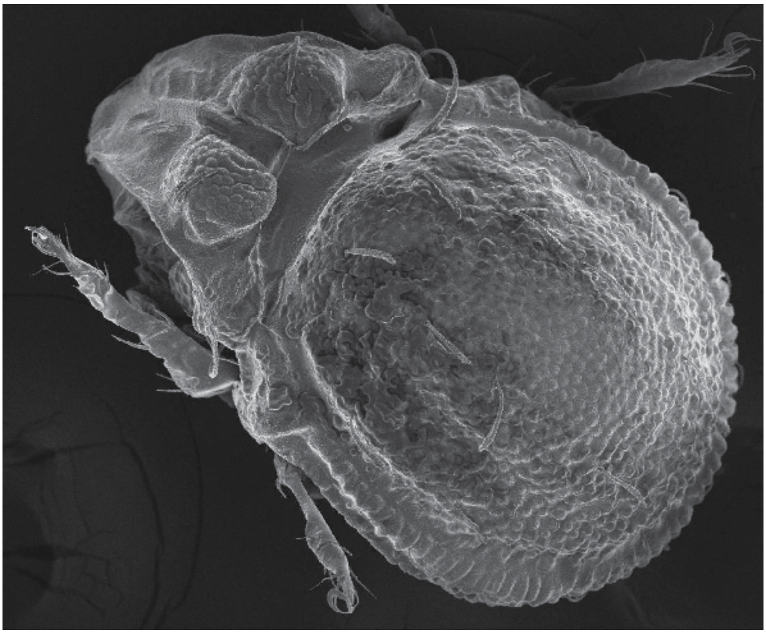

Fig. 11. A cryptostigmatic mite belonging to the genus *Carabodes.*

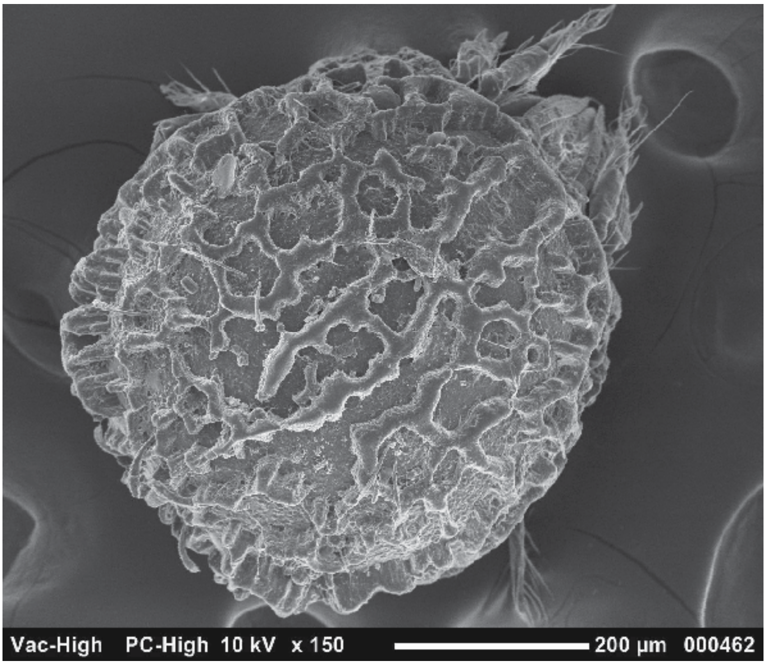

Fig. 12. A cryptostigmatic mite belonging to the genus *Pelops.*

Some soil mite groups have greater numbers of individuals in the boreal then in more southern zone. For exemple Oribatid and Prostigmatid mites are better represented in coniferous then in deciduous or tropical forest soil, and provide a significant share of total soil biomass (Petersen & Luxton, 1982).

Nematodes, perfectly adapted morphologically to interstitial habitats, are considered the most abundant animals on the Earth. The species found in soil are usually small, live in films of water lining soil and detritus particles, and feed on a wide range of substrata, including other nematodes preyed upon by many species of the same group. From the few data available, we can infer that the nematode communities of forest soils play a fundamental role in the control of microbial populations, carrying out this function even more effectively than protozoa. In some soils, microbivorous nematodes are the most numerous component of the nematode fauna (Anderson *et al*., 1978) and act not only as consumers but also as vectors of both pathogenic and useful micro-organisms, in some cases showing specific associations with particular soil bacteria.

In table 3 are reported the distributions of nematode genera, in according of your feeding behaviour, in forest soils of central Europe.

Trophic group	Genera
Nematode bacteriophages	11-18
Nematode mycophages	2-5
Nematode phytophages	7-11
Nematode predators	2-8

Table 3. Distributions of nematode genera in groups feeding on different substrata recorded in forest soils of central Europe (from Wasilewska, 1979).

Large nematode populations are found in decomposing plant detritus, inside the tissues following the action of bacteria and protozoa. By their activity, they favour the humification and structural stability of the soils.

In general, micro-arthropods that feed on micro-organisms or behave functionally as detritivores are difficult to assign to only one of either primary or secondary decomposers. Both categories include Lumbricidae, Diplopoda, Isopoda, Collembola and Acari Oribatida, whereas Enchytraeidae and Coleoptera Elateridae are assigned to the secondary decomposers.

A similar model is used for soil-living predators, with several distinct levels: indeed, we can speak of first-, second- and third-level predators. Generally Chilopoda, Araneidae, Coleoptera Staphylinidae, Acari Gamasida and Uropodina, Pseudoscorpionida and Diplura are assigned to the first two levels, while third-level predators usually include higher animals such as micromammals and birds.

5. Conclusion

Animals included among consumers, demolishers and degraders actively participate in the cycles of organic matter and mineral elements, which without the intervention of these organisms would be destined to prolonged immobilization, especially in regard to the amounts conserved in durable wood structures (Dajoz, 2000). These organisms also establish complex interactions with predators and parasitoids forming part of the next trophic levels, which in turn are often subjected to predation and parasitism. This system of relationships is fundamental for the maintenance of homeostasis of forest ecosystems since it allows the species involved in the consumption and recycling of organic matter to play their role while at the same time maintaining their population numbers within strict limits so as not to jeopardize the equilibrium of the entire system. The last aspect is particularly important because of the necessity to keep primary consumer arthropods and nematodes, which feed on green photosynthesizing organs and subcortical tissues, within the carrying capacity of the ecosystem.

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3

Advances in Molecular Diversity of Arbuscular Mycorrhizal Fungi (Phylum Glomeromycota) in Forest Ecosystems

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1. Introduction

Glomeromycota is a fungal phylum scientifically recognized in 2001 as monophyletic group which probably diverged from the same common ancestor as the Ascomycota and Basidiomycota (Schüssler et al., 2001). Glomeromycota comprises arbuscular mycorrhizal fungi (AMF), important simbiont of land plants and the endocytobiotic fungus, *Geosiphon pyriformis*. Despite of fungi worldwide distribution, relatively few species have been described. The AM fungi are an interesting case: like other fungi they are distributed organisms with apparently widespread mycelial networks, but no sexual stage has been identified in any species in the phylum, they cannot easily be observed or located in situ as they have no conspicuous above-ground fruiting body, and they cannot yet be grown in axenic culture in the absence of plant roots. From 1,5 million microbial fungal species in soils worldwide estimated (Torsvik et al., 1990), about 214 currently described species are glomeromycetes within a universe of 97,000 species of fungal kingdom described so far.

Mycorrhizas are ubiquitous in terrestrial ecosystems. Around 80% of plant species that have been studied form the symbiosis (Wang & Qiu, 2006). There are several different types of mycorrhiza, in which different plant and fungal taxa are involved, but the arbuscular mycorrhizas (AMs) form a monophyletic group of obligate plant symbiotic fungi belonging to the Phylum Glomeromycota and around two-thirds of plant species, is both the most widespread and ancestral: all modern plants have ancestors that formed AM symbioses (Helgason & Fitter, 2009).

The AM fungi are an interesting case: like other fungi they are distributed organisms with apparently widespread mycelial networks, but no sexual stage has been identified in any species in the phylum, they cannot easily be observed or located in situ as they have no conspicuous above-ground fruiting body, and they cannot yet be grown in axenic culture in the absence of plant roots. Initially, the AM species were described only based on asexual spore's morphology. However, new findings showed problems related to dimorphic spores in some species, as for example, spores with morphs from *Glomus intraradices*, i.e., spore with wall simple and Scutellospora spp. morphs, i.e., spores containing several inner membranous walls and develop complex germination shields at the same species.

Furthermore, the scientific community remains discussing several morphologic characters and its limitations to the species identification. Studies based on rDNA sequence have often confirmed the morphologically defined species and the molecular data have erected new genera and families, revealing a considerable unknown AM diversity. To identify fungi from various substrates and in different life stages to species level, the most frequently sequenced region is the internal transcribed spacer (ITS) region of the nuclear ribosomal DNA, however other regions are informative as 18S rRNA, small subunit ribosomal of rRNA (SSU), large subunit ribosomal of rRNA (LSU). Thus, molecular methods are potential tools to cover the diversity of this group.

It is well known that mycorrhizal associations take up mineral nutrients from the soil and exchange nutritional elements with plants for photosynthetically fixed carbon (Smith & Read, 2008). The main nutrient is phosphorous (P) and AMF structures assimilates P from lower concentrations in the soil at which normal plant roots fail (Jefferies et al., 2003). Moreover, these fungi can uptake K, Zn, Fe, Cu, Mg and Ca. The mechanism of absorption is based on major surface area of roots of plants and exploring soil by extraradical hyphae beyond the root hair. The element is then biochemically transformed at external hyphae and passed to the arbuscules for being ultimately transferred to the host plant (Azcon-Aguilar & Barea, 1996).

The plant hosts of AMF are mostly angiosperms, some gymnosperms, pteridophytes, lycopods and mosses (Smith & Read, 1997) which comprises over 80% of all terrestrial plant species. The AM symbiosis is associated with a range of additional benefits for the plant including the acquisition of other mineral nutrients, such as nitrogen and resistance to a variety of stresses (Kaapor et al., 2008) or pathogens (Rabie, 1998), soil aggregation, and carbon sequestration (van der Heijden et al., 2008). AMF can mitigate the effects of extreme variations in temperature, pH and water stress (Michelsen & Rosendahl, 1990; Siqueira, 1994; Augé 2001). For water stress, recent studies have also addressed how symbiosis and water stresses interact to modify the function and expression of plant aquaporins.

Aquaporins are integral membrane proteins that function as gradient-driven water and / or solute channels present in plants. The effect of mycorrhiza interaction in aquaporin expression was described for several plant species, including the tree poplar (Marjanovic et al., 2005), though the microsymbiont was an ectomycorrhizal fungus. An aquaporin protein was recently cloned from an AMF, *Glomus intraradices*, by Aroca et al. (2009), but the interaction between the plant and fungi aquaporins remains unclear, as suggested by the authors, that the fungus aquaporin expression is due to plant. These results came from studies with culture plant species, opening a new view to investigate the expression profile of aquaporins from tree species and its rules at different ecosystems. An aquaporin (water channel) gene from an AM fungus (*Glomus intraradices*), which was named GintAQP1, was reported from experiments in different colonized host roots growing under several environmental conditions. It seems that gene expression is regulated in a compensatory way regarding host root aquaporin expression (Aroca et al., 2009). At the same time, from in vitro experiments, it was shown that a signaling communication between NaCl-treated mycelium and untreated mycelium took place in order to regulate gene expression of both GintAQP1 and host root aquaporins. The authors suggested that specific communication could be involved in the transport of water from osmotically favorable growing mycelium or host roots to salt-stressed tissues.

Despite their importance to plant productivity and sustainability of agricultural systems (Barea, 1991; Smith & Read, 1997), AMF are widely distributed through the most diverse forest ecosystems, as rain forest in southern Queensland-Australia (Gehring & Connell, 2006), Clintonia borealis roots from a boreal mixed forests in northwestern Québec (DeBellis & Widden 2006), hot-dry valley of Jinsha River, southwest China (Dandan and Zhiwei, 2007), forest with *Araucaria angustifolia* in Brazil (Moreira et al., 2007; Moreira et al. 2009; Patreze et al., 2009), in the Atlantic Forest in Southeastern Brazil (Zangaro et al., 2007, 2009), *Hepatica nobilis* Mill. site type spruce forest at central Estonia (Uibopuu et al., 2009), semi-evergreen tropical forest at southeast Mexico (Ramos-Zapata et al., 2011a), *Podocarpus cunninghamii* forests from New Zealand (Williams et al., 2011), young and old secondary forest in Western Brazilian Amazon (Stürmer & Siqueira, 2011), coastal dunes of Sisal, Mexico (Ramos-Zapata et al., 2011b) and floodplain islands as recently related at northeastern Italy (Harner et al., 2011). The observations of AMF occurrence in aquatic environment corroborate the hypothesis of coevolution with the first established plants (Berbee & Taylor, 1993).

Arbuscular mycorrhizas are abundant in herbaceous species as well as in tropical and temperate forest tree species (Harley & Harley, 1987; Newman et al., 1994). The temperate and boreal forest ecosystems are the best studied; however, AM are poorly investigated in these ecosystems since the most of tree species form ectomycorrhizas, a fungal polyphyletic group. In the Pinaceae family, for example, very common in temperate forests, a few species are able to form both ecto- and arbuscular mycorrhizas, e.g., *Pinus muricata*, *Pinus banksiana*, *Pinus strobus*, *Pinus contorta* and *Picea glauca x Picea engelmannii* (O'Dell et al., 1993; Horton et al., 1998; Wagg et al., 2008). Another temperate tree species, Douglas fir, showed over 200 morphologically distinct ectomycorrhizas in southern Oregon (Luoma et al., 1997). The authors reported that after disturbance such as fire burning or logging, roots of Douglas fir seedlings can also be colonized by arbuscular mycorrhizas.

On the other hand, the tropical forests are an outstanding biodiversity hotspot for vascular plants and consequently it is expected a high fungal diversity, including the AM which are symbiotic organisms of vascular plants. These fungi are important as they play a key role for nutrient cycling and nutrient retention in the humus layers. Then, tropical forests rich in plant species from diverse families are considered to be dominated by AM-forming trees; however, relatively few studies have focused at the molecular AM diversity in natural ecosystems and this knowledge is a major bottleneck in mycorrhizal ecology.

In tropical areas, most AMF propagules have shown seasonal fluctuations in abundance either as spores (Guadarrama & Alvarez-Sánchez, 1999, Silva-Júnior & Cardoso, 2006) or in colonized roots (Ramos-Zapata et al., 2011b). The approach which has been conducted is the evaluation of soil quality by direct counts of spores extracted from soil (Carvalho et al., 2003; Moreira et al., 2009), through assessment of percentage of colonized roots (Moreira et al., 2007, Patreze et al., 2009), and estimation of length and biomass of hyphae in the soil using hyphal ^{32}P-labelling (Pearson & Jakobsen, 1993). According to Rosendahl (2008), quantitative studies of arbuscular mycorrhizal fungal communities based on the presence of spore numbers are complicated as some species produce few spores on the mycelium, whereas species such as *G. intraradices*, *G. versiforme* or *G. fasciculatum* produce hundreds of spores on the same hypha. Another technique, the Most Probable Number (MPN) method is a microbiological approach that allows the detection of AMF species which do not produce spores (Troeh & Loynachan, 2003) by soil dilution. However, there are several experimental variables which may influence the final estimations. Several experiments have been carried out at greenhouse for evaluation of dependency and responsiveness to arbuscular mycorrhizal fungi in tree species, as cedar, *Cedrela fissilis* Vell. (Rocha et al., 2006), that occurs in different biomes from Brazil. Siqueira et al. (2010) published recently a book summarizing 30 years of research with mycorrhizal fungi in Brazil. The mycotrophic tree species was discussed in respect to potential use for restoration of degraded land (Soares & Carneiro, 2010) in tropical and arid ecosystems. The use of mycotrophic species in agroforestry systems was also discussed and several examples were discussed, as the studies for peach palm (*Bactris gasipaes* Kunth) and cupuaçu (*Theobroma grandiflorum* (Willd ex Spring) K. Schum) at the central part of the Amazon region in Brazil (Silva-Júnior & Cardoso, 2006).

We propose in this chapter to discuss the advances in molecular diversity of Glomeromycota in forest ecosystems focusing on some aspects related to DNA target regions for sequencing tools, on different approaches on molecular diversity applied to fungal researches and the presence of Glomeromycota in natural and impacted forests. Finally, we will address the challenges to the development of new areas, as genomic and metagenomic applied to mycorrhizal studies.

2. New approaches from molecular techniques

Studies in planta have shown the inability to obtain axenic cultures and the difficulties associated with identifying AMF, made more difficult to establish in the past, advanced studies on their ecology, genetics, and evolution. In the past decade, considerable effort has been expended to understand the keystone ecological position of AM symbioses, most studies have been limited in scope to recording organism occurrences and identities, as determined from morphological characters and ribosomal sequence markers for characterization of AMF, leading to important advances in our understanding of the phylogeny (Schüssler et al., 2001; Schwarzott et al., 2001), ecology (Helgason et al., 1998; Helgason et al., 2002; Husband et al., 2002a, b; Kowalchuk et al., 2002), genetics (Gianinazzi-Pearson et al., 2001; Harrison, 1999), and evolution (Gandolfi et al., 2003; Sanders, 2002) of this group of obligatory symbiotic fungi. rRNA genes have become the most widely use targets for detection of AMF in environmental samples (Clapp et al., 2002). Several PCR-based strategies targeting rRNA genes have more recently been developed to detect AMF in DNA extracted from roots, soil, or spores (van Tuinen et al., 1998; Helgason et al., 1998; Kjoller & Rosendahl, 2000; Kowalchuk et al., 2002; de Souza et al., 2004). Gamper et al. (2010) proposed a shift toward plant and fungal protein-encoding genes as more immediate indicators of mycorrhizal contributions to ecological processes. A number of candidate target genes, involved in the uptake of phosphorus and nitrogen, carbon cycling, and overall metabolic activity were proposed, and advantages and disadvantages of future protein-encoding gene marker and current (phylo-) taxonomic approaches are offered as new strategy for studying the impact of AM fungi on plant growth and ecosystem functioning.

Molecular approaches to community ecology may minimize data variation in the morphological characters that hamper traditional taxonomy and have revealed a considerable unknown AM diversity from colonized roots (Rosendahl, 2008) and soils under different land uses. In forest ecosystems, different groups of fungi, bacteria, algae, and microfauna communities living within the first soil layers can be altered by several factors. The relationship between diversity of fungal communities and resource available and the relation of fungal communities to the greater plant diversity remains under discussion. Using the Ribosomal Intergenic Spacer Analysis (RISA), Waldrop et al. (2006) found no significant effect of plant diversity on the number of fungal ITS bands. However, many other factors unrelated to plants, but inherent to soil (climate, parent material, slope), may influence fungal diversity and they are not easily controlled (Waldrop et al., 2006). The opposite also is possible, i.e. the existence of effects of AM on plants composition and development of plant communities, despite your action to the nutritional status of individual plants (Grime et al., 1987; van der Heijden et al., 1998).

The first steps to better understand the plant host-arbuscular mycorrhizal fungus (AMF) interaction in forest ecosystems could be the deeper studies on plant growth response to different natural soil inocula and upgrading of knowledge about the AM species composition from each community. Williams et al. (2011) observed that pre-inoculation of tree seedlings of *Podocarpus cunninghamii* propagated in glasshouse from cuttings with forest AMF-inoculums collected from a remnant *P. cunninghamii* forest could improve restoration success in comparison to the ex-agricultural AMF community used as inoculums. This last community was less mutualistic than the forest AMF community. These results have potential implications for forest restoration, predicting for example the effect of future forest management on understory forest vegetation. The molecular tools might complement such data helping the identification of mycorrhizal species in different forest communities. An accurate assessment of species richness and community composition is crucial to understanding the role of AMF in ecosystem functioning.

2.1 DNA target regions for sequencing tools

Molecular techniques were developed primarily for the identification of ectomycorrhizas (Gardes et al., 1991; Gardes & Bruns, 1993), and later for the analysis of arbuscular mycorrhizal fungi (AMF) (Lanfranco et al., 1999; Schüssler et al., 2001). Ectomycorrhizal fungi are a large diverse group of an estimated 5000–6000 different species belonging to the Basidiomycota and Ascomycota (Molina et al., 1992), which are very common in forest ecosystems, mainly in temperate and boreal forest ecosystems, where most tree species form ectomycorrhizas (Ducic et al., 2009).

All ribosomal genes (rRNA) are conserved in eukaryotes genomes and they are present in tandem repetition. The regions 18S, 5.8S and 28S are the most conserved, which allows the primer design to amplify the variable and informative sequences (internal transcribed spacer -ITS and intergenic spacer rRNA –IGS).

The fungal internal transcribed spacer (ITS) region of genomic DNA was characterized from single AMF spores by restriction fragment length polymorphism analysis (PCR-RFLP) (Sanders et al., 1995). Then, the ITS region was used to detect AMF in different roots systems (van Tuinen et al., 1998; Colozzi-Filho & Cardoso, 2000; Redecker, 2000) and in the field (Renker et al., 2003, Mergulhão et al., 2008). Using specific PCR primers to identify AMF within colonized roots of *Plantago media* and *Sorghum bicolor*, Redecker (2000) defined five groups of AMF. Later on, the same groups were detected by Shepherd et al. (2007) in roots of twelve tree legumes and non-legume trees, but these primers did not discriminate the AMF species. A set of primers amplifying a SSU-ITS-LSU fragment was developed (Kruger et al., 2009) allowing phylogenetic analyses with species level resolution. Such primers are useful to monitor entire AMF field communities, but they present a drawback related to their size of 1500 bp. Candidate regions to be DNA barcoding of arbuscular mycorrhizal fungi were analysed (Stockinger et al., 2010), but there was intraspecific variation heterogeneous and high in some groups.

Glomeromycota has a distribution of ITS fragment lengths concentrated between 550 and 650 bp, found in 96.4% of in silico analyzed sequences by Patreze et al. (2009). These authors rescued eight Glomeromycota genera and 31 species from 422 ITS sequences. The sub-regions ITS1 and ITS2 show high evolution rate and they are typically specific-species (Bruns & Shefferson, 2004). Furthermore, the great number of ITS copies per cell (more than 250) characterize this region as good target to sequencing where the DNA initial quantity is low, as environmental samples (Nilsson et al., 2009a). Due some taxonomic discrepancies between ITS1 and ITS2 analyzed separately and also in relation to the full ITS region (Nilsson et al., 2009b), it is suggested starting the study using the ITS2 region because it is as variable and long as ITS1, but ITS2 (White et al., 1990) has a major number of access at INSD (International Nucleotide Sequence Databases; Benson et al., 2008) to perform comparisons. Although the ITS sequencing allows species identification, the number of samples required for environmental studies can be unviable. The region ITS1-5.8-ITS2 was used to assess the genetic diversity of geographical isolates of *Glomus mosseae* (Avio et al., 2009).

The target regions Large Subunit (LSU) rDNA and the Small Subunit (SSU) rDNA have been useful at AMF's detection, whereas most studies are based on this last one. The resolution of these genes is different, and a direct comparison of phylogenetically defined taxa is not possible. Van Tuinen et al. (1998) detected four AMF species using one region from LSU rDNA in stained mycorrhizal root fragments by nested PCR. Species and in some cases isolates, also were separated based on polymorphism found in the gene coding for the large ribosomal subunit (LSU) by Single Stranded Conformation Polymorphism (SSCP) method (Kjøller and Søren Rosendahl, 2000). In this later method, nucleotide differences between homologous sequence strands are detected by electrophoresis of single-stranded DNA under non-denaturing conditions (Orita et al., 1989). The question was if it was possible to apply to field roots with unknown arbuscular mycorrhizal symbionts. Some years after, Rosendahl & Stukenbrock (2004) used with success the LSU rDNA sequences to analyze the community structure in coastal grassland in Denmark. The LSU provides a better resolution, but several primers are necessary for amplifying all genera of Glomeromycota. Lee et al. (2008) developed new primers using the small subunit rRNA gene (SSU) as target, providing another alternative to detect AMF directly from field roots. The sequencing of DNA target regions can reveal high variability of taxon richness and composition between particular ecosystems. Öpik et al. (2006) surveyed 26 publications that report on the occurrence of natural root-colonizing AM fungi identified using rDNA region (ITS, SSU and/or LSU), of which nine reports were in forest ecosystems. The number of AM fungal taxa per host plant species in tropical forests was 18.2 and temperate forests were 5.6. The Table 1 summarizes the results of surveys about AMF detection using rDNA regions in forest ecosystems after 2006. Data from two reports were obtained using second-generation sequencing technologies where taxa at very low abundances may be recorded.

Forest ecosystem	**Plant species**	**N° of root samples**	**N° of clones screened**	**N° of AMF sequenced**	**OTU**	**Diversity index**	**Marker region**	**Primers used**	**Reference**
seminatural woodland, North Yorkshire	*Hyacinthoides non-scripta*	33	141	62	**	**	SSU	NS31/AM1	Helgason et al. 1999
	Cajanus cajan	5			48	2.67			
	Heteropogon contortus	5			24	1.88			
boreonemoral forest, Central Estonia	10 species	458	*	158 358	47	9.96 to 38.32	SSU	NS31/AM1	Opik et al. 2009
gypsum area, Southern Spain	*G. struthium* L.	24	3072	1443	19	1.13	SSU	NS31 and AM1+AM2+AM3	Alguacil et. al 2009
	Teucrium libanitis Schreber	24						Nested PCR (NS31 / NS41 and ARCH1311/NS8)	
	Ononis tridentata L.	24							
	Helianthemum squamatum (L.) Dum.Cours	24							
hot and arid valley, Southwest China (undisturbed land)	*Bothriochloa pertusa*	5	1168	241	25	2.38	LSU	Nested PCR (LR1/FLR2 and 28G1/28G2)	Li et al. 2010
northern hardwood forests, Michigan, USA	maple (*Acer* spp.) roots	144	2160	38	27	1.94	18S	AM1/NS31	Van Diepen et al. 2011
mosaic of grassland, wood and heath, UK	soils (area of 7 m^2)	66 soil cores	*	108 245	70	2.45	SSU	Nested PCR (NS31/AM1 and WANDA/AM1)	Dumbrel et al. 2011

Table 1. Overview of arbuscular mycorrhizal (AM) fungal community surveys from forest ecosystems. Data from sampling and sample screening were included. The asterisk means that the manuscript applied the pyrosequencing approach.

The fungal communities analyses by sequencing is based on PCR amplification using specific primers for the taxa in study, followed of cloning of fragments which represent the species richness. This kind of approach generates a library of clones, which many times are high (above one hundred). In order to minimize costs, the clones obtained can be select by restriction fragment length polymorphism (RFLP), grouped according a restriction standard revealed using restriction enzymes. Helgason et al. (1998) made use of this technique for the first time to evaluate the AMF diversity changes comparing agriculture soils and forest adjacent. They suggested that the low taxonomic diversity of arbuscular mycorrhizal fungi in arable fields indicates that their functional contribution may be less there than in woodland.

To date, almost all information on sequence differences in this interesting fungal group comes from ribosomal genes. Other coding regions of the genome were investigated as the variability of β-tubulin and H^+-ATPase genes in the AMF *Glomus intraradices* (Corradi et al., 2004). For this purpose, the authors used degenerate primers in order to sequence the most gene variants possible including any that might have originated from other fungal and eukaryotic groups. Following this idea, it is important to check the sequences available on databases of additional fungal groups to improve the consistence of phylogenetic analysis for arbuscular mycorrhizal fungi, mainly when the objective is evaluate the variability in other than ribosomal genes.

2.2 Molecular methods for fungal diversity and applications

Many methods allow the elucidation of microbial structure has been intensively applied to bacterial and fungal communities, as PCR-Restriction Fragment Length Polymorphism (PCR-RFLP), Denaturing Gradient Gel Electrophoresis (DGGE), Temperature Gradient Gel Electrophoresis (TGGE), Terminal-Restriction Fragment Length Polymorphism (T-RFLP), or Oligonucleotide Fingerprinting of rRNA Genes (OFRG). Here, we select studies which were developed from these methods in Glomeromycetes communities which were applied or have a potential for assessment in natural ecosystems, as forests. All possibilities are described in Figure 1, in an adaptation from Theron & Cloete (2000). The actual function of AMF symbiosis in nature should be considered at the community level of both the AMF and host plants, but we are focusing at fungal partner. All primers sequences and regions of ribosomal RNA genes used in such molecular approaches are shown at Figure 2.

2.2.1 PCR-RESTRICTION Fragment Length Polymorphism (PCR-RFLP) and Single Stranded Conformation Polymorphism (SSCP)

The technique PCR-RFLP was employed with success (Sanders et al., 1995) to distinguish AMF species from DNA isolated of spores; however, when applied to field samples, this technique can generate polymorphism in not target organisms. Avio et al. (2009) were able to discriminate *Glomus mosseae* isolates from G. coronatum, *G. intraradices* and G. viscosum by using of a single enzyme (HinfI) with ITS-RFLP profiles. For field samples, this technique remains insufficiently tested, Mergulhão et al. (2008) detected AMF species in an impacted semiarid soil using the ITS1-5.8S-ITS2 region and Börstler et al. (2010) analyzed for the first time the intraspecific genetic structure of an AMF directly from colonized roots in the field comparing between agricultural and semi-natural sites. To our knowledge, there are not studies using solely PCR-RFLP to characterize AMF communities in forest ecosystems. The work from van Diepen et al. (2011) used the PCR-RFLP to select clones representatives of each type to be re-amplified and sequenced.

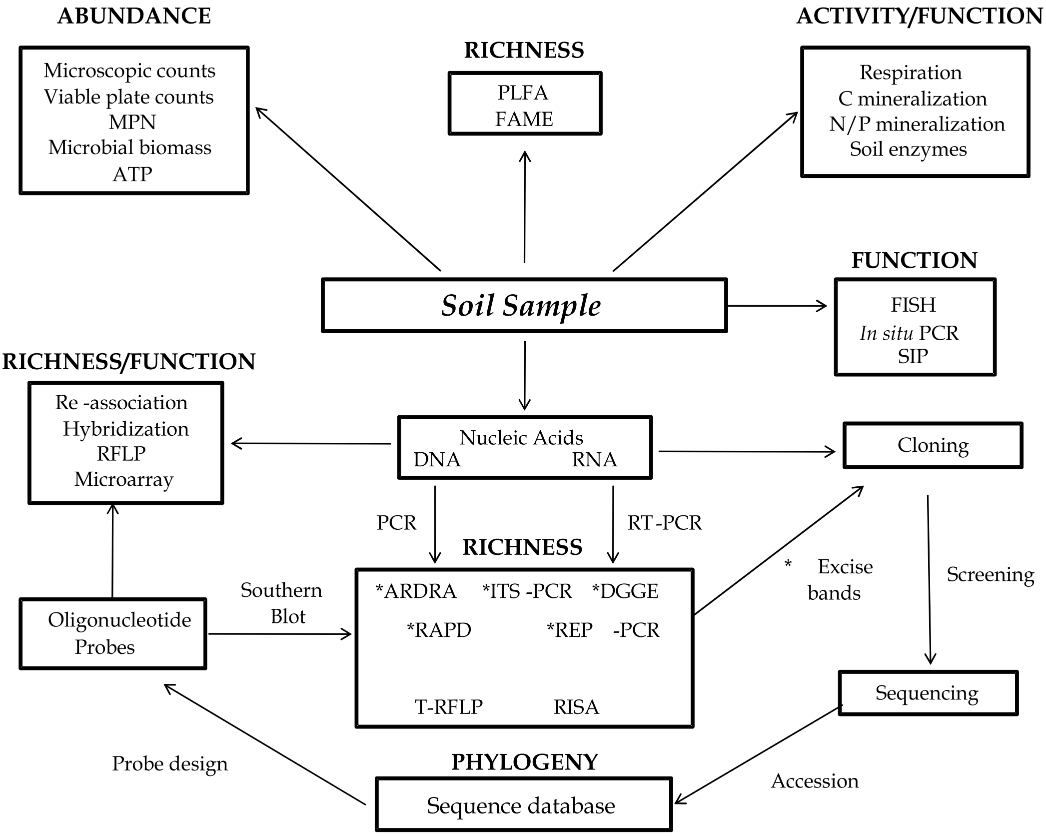
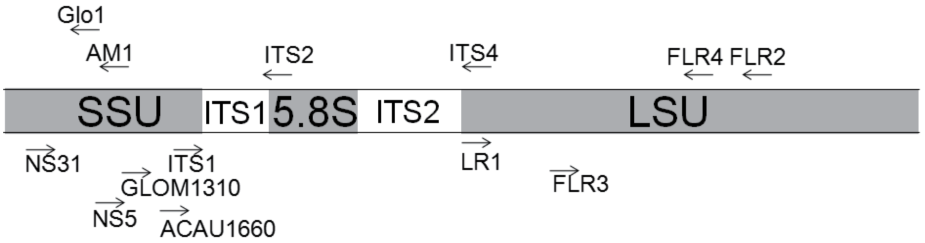


Fig. 1. Commonly used molecular approaches in microbial ecology. PLFA - Phospholipid Fatty Acids; FAME – Fatty Acid Methyl Ester; FISH – Fluorescence in Situ Hybridization; SIP - Stable Isotope Probing; RFLP - Restriction Fragment Length Polymorphism; PCR - Polymerase Chain Reaction; RT-PCR – Real Time Polymerase Chain Reaction; ARDRA – Amplified Ribosomal DNA Restriction Analysis; ITS-PCR – Internal Transcribed Spacer Polymerase Chain Reaction; DGGE – Denaturing Gradient Gel Electrophoresis; RAPD – Random Amplified Polymorphic DNA; T-RFLP – Terminal Restriction Fragment Length Polymorphism; REP-PCR – Repetitive Element Palindromic Polymerase Chain Reaction; SIP – Stable Isotope Probing.



Primer	Sequence (5’-3’)	Reference
ITS1	TCCGTAGGTGAACCTGCGG	White et al. 1990
ITS2	GCTGCGTTCTTCATCGATGC	White et al. 1990
ITS4	TCCTCCGCTTATTGATATGC	White et al. 1990
NS5	AACTTAAAGGAATTGACGGAAG	White et al. 1990
NS31	TTGGAGGGCAAGTCTGGTGCC	Simon et al. 1992
LR1	GCA TAT CAA TAA GCG GAG GA	van Tuinen et al. 1998
AM1	GTTTCCCGTAAGGCGCCGAA	Helgason et al. 1998
FLR2	GTC GTT TAA AGC CAT TAC GTC	Trouvelot, et al. 1999
ACAU1660	TGAGACTCTCTCGGATCGG	Redecker et al. 2000
GLOM1310	AGCTAGGYCTAACATTGTTA	Redecker et al. 2000
FLR3	TTGAAAGGGAAACGATTGAAGT	Gollotte et al. 2004
FLR4	TACGTCAACATCCTTAACGAA	Gollotte et al. 2004
Glo1	GCCTGCTTTAAACACTCTA	Cornejo et al. 2004

Fig. 2. Diagram of the ribosomal DNA cluster of fungi containing the location and sequences of the primers cited in this chapter and used in molecular methods to fungal community studies. The ribosomal RNA (rRNA) gene is a tandem array of at least 50–100 copies in the haploid genome of all fungi. SSU=small ribosomal subunit; ITS1=intergenic transcribed spacer region 1; ITS2=intergenic transcribed spacer region 2; LSU=large ribosomal subunit. The arrows refer to the approximate annealing sites of primers, but the diagram is not to scale.

In order to detect AMF species, nested-PCR, based on sequence differences in the gene coding for the large ribosomal subunit can be coupled to a method known as SSCP (Single Stranded Conformation Polymorphism) and the differences among species are visualized in polyacrylamide gels under non-denaturing conditions. This method allowed Kjøller & Rosendahl (2000) detect four species of Glomus in root tissues of four culture plant species. Jansa et al. (2002) could detect different ITS sequences types within of the single-spore isolates of *Glomus intraradices* using the SSCP technique. A recent study assessed the AMF community at field, in arid gypsophilous plant communities in south-eastern Spain (Alguacil et al., 2009) by sequencing (Table 1), using SSCP to select clones. In such work, representatives of each SSCP pattern were chosen for sequencing while the remaining clones (almost two thousand) were classified by SSCP typing. These sequences showed high degree of similarity to sequences from taxa belonging to the phylum Glomeromycota. In a savanna area, Alguacil et al. (2010) related the AMF diversity in roots of *Centrosema macrocarpum* to soil parameters and sources of phosphorus. The authors amplified by PCR the AM fungal small-subunit (SSU) rRNA genes and selected clones by SSCP to sequencing and phylogenetic analyses. They identified nine fungal types: six belonged to the genus Glomus and three to Acaulospora. The single-stranded conformation polymorphism (SSCP) approach is a very sensitive and reproducible technique that has potential to be applied successfully in studies in order to analyze the sequence diversity of AM fungi within roots from forest ecosystems, not reported so far.

2.2.2 Terminal-Restriction Fragment Length Polymorphism (T-RFLP)

Another technique, derived from a combination of PCR, RFLP and electrophoresis of nucleic acids (Liu et al., 1997) nominated as Terminal-Restriction Fragment Length Polymorphism (T-RFLP) use oligonucleotides fluorescent-labeled that enables generation of fingerprinting data of microbial communities efficiently (Marsh, 1999). Figure 3 exemplifies the steps needed for the T-RFLP analysis. As PCR-RFLP, the selection of restriction enzymes is a fundamental step. It is important to use 2-4 enzymes in each study for obtaining of different amplicons (Tiedje et al., 1999). These authors recommend the enzymes HhaI, RsaI, and MspI, which have given the greatest resolution based on restriction analysis of the database as well as natural communities for soil microbial, but others may be of use under special circumstances, as specific AMF communities. The initial works using T-RFLP for fungal community analysis focused on temperate forests (Klamer et al., 2002) or ectomycorrizas (Zhou and Hogetsu, 2002; Dickie et al., 2002). Combining LSU rDNA sequencing and T-RFLP analysis, Mummey et al. (2009) investigated if the pre-inoculation may play a role in arbuscular mycorrhizal fungi (AMF) community assembly within the roots. Another application of T-RFLP for arbuscular mycorrhizal can be developed to measure the effect of soil inoculums representing different AM fungal communities on the growth of three plant species. Uibopuu et al. (2009) used Glomeromycota specific primers NS31 and AM1 labeled with fluorescent dyes to perform the method known as T-RFLP, comparing the inoculums from a young forest stand, an old forest stand and an arable field at growing of the three plant species and showed that the old and young forest resulted in similar root AMF communities whilst plants grown with AM fungi from arable field hosted a different AMF community from those grown with old forest inocula. However the AMF richness in plant roots was not related to the origin of AMF inoculums. Previous works using the T-RFLP technique were performed in AMF community colonizing roots from herbaceous (Wu et al. 2007), grass (Mummey et al., 2005, Mummey and Rillig, 2008; Hausmann and Hawkes, 2009), addressing studies of impact of various agricultural practices on AMF biodiversity (Lekberg et al., 2007; Verbruggen et al., 2010). The average number of AMF taxa reached in this work was 8.8 OTU and the authors stressed the importance of organic management in agro-ecosystems maintenance of mycorrizal fungi. Van de Voorde et al. (2010) compared the AMF communities from roots of one species of interest in both situations: bioassay plants and plants collected from the field. Although the species had not been a forest, wood or tree plant, this kind of study can be applicable to address similar questions for them.

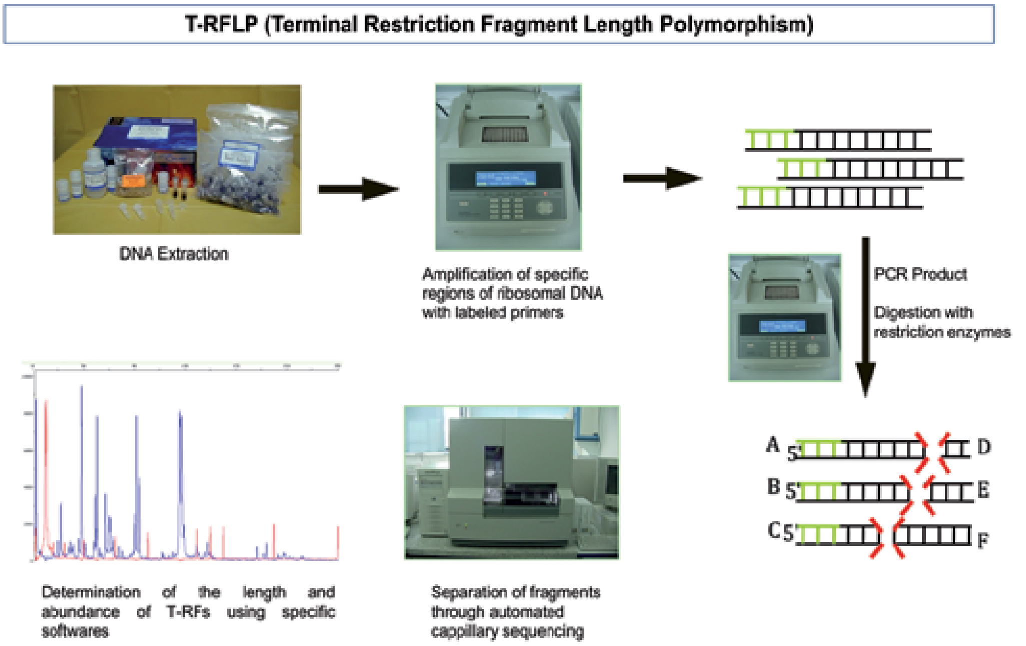


Fig. 3. A schematic design for the steps of a T-RFLP analysis on the soil microbial community structures or for determination of the presence of a target species using specific primer.

Once the belowground feedbacks may lead to changes in species diversity, the knowledge about AMF diversity and distribution both in soil and roots, as well as plant performance is very useful to sustainability of an ecosystem. Evaluating the AMF diversity in roots from seven different shrub species, Martínez-García (2011) suggested that the generate islands of fertility which differ in nutrient content and, therefore, support different AMF communities, increasing AMF diversity at the landscape level. These authors used the primers sequences LR1 and FLR2 for the amplification of the 5′ end of LSU rDNA sequences in general fungi (Van Tuinen et al., 1998; Trouvelot et al., 1999) and in the second amplification, they used the AMF specific primers FLR3 and FLR4 (Gollotte et al., 2004). The same set of primers were used by Koch et al. (2011) to investigate the impacts of introduced plants and exotic AM fungi on local AM fungi at Canada.

2.2.3 Denaturing Gradient Gel Electrophoresis (DGGE), Temperature Gradient Gel Electrophoresis (TGGE)

Denaturing gradient gel electrophoresis (DGGE) and terminal-restriction fragment length polymorphism (T-RFLP) approaches also were applied to AMF studies. These techniques are based on extraction of community DNA followed by the PCR amplification of rRNA genes from the community DNA using universal, domain or group specific primers. The resulting products are separated based on relative helix stabilities in a denaturant (DGGE) or thermal (TGGE) gradient gel (Muyzer et al., 1993). Such techniques are very sensitive and have been used to detect single base differences. However, the gel system employed has low resolving power and there is no way of defining with accuracy the Tm of the helix.

Moreover, there is no comparative sequence database for AMF. In addition, reports have been published and stimulate to better focus on this issue. Kowalchuk et al. (2002) first coupled an AMF-specific PCR strategy targeting the 18S rRNA gene (Helgason et al., 1998) with denaturing gradient gel electrophoresis (DGGE) to detect AMF in roots of a grass species at two coastal sand dune locations in the Netherlands. In this report, the primer reverse NS31, described by Simon et al. (1992) had a GC clamp sequence, as described by Kowalchuk et al. (1997). The same gene (18S rRNA), though a different sub-region, was used by de Sousa et al. (2004) who applied the DGGE method to discriminate Gigaspora isolates and Gigasporaceae populations from environmental samples. Although the environmental samples were collected in a grassland field, a cattle farm in Brazil, that work brings new possibilities for studying the ecology of Gigaspora under field conditions, including forest ecosystems, without the need for trap cultures.

The DGGE from sequential amplification of 18S rDNA fragments by nested PCR using primer pairs AM1-NS31 and Glo1-NS31GC yielded a high-resolution band profile to soil samples from different ecosystems, including a eastern red cedar (Juniperus virginiana L.) forest ecosystems (Liang et al., 2008). The primer Glo1 was described by Cornejo et al. (2004). Although the primer pair AM1/NS31 is one of the most widely used group-specific primer pairs in studies of AMF communities, amplifying the three well-established families of the Glomeromycota (Glomaceae, Acaulosporaceae, and Gigasporaceae), this primer pair does not amplify 18S rDNA fragments from all known AMF or they can amplify some non-AMF sequences. Nevertheless, an advantage for the use of primer pair AM1/NS31 is the relatively large amounts of DNA sequence information derived from this primer pair available. A subsequent study (Zhang et al., 2010) was aimed the variable V3-V4 region of the 18S rDNA of AMF gene, by using nested PCR in three steps: (1) first round PCR, using primers GeoA2 and Geo11 (Schwarzott and Schüssler, 2001); (2) second round, using primers above-mentioned AM1/ NS31-GC; and (3) third round using NS31-GC/Glol. In that study, the AMF community from rhizosphere of two shrubs species was investigated and the species richness ranged from 17 to 25 AMF species. Internal Transcribed Spacer (ITS) specific primers for Acaulosporaceae (ACAU1660/ITS2) and Glomaceae (GLOM1310/ITS2) (Redecker et al., 2000; White et al., 1990) have been used successfully in DGGE analysis on differentiating of composition of mycorrhizal communities in maize genotypes (Oliveira et al., 2009; Pagano et al., 2011).

Two other studies aiming at the molecular community analysis of AMF had as target the fungal small subunit (SSU) rRNA gene. Their objectives were related to role of AMF in plant tolerance to heavy metals stress (Long et al., 2010) and the interplay between soil properties and crop yield (Wu et al., 2011).

Few studies have applied molecular tools as DGGE analysis in forest species. The scarcity of works of this nature in forest species reinforces our goal of encouraging research in this area. Öpik et al. (2003) had surveyed the mycorrhizal status of plants grown in soils from a boreal forest by DGGE plus restriction analysis and sequencing. The region analyzed by them was the SSU region. Recently, using specific PCR conditions for Glomaceae family (nested system with NS5/ITS2 and GLOM1310/ITS2 primers) in DGGE system, Pagano et al. (2011) showed the applicability of this technique to understand the role of AMF in woody and shrub species from Caatinga, a dry deciduous forest at Brazil. The region studied had different agroforestry systems which were implanted in a degraded area in order to be an attractive alternative to conventional afforestation systems. An important conclusion from this work is the existence of functional diversity among AMF, supporting the theory that the AMF are considered as one of the factors that determine how plant species coexist. As observed by Pagano et al. (2011) for semi-arid soil, the analysis of AMF population of an experimental area may inform the state of land restoration depending how close they are from those of climax vegetation.

2.2.4 F-RISA and Automated-RISA (ARISA)

The Fungal Ribosomal Intergenic Spacer Analysis (F-RISA) method exploits the variability on the length of the nuclear ribosomal DNA (rDNA) region that contains the two internal transcribed spacers (ITS1 and ITS4) and the 5.8S rRNA gene (ITS1-5.8S-ITS2). Gleeson et al. (2005) characterized the fungal community structure on mineral surface using this region and Hong, Fomina and Gadd (2009) showed the applicability of this assay to examine the potential role of fungi as bioindicator of effects of organic and metal contamination in soil. It is possible to use the same approach to Glomeromycetes, but it is suggested to sequence some F-RISA fragments from AMF species known to establish standards. Thus, differential fragments when experimental communities are compared can be excised from gel, purified and sequenced in order to detect core AMF species in each environment or ecosystem.

To improve the resolution of this technique was developed an automated variation (ARISA) by Fisher & Triplett (1999) for characterization of bacterial communities. This PCR-based technique is based on the use of a fluorescent primer in the amplification of microbial ribosomal intergenic spacers, using DNA extracted from environmental samples as a template. ARISA was first used to fungal soil communities by using a pair of primers that targeted the 3’end of the 18S rDNA sequence and the 5’end of the 25S rDNA sequence (Ranjard et al., 2001). These authors examined the fungal database for the size of the ITS1-5.8S-ITS2 region in fungi, totalizing 104 genera and 251 species. However, the Glomeromycetes were not recognized as a phylum that date. Patreze et al. (2009) repeated the same in silico analysis including data updated to January 2008. The authors followed the classification of Hibbett et al. (2007), which consider the Glomeromycota as a phylum. Representatives of this phylum have a distribution of ITS fragment lengths concentrated between 550 and 650 bp (Patreze et al., 2009). The authors concluded that a clear distinction among the fungi kingdom is not possible considering the ITS sequence length. However, the method RISA was useful to characterize soil fungal communities from three forest ecosystems from Brazil: a native forest of *Araucaria angustifolia* and two replanted forest.

2.3 Microsatellites

Genetic diversity of arbuscular mycorrhizal fungi also can be investigated from the viewpoint of the population or individual, aside from the community level. Multilocus genotyping of AMF using microsatellites have been useful as marker suitability for population genetics. Microsatellites or Simple Sequence Repeats (SSRs) are regions with at least five identical repeats of two, three or four nucleotides, or a stretch of at least 10 identical single nucleotides. The length polymorphisms at microsatellite regions are caused by changes in the numbers of repeat lengths, which are repeated up to about 100 times (Tautz, 1989). This marker was used to explore the AMF diversity, simultaneously published by Croll et al. (2008a) and Mathimaran et al. (2008a) for the *Glomus intraradices* species. Previous works of distinct nature had reveled genetic variation within AMF species (Vandenkoornhuyse & Leyval, 1998), which affect plant growth and nutrition (Koch et al., 2006). Previously, the possibility of using a tandem repeated DNA sequence as a diagnostic probe for detection in colonized roots was demonstrated from the arbuscular mycorrhizal fungus *Scutellospora castanea* (Zézé et al., 1996). Then Zézé et al. (1997) employed the M13 minisatellite-primed PCR technique to explore the intersporal genetic variation of *Gigaspora margarita*. In the same year, the microsatellites were used as target to detect mycorrizal fungi (ecto and endo-mycorrhiza), including AMFs, however the isolates of *Glomus mosseae* could not be separated by microsatellites analysed (Longato & Bonfante, 1997). In addition, Douhan and Rizzo (2003) had developed a technique to isolate and detect microsatellite loci in AM fungi from single spores of *Glomus etunicatum* and *Gigaspora gigantea*. The authors were not certain that the microsatellite motifs found by them were from the target organism due the possible contaminants. A fingerprinting technique widely used in studies of closely organisms (Lim et al., 2004) known as Inter-Simple-Sequence Repeat (ISSR-PCR) allowed

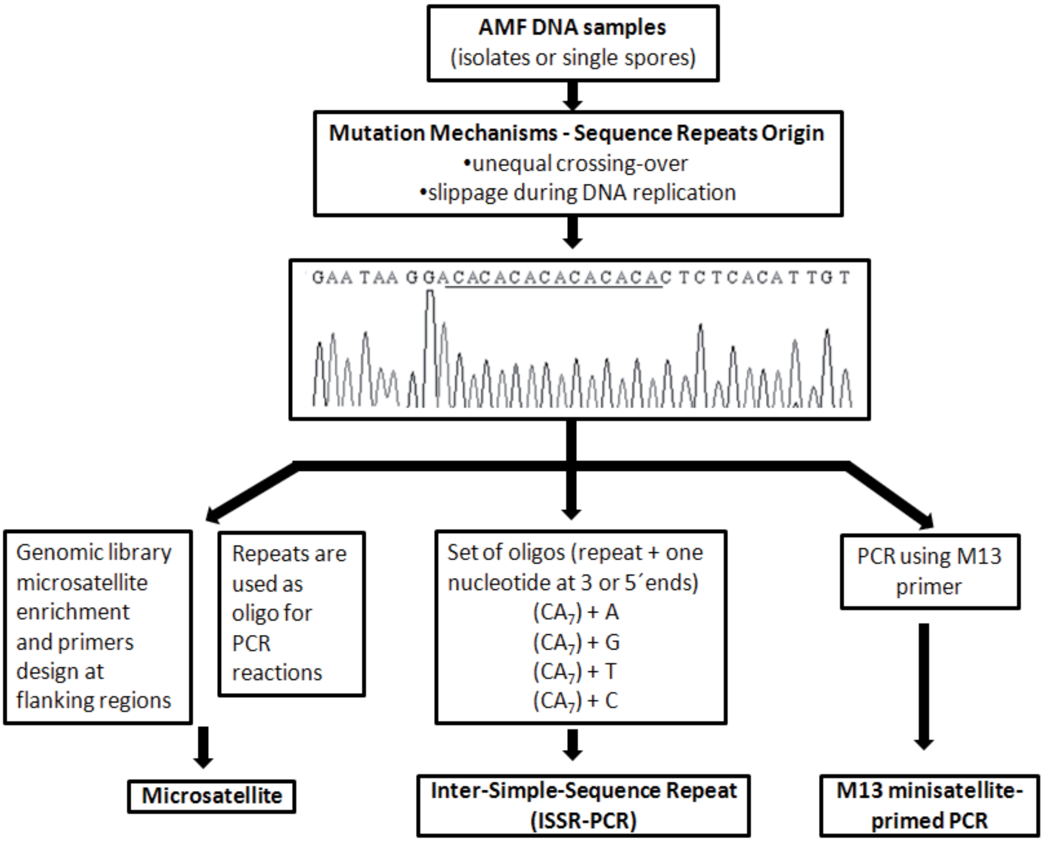


Fig. 4. Microsatellites regions origin and different approaches to explore the variation at length repeats: Microsatellite or Simple Sequence Repeats; Inter-Simple-Sequence Repeat and M13 minisatellite-primed PCR. These techniques were applied to arbuscular mycorrhizal fungi studies.

the characterization of genetic diversity of *Glomus mosseae* isolates (Avio et al., 2009). The authors amplified the minisatellite and microsatellite regions from fungal extracted DNA using the primers M13, $(GTG)_5$ and $(GACA)_4$. The same strategy above-described has potential application to several AMF species. In our opinion, this study can be a precursor of a field research related to the functional diversity of arbuscular mycorrhizal fungi, which remains poorly explored.

Taking into account the AM fungal populations, the molecular techniques have also shown that natural populations exhibit unexpectedly high genetic diversity, despite the assumption that diversity in these seemingly asexual fungi should be low. Thus, microsatellites are an interesting alternative as markers since the ribosomal gene sequences in AM fungi present high diversity, which might cause problems in their use in field studies.

3. Conclusion

Advances at understanding of genome structure of AMF were done in specifics and common species, as *G. intraradices*, which can easily be cultured in large amounts. Analyzing the regions of both LSU rDNA (*Glomus intraradices*) and POL1-like (PLS) sequences (*Glomus etunicatum*), Boon et al. (2010) confirmed high intra-isolate genetic polymorphism at the genome level. Their showed that genetic variation persists at the transcript level and suggested that in AMF, multiple nuclear genomes contribute to a single phenotype. Thus, it is supposed AMF connect plants together by a hyphal network, and that these different genomes may potentially move around in this network. In addition, genomic changes do not only appear among highly divergent lineages but can also occur among highly related species and individuals from the same population (Corradi et al., 2006).

The reassociation kinetics on *G. intraradices* experiments conducted by Hijri and Sanders (2004) revealed that 1.59% from haploid genome size is repetitive DNA, the category that includes the microsatellites regions. However the repetitive regions had low frequency, these authors had suggested that the very small genome size of *G. intraradices* makes it an excellent candidate for a genome sequencing project, beyond this species to be one of the most commonly studied AM fungi which colonizes host plants rapidly. The production of a completely annotated and assembled *G. intraradices* genome was initiated in 2004, having been shown especially arduous challenge. Martin et al. (2008) summarized the main difficulties found to complete this project and presented a nice historical perspective about the advances and approaches used to sequencing.

The recently developed massively parallel ('454') pyrosequencing enables metagenomic and metagenetic analyses in a manner that increase the capacity of traditional Sanger sequencing-based approaches by several orders of magnitude (Tedersoo et al., 2010). Pyrosequencing of fungi in diverse environments, such as soil or roots, elevates the number of recovered taxa several fold (Table 1). Similarly to study of Tedersoo et al. (2010) which compares a ectomycorrhizal fungi community of a tropical rainforest ecosystem by pyrosequencing and Sanger's sequencing, such analysis need to be performed to arbuscular mycorrhizal fungi in order to improve technical biases and to interpreted the data accordingly. Recently, the suitability of species abundance models in arbuscular mycorrhizal fungi were addressed (Unterseher et al., 2011) using output data from a boreonemoral forest in Estonia (Öpik et al., 2009), described in the Table 1. The authors proposed the use of lognormal species abundance distributions (SAD) as a working hypothesis to elucidate MOTU richness and biodiversity of AMF communities with low to medium sampling coverage. Such analyses are recommended to new studies in AMF communities emerging from pyrosequencing.

Studies on the evolutionary ecology of the AMF are on demand in order to approach measuring selection and host specificity as variations in AMF phenotypes were observed more recently with the development of molecular techniques. New approaches based on protein-encoding genes are expected to open opportunities to advance the mechanistic understanding of ecological roles of mycorrhizas in natural and managed forest ecosystems as well. And the idea that direct selection on AM fungal traits related to their survival and performance in the environment independent of the host is being reviewed as extraradical mycelium can be shown to be responsible for a significant part of the diversity of the AM fungi. As proposed by Helgason & Fitter (2009), the fungal response to the abiotic environment is that it would be expected for there to be substantial uncharacterized diversity in the Phylum Glomeromycota, since its members are globally distributed but poorly dispersed, and soil conditions vary greatly in time and space.

There have been significant advances in the plant-microbe interaction studies. As example, laser microdissection (LMD), a method which has been used widely by human and animal biologists to study gene expression in specific cell types and to elucidate the associated molecular events, has been adapted to plant tissues (Day et al. 2005; 2006) and applied successfully to study root-mycorrhizal fungus interactions for the identification of differentially expressed transcripts from LMD-derived RNA for the development of the arbuscule–cortical cell interface (Gomez & Harrison, 2008) or identify transcripts of different phosphate transporters in the same arbusculated cell population provides (Balestrini et al., 2007). The special advantage of LMD for arbuscular mycorrhiza is the isolating of cortical cells containing the fungus from the rest of the root cells. One objective is to rescue the RNA to perform transcript profiles analysis. LMD opens a new scenario for the understanding of the molecular basis of the AM symbiosis. Although the preparation protocols needs to be optimized for each tissue type and plant species, LMD can be adapted to detect and quantify mycorrhizal fungus in forest roots.

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5. Glossary

AMF = Arbuscular Mycorrhizal fungi
ARISA = Automated Variation
DGGE = Denaturing Gradient Gel Eletrophoresis
F-RISA = Fungal Ribosomal Intergenic Spacer Analysis
ITS = Internal Transcribed Spacer
LMD = Laser Microdissection
LSU = Large Subunit ribosomal of rRNA
OFRG = Oligonucleotide Fingerprinting of rRNA Genes

PCR = Polymerase Chain Reaction
RFLP = Restriction Fragment Length Polymorphism
RISA = Ribosomal Intergenic Spacer Analysis
rRNA = Ribosomal RNA
SSCP = Single Stranded Conformation Polymorphism
SSRS – Microsatellites or Single Sequence Repeats
SSU = Small Subunit ribosomal of rRNA
TGGE = Temperature Gradient Gel Eletrophoresis
T-RFLP = Terminal Restriction Fragment Length Polymorphism

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4

Deadwood in Forest Ecosystems

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1. Introduction

Until recently, deadwood was perceived as a negative element of forest ecosystems, that indicates "mismanagement, negligence, and wastefulness" of the applied forest management (Stachura et al., 2007). It was regarded as a potential source of biotic pests, mainly insects (Bütler, 2003; Marage & Lemperiere, 2005), to remaining trees in a forest as well as to adjacent stands (Pasierbek et al., 2007). The presence of deadwood was also seen as a threat of the spread of abiotic disturbances, e.g fire (Thomas, 2002; Travaglini et al., 2007). In managed stands, deadwood represented an obstacle to silvicultural activities (Travaglini & Chirici, 2006; Travaglini et al., 2007), and reforestation (Thomas, 2002). Considering forest workers and visitors, standing dead trees have been seen as a threat to public safety (Peterken, 1996; Thomas, 2002) that had to be removed immediately after they had occurred (Pasierbek et al., 2007). For these reasons, sanitary cuttings have been common forestry activities not only in managed forests, but also in protected areas (Pasierbek et al., 2007; Stachura et al., 2007). In Europe, the maintenance of "hygienic standards" of a forest through systematic removal of sick, dying, and dead trees has been a common practice for more than 200 years (Stachura et al., 2007). In traditional systems, nearly every piece of wood would have been utilised (Mössmer, 1999; Butler et al., 2002). While large deadwood was usually extracted from the forests during stand tending (Radu, 2007), small wood pieces and leftovers were often burnt (Travaglini & Chirici, 2006). This intense forest exploitation has led to a substantial decrease of deadwood quantities (Travaglini & Chirici, 2006).

Over the last decades, the perception of deadwood in forest ecosystems has gradually changed as the scientific research gained information about the functions of deadwood in forests. North American researchers were the first to recognise the importance of deadwood presence in forest ecosystems (Radu, 2007). Already in the first half of the twentieth century several authors (e.g. Graham, 1925; Kimmey & Furniss, 1943; Savely, 1939, as cited in Thomas, 2002) identified deadwood as an important habitat for wildlife. In 1966 Elton (1966) described the role of deadwood in forests as a critical habitat component for a great number of species. In America, researchers as well as forest managers recognised the importance of deadwood in the ecology of a forest as early as in the 1970s (Thomas, 2002). This triggered additional research to further expand knowledge about the role of deadwood in forest ecosystems. Since then, a number of publications have documented its importance particularly for biodiversity (Ferris & Humphrey, 1999; Humphrey et al., 2004; Müller & Schnell, 2003; Schuck et al., 2004), nutrient cycling (Harmon et al., 1986; Krankina et al., 1999; Lexer et al., 2000; Pasinelli & Suter, 2000), natural regeneration (Harmon & Franklin, 1989; Mai, 1999; Ulbrichová et al., 2006; Vorčák et al., 2005, 2006; Zielonka, 2006) and other processes.

Nowadays, deadwood is of interests not only to ecologists, but also to mycologists, foresters, and fuel specialists (Rondeux & Sanchez, 2009). It is increasingly recognised as an important component in the functioning of forest ecosystems (Vandekerkhove et al., 2009) and is becoming an integrated part of forest management (Marage & Lemperiere, 2005). This is proved by the fact that deadwood has been selected as a Pan-European indicator of sustainable forest management (Ministerial Conference of Protection of Forest Ecosystems [MCPFE], 2002). Deadwood is also one of 15 main indicators of biodiversity proposed by European Environmental Agency (Humphrey et al., 2004). Within the Forest Inventory and Analysis program in the USA, deadwood is an indicator of forest structural diversity, carbon sources and fuel loadings (Woodall & Williams, 2005).

Hence, the objectives of the presented paper are (i) to review the approaches for deadwood description, characterisation, and evaluation, (ii) to review the importance of deadwood for sustainable forest management.

Fig. 1. Deadwood as a part of natural forest ecosystem. (photo by J. Vorčák)

2. Definition and types of deadwood

Schuck et al. (2004) and Rondeux & Sanchez (2009) presented several definitions of deadwood that were gathered within the activities of COST Action E272, and thus showed the variability in understanding of this term, which mainly depends on the aim of the particular study (Rondeux & Sanchez, 2009). However, from a general perspective the term deadwood encompasses all woody material in forests that is no longer living including stems, or their parts, branches, twigs, and roots, but excluding deadwood parts of living trees. Hence, it includes both aboveground and belowground woody material (Harmon & Sexton, 1996). It can originate either from the natural mortality caused by senescence, competition, or disturbances (windthrow), or from silvicultural treatments (Rondeux & Sanchez, 2009).

The aboveground woody debris can occur as standing dead trees or shrubs or their partial remains, or as material lying on the forest floor (Pyle & Brown, 1999). Belowground material include dead woody roots and buried wood, which is very decayed woody detritus found in the mineral soil or forest floor (Harmon & Sexton, 1996). However, since belowground material is difficult to quantify (Schuck et al., 2004), it is only rarely accounted for in the studies; although its proportion may be particularly in managed forest stands significant (Debeljak, 2006).

As vary the definitions of deadwood between the studies, so do the types specified in individual works. While some authors (e.g. Atici et al., 2008; Fridman & Walheim, 2000; Christensen et al., 2005; Vacik et al., 2009) distinguish only two types of deadwood, namely standing and lying deadwood, other works use a more detailed classification with four or five deadwood components (Kirby et al., 1998; Schuck et al., 2004; Travaglini et al., 2007). The basic classifications distinguish between standing and downed or fallen deadwood, while the common separation limit is at a 45-degree angle (Harmon & Sexton, 1996; Rondeux & Sanchez, 2009). There is a clear difference in the decomposition process between the two types of deadwood and in the host species. While birds and lichens are almost entirely associated to standing dead trees, fungi and moss species primarily colonise lying deadwood (Stokland et al., 2004).

Standing deadwood consists of standing dead trees, snags, and stumps. Snags are defined as vertical pieces of dead trees. There exists a discrepancy in the understanding of snags and stumps between some authors. For example, Harmon & Sexton (1996) consider a snag any vertical piece irrespective of its height resulting from natural processes only, while Travaglini et al. (2007) require a snag to have a height equal to or greater than 1.3 m. Consequently, in the first work, a stump is defined as a short vertical piece resulting from cutting (Harmon & Sexton, 1996), but in the second paper, it is a piece shorter than 1.3 m irrespective of its origin. Lying deadwood includes downed dead trees, and lying deadwood pieces, which are often called logs. The specification of log parameters depends on a particular study. For example, Pyle & Brown (1999) define a log as a piece at least 1.5 m in length, while Debeljak (2006) considers a log any lying woody piece with length 1 m or more.

The most important size distinction is between coarse and fine woody debris (Harmon & Sexton, 1996) representing large and small pieces, respectively. The two categories are separated depending on the diameter at a specific point on a tree or a log. However, the threshold value varies from 0 to 35 cm (Cienciala et al., 2008). According to IPCC (2003), the border diameter is 10 cm. Harmon & Sexton (1996) found that below this diameter the decay rate increases exponentially, while above this diameter the decay rate decreases only slowly. Due to this fact, the decomposition process of coarse woody debris (CWD) can sometimes take up to 1,000 years (Feller, 2003) depending on wood characteristics (tree species, dimensions), climate characteristics (temperature and moisture, Woodall & Liknes, 2008) and the position on the ground (i.e. contact with the ground, Radtke et al., 2004). Since CWD persists a substantial time in the ecosystem, it is regarded as a more significant component of deadwood than fine woody detritus. Hence, most inventories do not account for fine woody debris and deal only with the components of coarse woody debris.

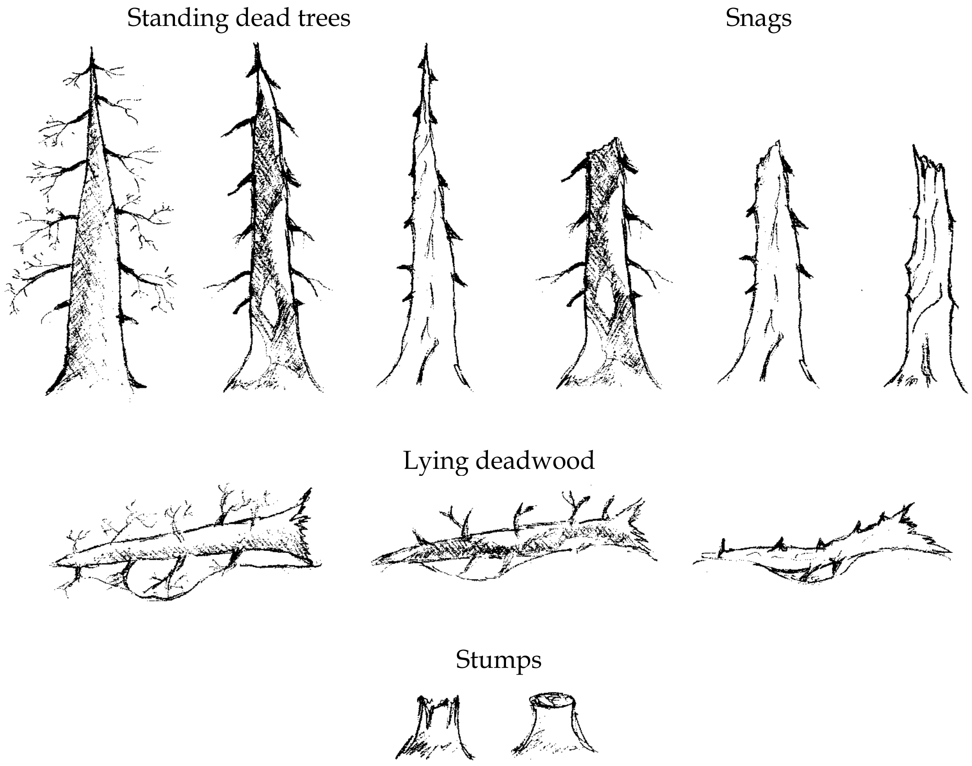

Fig. 2. Types of aboveground deadwood.

3. Deadwood assessment

Nowadays, deadwood is assessed in many countries of the world within national inventories, and through various forest research activities. However, there is no accepted standard for the assessment of deadwood (Fridman & Walheim, 2000; Schuck et al., 2004; Stokland et al., 2004). A thorough analysis was performed by Schuck et al. (2004), who identified seven general deadwood attributes. From them, Rondeux & Sanchez (2009) selected three basic parameters: tree species, dimensions (diameter, height or length), and decay stage. Other attributes, such as cause of death, presence of cavities, or amount of bark left, are less frequently used (Rondeux & Sanchez, 2009).

3.1 Parameters of deadwood

3.1.1 Tree species

Tree species is important particularly because it determines the decay rate of deadwood (Rondeux & Sanchez, 2009) and the habitat qualities for colonising species (Schuck et al., 2004). For recently dead trees, the identification of tree species is quite easy, but as decomposition advances, the identification becomes more difficult (Rondeux & Sanchez, 2009; Stokland et al., 2004). The best criteria are bark surface, and wood structure (Stokland et al., 2004). In Scandinavia, the angle between the trunk and the branches is also used as an identification criterion for separating between Pinus sylvestris and Picea abies, or between coniferous and broadleaved species (Stokland et al., 2004). If a tree species or a genus is impossible to determine, it is recommended to distinguish between conifers/broadleaves and/or hardwood/softwood (Rondeux & Sanchez, 2009; Schuck et al., 2004; Stokland et al., 2004), as many colonising species show preferences for a certain tree species or a group of species (Stokland et al., 2004). From 16 examined tree genera, Quercus was found to have the highest number of specialists (58 species, Jonsell et al., 1998). However, almost all tree genera have some monophagous species, i.e. species restricted to a single tree genus (Jonsell et al., 1998). According to Stokland et al. (2004), only 10% of the colonising species are generalists that utilise both coniferous and broadleaved tree species. As the wood decays, the host range broadens (Jonsell et al., 1998). In the latest stage of decomposition, when it is clearly impossible to determine tree species or a group, deadwood is classified as "unindentified" (Rondeux & Sanchez, 2009; Stachura et al., 2007; Stokland et al., 2004).

3.1.2 Dimensions

Dimensions are necessary attributes to calculate approximate volume of deadwood (Stokland et al., 2004). They are also used to distinguish between individual types of deadwood, e.g. coarse and fine woody debris, or snags and stumps. According to Stokland et al. (2004), diameter is one of the most important biodiversity attributes of deadwood, since a majority of species colonising deadwood respond to its value. While some species prefer small diameters up to 20 cm, other species colonise only deadwood with diameters greater than 20 cm or even 40 cm. Only about 20% of the examined species were found to be generalists (Stokland et al., 2004).

As already mentioned, the variability of minimum threshold diameter between coarse and fine woody detritus is large. In the context of forest management dead wood with diameter of more than 6-7 cm is generally accepted as "deadwood" (Atici et al. 2008), while smaller material is considered of lesser importance (Colak, 2002). Some authors (e.g. Debeljak, 2006; Travaglini et al. 2007; Vandekerkhove et al. 2009) use minimum threshold 5 or 7 cm, which equals the threshold diameter for living trees. Other authors (e.g. Atici et al., 2008; Fridman & Walheim, 2000; Nordén et al., 2004) use the diameter limit 10 cm as suggested by Harmon & Sexton (1996). However, Vandekerkhove et al. (2009) showed that the differences in diameter thresholds did not significantly affect the results, and concluded that unlike stand density, deadwood volume is less affected by size thresholds.

The main attributes used for describing standing deadwood are diameter and height (Rondeux & Sanchez, 2009). In case of standing dead trees and snags with height 1.3 m or more, diameter at breast height is measured. In case of stumps and snags shorter than 1.3 m, diameter at the level where the tree was cut or where the stem was broken off is measured (Travaglini et al., 2007). For lying deadwood, a diameter in the middle of the log (a so called mid diameter) and its length are the main attributes (Rondeux & Sanchez, 2009). Alternatively, diameters at the top and bottom ends of the log (i.e. top and basal diameter, respectively) can be measured in order to produce more precise volume calculations (Harmon & Sexton, 1996).

3.1.3 Decay stage

Decomposition is the process by which organic material is broken down into simpler forms of matter. If the decomposition is driven by physical and chemical processes, it is referred to as abiotic decomposition, while biotic decomposition is the degradation by living organisms, particularly microorganisms. It usually occurs in a number of sequential stages. As presented by Stokland et al. (2004), decay stage is an important quality influencing the associated species composition. In case of decay fungi, Veerkamp (2003) stated that it is the most important factor affecting their occurrence.

The decomposition of deadwood has been studied in many forests of the world (Bütler et al., 2007; Harmon et al., 2000; Jonsson, 2000; Krankina & Harmon, 1995; Kruys et al., 2002; Morelli et al., 2007; Næsset, 1999; Storaunet & Rolstand, 2002; Yatskov, 2001; etc.). The results of these studies showed that the rate/speed of decomposition of deadwood depends on a number of factors (Næsset, 1999), which can be divided into wood characteristics (tree species, dimensions) and site environmental factors (Radtke et al., 2004). Temperature and moisture seem to be the driving site parameters (Yin, 1999), but also the aspect of slope has an effect on the decomposition rate (Harmon et al., 1986). The contact of the deadwood with the ground is another important factor increasing the decay rate (Hytterborn & Packham, 1987, as cited in Næsset, 1999; Duvall & Grigal, 1999; Mattson et al., 1987).

Visual classification of deadwood is the most common approach of decomposition assessment (Bütler et al., 2007). The classification schemes generally distinguish several (3-7) decay stages (e.g. Holeksa, 2001; Lee et al., 1997; Maser et al., 1979; Næsset, 1999; Sollins, 1982). Each study defines its own class specification according to its objectives (Rondeux & Sanchez, 2009). The characterisation of decay stages/classes is usually based on the morphological features (log shape, wood texture, bark adherence, presence or absence of twigs and branches), hardness of the wood, and position with respect to the ground. The hardness of the wood, or the level of rottenness, is assessed by the depth a pushed knife penetrates the wood (Holeksa, 2001; Kuuluvainen et al., 2002; Rouvinen et al., 2005; Pasierbek et al., 2007). Other characteristics that have proven useful to distinguish decay classes include colour of wood, sloughing of wood, friability or crushability of wood (Harmon & Sexton, 1996). Some studies also use the presence of biological indicators (e.g. moss or plant cover, Holeksa, 2001), but Harmon & Sexton (1996) argue that they are of little value because they significantly vary even within a limited area.

Usually, the first decay class represents recently dead wood, which is least decayed with intact bark, present twigs and branches, round shape, smooth surface, intact texture, and the position elevated on support points. As the decay process proceeds the twigs, parts of branches and bark become traces to absent, wood becomes softer and fragmented, and the round shape becomes elliptical. The last decay class represents the most decomposed dead wood with no bark, twigs or branches, which is very soft, strongly fragmented and in contact with the ground along the whole length.

In order to quantify the decomposition process in a more objective way, it may be more straightforward to measure target variables. One method that involves ultrasonic measurements to characterize the wood quality of timber has been described by Sandoz (1989).

3.1.4 Volume, biomass, carbon

The volume of deadwood can either be calculated from the basic dimensions (diameter and height) or estimated on the base of the ocular judgement, which is the simplest and the most cost-effective, but a less accurate method. A thorough analysis of deadwood volume calculations is presented in Rondeux & Sanchez (2009). In general, the calculation of volume of individual standing and fallen dead trees follows the approaches applied to living trees (Rondeux & Sanchez, 2009). The most precise method is the volume equation derived for a particular species and region. Volume tables represent an easier, but a less precise approach (Šmelko, 2010).

In case of snags higher than 1.3 m, some authors (e.g. Travaglini & Chirici, 2006; Vacik et al., 2009) use the same approaches as for the living trees multiplied by a reduction factor representing the reduction of the tree height due to the top breakdown. Other studies approximate the volume of snags by common geometric solids (cylinders, cones, paraboloids), which the wood pieces resemble most (Rondeux & Sanchez, 2009). For example, Vandekerkhove et al. (2009) used the formulas of truncated cones. Merganičová & Merganič (2008) used an integral equation based on the models of stem shape derived by Petráš (1986, 1989, 1990).

Logs, i.e. lying deadwood pieces, usually resemble cylinders. There are three possibilities to calculate their volume depending on which diameters were measured. If only a mid diameter was measured, their volume is calculated using Huber´s formula. In case, top and bottom diameters are known, Smalian´s formula is used. Occasionally, all three diameters (top, middle, and bottom) are measured. In such cases, Newton´s formula can be applied. Concerning the question about the ideal formula to estimate log volume, Harmon & Sexton (1996) concluded that on average, all the formulae presented above should give satisfactory results. For individual logs, Newton's formula had the smallest average deviation from the "true" volume, but none of the formulae were biased (Harmon & Sexton, 1996). The volume of stumps is usually calculated using the formula of cylinder (e.g. Rouvinen et al., 2005).

Belowground volume of deadwood is usually omitted from the studies. Debeljak (2006) presented a method for the calculation of the belowground quantity of coarse woody debris based on the aboveground volume, ratio between the total volume to the root system volume, and the decay stage. Similarly, fine woody debris is only rarely included in the analyses.

Most of the above stated approaches dealt with the volume of individual deadwood pieces. To obtain a value representing the whole stand, the volumes of all occurring types of deadwood (dead trees, snag, logs, stumps) are summed up and converted to hectare values. The stand volumes of deadwood are used to compare different forests, regions, countries, and to evaluate the level of biodiversity, naturalness, or sustainability.

However, volume is not the best indicator if nutrient cycling and/or carbon sequestration are of primary interests, because during the decomposition process woody debris looses not only its volume, but also its mass and density (Coomes et al., 2002; Harmon et al., 2000; Krankina & Harmon, 1995). In such cases, biomass and carbon stock are estimated from volume. Carbon storage in wood is obtained by converting the volume mass into the amount of carbon stored in deadwood. For this conversion, carbon content in wood and wood density need to be known. Usually, carbon fraction in wood is approximated 50% of the woody dry mass (Coomes et al., 2002). Weiss et al. (2000) published more precise values for individual tree species of Central Europe. According to these authors, carbon content in Norway spruce wood is 50.1%, while in European beech 48.6%. This fraction remains stable during the whole decomposition process of deadwood (Bütler et al., 2007).

Unlike carbon fraction in wood, wood density decreases as wood decays (Harmon et al., 2000). While basic wood density of Norway spruce living trees fluctuates around 0.43 g·cm^{-3} (Bütler et al., 2007; Morelli et al., 2007, Weiss et al., 2000), the average density of the most decayed Norway spruce deadwood is only 0.138 g·cm^{-3} (Merganičová & Merganič, 2010). This is a significant reduction of wood density over the course of decomposition, which needs to be taken into account in the carbon stock studies. Merganičová & Merganič (2010) presented that when the volume of coarse woody debris was converted to carbon stocks using the basic wood density of fresh wood (i.e. 0.43 g·cm^{-3}), deadwood carbon stocks were overestimated by 40% or more.

3.2 Deadwood inventory

Initially, information about deadwood was collected to address wildlife habitat issues (Bütler, 2003). Nowadays, deadwood is considered relevant for a number of different issues including nature conservation, forest certification, sustainable forest management, carbon sequestration, etc. Hence, deadwood is now assessed in many parts of the world within national forest inventories and various research activities. However, no harmonised methodology for deadwood inventory exists, as the objectives and the needs differ between the studies (Rondeux & Sanchez, 2009). In spite of these differences, simple, fast and accurate methods are required for both research and management purposes (Bütler, 2003).

In general, the survey can be accomplished either in the whole area of interest, or only on a portion of the given area. Although complete enumeration can provide us with the information about each individual, in large populations, such as forests, this survey is usually not economically and practically feasible. Hence, complete field inventory has been applied very scarcely, e.g. for the repeated measurements of virgin forests in the Czech republic (Vrška et al., 2001a, 2001b, 2001c), or to compare different assessment methods (e.g. Bütler, 2003). Because of high time and cost demands, sampling is often applied instead, while its main condition is that the selected sample represents the whole population. As Shiver & Borders (1996) pointed out, in most cases sampling can be more reliable than complete inventory, because more time can be taken to measurements, while sampling error could be kept small. There exist a great number of publications devoted to sampling techniques in general, e.g. Cochran (1977), Hush et al. (2003), Kish (1995), Shiver & Borders (1996), Schreuder et al. (1993), Šmelko (1985), Thompson (2002), Zöhrer (1980), etc., presenting different sampling designs from simple random sampling, through systematic and stratified sampling, up to multi-stage or multi-phase sampling designs. Deadwood sampling methods present specific characteristics with regard to the spatial distribution and the variability of deadwood components (Rondeux & Sanchez, 2009). As already mentioned, deadwood consists of different types (standing/lying, aboveground/belowground, coarse/fine woody debris) several of which would ideally require their own survey method. Due to this complexity, the majority of studies usually account only for the selected components of deadwood. For example, Marage & Lemperiere (2005) studied standing dead trees only. Most often the aboveground coarse woody debris is the subject of interest, while belowground deadwood is conventionally excluded because its assessment and quantification is difficult (Rondeux & Sanchez, 2009).

Standing deadwood is usually inventoried with the same methodology as living trees (Rondeux & Sanchez, 2009). The common approach is the plot-based sampling, while the plots can either be of fixed or variable area. An example of plots with variable area is when the plots are selected depending on a certain pre-defined number of trees to be included, e.g. the optimisation study of Šmelko (1968) proposed to measure 20-25 trees. In some cases, a set of concentric circles is used (Oehmichen, 2007; Šmelko & Merganič, 2008). Bütler (2003) and Vacik et al. (2009) applied the Bitterlich relascope point sampling, which uses a fixed angle of sight to select the trees to be assessed.

Lying deadwood can also be assessed on the same sample plots as living trees or standing deadwood. The only exception is the Bitterlich sampling method, which cannot be applied to downed deadwood directly (Vacik et al., 2009). In case of plot-based sampling, a common approach is to inventory only the deadwood inside the plot, i.e. if the log crosses the plot border, the part outside the plot is not accounted for in the inventory (Oehmichen, 2007). The second widely used approach is the line intersect sampling firstly presented by Warren & Olsen (1964) and Wagner (1968) for the inventory of logging waste and fuel wood, respectively. The principle of the method is that only the deadwood that crosses the line/transect is inventoried.

Both plot-based and line-based sampling techniques have some advantages and disadvantages. Line sampling is fast and accurate (Harmon & Sexton, 1996), easy to use, more time efficient and more economical than plot-based approach (Oehmichen, 2007). However, plot-based sampling is applicable to all types of deadwood, while line intersect method includes only lying deadwood. Hence, if this method is to be used for the deadwood assessment, it must be coupled with another method to consider standing deadwood. Additionally, Oehmichen (2007) and Rondeux & Sanchez (2009) stated that line intersect sampling is not suitable for long-term monitoring.

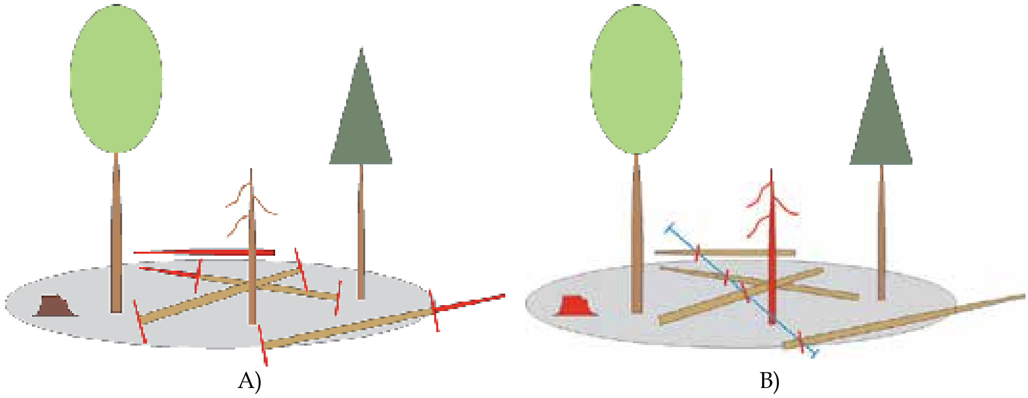
A) B)

Fig. 3. Assessment of coarse woody debris using fixed-area (A) and line intersection (B) sampling techniques. Red colour indicates the elements of coarse woody debris that are not inventoried with the particular method.

Apart from the measurement-based inventory methods, the approach of visual estimation is also used, particularly for the inventory of fine woody debris, as its measurement would be too time consuming. With the visual assessment we can either directly estimate the volume of fine woody debris. However, more frequently other parameters, from which the volume is calculated, are estimated, e.g. average diameter and length (Rondeux & Sanchez, 2009), and the coverage of the plot by fine woody fractions (Šmelko et al., 2006; Šmelko & Merganič, 2008; Šmelko, 2010).

The methods presented so far are field inventory techniques. With the progress of modern technology, new approaches based on remote sensing are promising for coarse deadwood inventory. Infrared aerial photos are suitable for mapping and quantifying of standing deadwood (dead trees and snags) (Bütler, 2003; Bütler & Schlaepfer, 2004), but lying deadwood is not possible to map unless their resolution is 20 cm (Frei et al., 2003, as cited in Oehmichen, 2007). Pesonen et al. (2008) and Vehmas et al. (2009) used airborne laser scanning to assess coarse woody debris characteristics and stated that this approach can be used for the preliminary mapping of forests with large amounts of downed deadwood.

4. Functions of deadwood in forest ecosystems

4.1 Biotope

A great number of different plant and animal species have been associated with deadwood as a space for their lives or the parts of their lives. Over the last decades, the scientific studies have shown that deadwood provides valuable habitats for lichens, bryophytes, fungi, invertebrates, small vertebrates, birds, and mammals (Humphrey et al., 2004). Although the exact numbers differ between regions and studies, in general it has been assumed that around 25% of species occurring in forests are dependent on decaying wood (Schuck et al., 2004). The same number was reported by Siitonen (2001) and Stokland et al. (2003) for Scandinavia.

For saproxylic organisms, dead and dying trees and their parts are the key elements of their life (Davies et al., 2008; Grove, 2002; Lonsdale et al., 2008; Zhou et al., 2007). The group of saproxylic species is the most diverse group in forest ecosystems (Schuck et al., 2004), as it includes all species that depend on deadwood during some part of their life, or upon other saproxylics (Speight, 1989). The main saproxylic taxa are fungi (Ferris et al., 2000; Pouska et al., 2010; Siitonen, 2001), bryophytes (Kruys et al., 1999; Kushnevskaya et al., 2007; Odor & Standovar, 2001; Zielonka & Piatek, 2004), lichens (Kushnevskaya et al., 2007), arthropods such as beetles (Davies et al., 2008; Jonsell & Nordlander, 2002; Persiani et al., 2010), and birds (Bütler et al., 2004). From other groups with a smaller number of saproxylic species we can name mammals such as bats and dormice (Maser & Trappe, 1984), amphibians (DeMaynadier & Hunter, 1995), and moluscs (Kappes et al., 2009).

For other species, deadwood is a source of food and/or construction materials, a nesting and/or breeding site, a shelter, and a hiding place (Bütler, 2003; Debeljak, 2006). The tunnels left after wood-destroying insects can be used as a hiding place for other insects, e.g. wasps (Ehnstrom, 2001). Deadwood can also be used as a lookout post by mammals, e.g. squirrels (Bütler, 2003), or lynx (Bobiec et al., 2005).

4.2 Substrate

Coarse downed deadwood represents favourable environment for the natural regeneration of plant species starting from moss, ferns, and herbs (Franklin et al., 1987; Harmon et al., 1986; Radu, 2007). It is also a primary site to be colonised by fungi and an important seedbed for regenerating tree species. In some forests, the regeneration of tree species is exclusively dependent on the presence of deadwood (Nakagawa et al., 2001; Narukawa & Yamamoto, 2002; Narukawa et al., 2003; Takahashi et al., 2000). In some cases, tree seedlings occur only on the logs of the same tree species (Hofgaard, 1993), while in other cases they colonise the logs of other tree species (Harmon & Franklin, 1989). On deadwood, seedlings are provided with better temperature and moisture conditions (Mai, 1999). Due to these qualities, deadwood is an important rooting substrate particularly in cool climate and severe conditions of boreal (Harmon & Franklin, 1989) and mountain forests (Szewczyk & Szwagrzyk, 1991; Vorčák et al., 2005). Lepšová (2001) and Jaloviar et al. (2008) reported that the root system of the seedlings growing on woody debris was better developed. In ecosystems with abundant herb layer, the regeneration established on such "nurse logs" (Harmon et al., 1986) is favoured against the competing plants (Mai, 1999). However, not all coarse woody debris is a suitable place for regeneration. The suitability of downed deadwood for the regeneration depends on its qualitative parameters, mainly the decay stage, which is closely coupled to other characteristics (moisture, nutrient content). More decayed wood is more appropriate than fresh or slightly decayed deadwood (Merganič et al., 2003).


A) B)

Fig. 4. Deadwood as biotope for saproxylic fungi (A) and substrate for new generation (B), photo by J. Vorčák.

4.3 Nutrient source

Deadwood significantly affects the flow of mass, energy and nutrients in ecosystems. The accumulation and decomposition of organic material on soil surface and in soil is closely coupled to nutrient cycling (Green et al., 1993). Although the relative concentration of nutrients in wood and bark is low, due to the large biomass amount of deadwood it is the main source of nutrients and carbon in forest ecosystems (Caza, 1993; Harmon et al., 1986). Nutrients are released from deadwood slowly over a long time; hence deadwood acts as a natural fertiliser (Holub et al., 2001; Hruška & Cienciala, 2002; Janisch & Harmon, 2001; Mackensen & Bauhus, 2003; Turner et al., 1995). Stevens (1997) reported that coarse woody debris is a nutrient source for more than 100 years. The release of nutrients can be performed by several different ways. Fungi and mosses growing on the surface take nutrients from deadwood, and hence, create a so-called zone of active nutrient cycling (Nadkarni & Matelson, 1992). The flow of nutrients runs through the mycelia of wood decomposing fungi (Zimmerman et al., 1995) as well as through the mycelia of ectomycorrhizal fungi (Lepšová, 2001). It is assumed that the colonisation of deadwood by fungi and microbes is one of the main phases of nutrient cycling (Caza, 1993). The microorganisms and wood-decomposing fungi decompose organic molecules of wood, and thus release the nutrients for plants (Stevens, 1997). All ways of nutrient release are directly or indirectly coupled to the processes causing wood decay. In addition, deadwood is also an important resource of water, especially in dry periods (Harmon & Sexton, 1995; Pichler et al., 2011).

5. Importance of deadwood

5.1 Productivity

The presence of deadwood in forest ecosystems increases their productivity (Marra & Edmonds, 1994; Mcminn & Crossley, 1993). Debeljak (2006) compared managed and virgin forest stands and found that the maximum tree height was significantly lower in the managed stands which may indicate the reduction of forest productivity due to the reduction of coarse woody debris.

5.2 Biodiversity

Since deadwood has been recognised as a habitat of great importance for many species of forest ecosystems, it is considered to be a key element of biodiversity in forests. In many cases, deadwood is associated with relict, rare and protected species (Radu, 2007), and therefore, it is regarded as a key feature for the preservation of many threatened species (Ranius et al., 2003). The recognition of the deadwood importance for biodiversity has led to the incorporation of its quantitative parameters in biodiversity monitoring programmes (Humphrey et al., 2004), e.g. the European Environmental Agency includes deadwood as one of 15 core biodiversity indicators (Kristensen, 2003). The results of the different studies suggest, that the importance of deadwood and its individual parameters differs between the sites and cannot be generalised. According to Humphrey et al. (2004), coarse woody debris is an important biodiversity indicator in conifer-dominated forests in the Atlantic and Boreal biogeographical regions, but is less applicable to Mediterranean forests.

The biological importance of deadwood depends on several factors, in particular on tree species, dimension, vertical and horizontal position, decay stage, and micro-environmental conditions (Radu, 2007). From all deadwood characteristics, the amount of deadwood is usually taken as an indicator of biodiversity (Stokland et al., 2004; Vandekerkhove et al., 2009). A higher amount of deadwood in forests increases the number, and the density of species, and hence, species richness, because higher deadwood amount means greater surface and area in forests, and hence, its higher availability for potential users (Müller & Bütler, 2010). This is in accordance with the island theory (Cook et al., 2002) according to which we can expect higher number of species in a unit with a larger "island". Secondly, larger surface means greater possibilities of its differentiation (Müller & Bütler, 2010) providing species with a greater variability of habitats.

Several studies detected the correlation of species richness to deadwood amount (Müller & Bussler, 2008; Müller & Bütler, 2010). It is widely agreed that 20-30 $m^3 \cdot ha^{-1}$ is the required amount that can safeguard the complete spectrum of deadwood-depending species (Angelstam et al., 2003; Humphrey et al., 2004; Siitonen, 2001; Vandekerkhove et al., 2009), although some authors presented higher values. For example, according to Müller & Bussler (2008), the critical threshold for saproxylic Coleoptera is between 40 and 60 $m^3 \cdot ha^{-1}$. Other studies argued that for some taxa the diversity of deadwood components, and its continuity in space and time is a more important feature than its amount (Heilmann-Clausen & Christensen, 2004; Schiegg, 2000a; Similä et al. 2003). Hence, for biodiversity conservation it is also important to balance the proportions of individual deadwood types and decay stages (Hagan & Grove, 1999), as each type represents quite different habitats suitable for different species.

5.3 Naturalness

Deadwood characteristics are also common attributes used for assessing forest naturalness (Laarmann et al., 2009; Winter et al., 2010), since the differences in deadwood between managed and unmanaged forests are in most cases notable (Kirby et al., 1998; Liira et al., 2007). In general, the amount of deadwood is lower in managed in stands than the stands left to self-development (Rahman et al., 2008; Rondeux & Sanchez, 2009; Travaglini & Chirici, 2006), because most of large-sized wood is extracted from the forest. Therefore, to determine the level of naturalness of forest ecosystems, the amount of coarse woody debris has become an important indicator (Rahman et al., 2008). However, for the proper application of deadwood as an indicator, reference values representing the "natural" state are needed. Such values can be obtained from natural unmanaged forests (virgin/old-growth forests) (Hahn & Christensen, 2004; Humphrey et al., 2004). However, when using the reference values it must be considered that the volume of deadwood varies considerably among forest sites. While in North America the volume of coarse woody debris in old-growth forests may exceed 1,000 $m^3 \cdot ha^{-1}$ (Harmon et al., 1986), in Europe the average values between 40 and 200 $m^3 \cdot ha^{-1}$ have been reported (Albrecht, 1991; Christensen et al., 2005; Hort & Vrška, 1999; Karjalainen et al., 2002; Siitonen et al., 2000; Vallauri et al., 2003; Vandekerkhove et al., 2009). Larger values (more than 400 $m^3 \cdot ha^{-1}$) have been found in virgin forests of Central Europe, e.g. Slovakia (Saniga and Schütz, 2001), Poland (Bobiec, 2002), Slovenia (Debeljak, 1999, 2006). Even in Europe, there is a large variability of deadwood accumulation, when northern boreal and southern Mediterranean forests are characterised by a lower deadwood amount than Central European mixed forest types (Hahn & Christensen, 2004).

Large amount of deadwood does not necessarily indicate the high level of naturalness of forest ecosystems (Laarman et al., 2009; Marage & Lemperiere, 2005; Rouvinen et al., 2005; Pasierbek et al., 2007), particularly in cases when it is the result of the accelerated breakdown of forest stands (Jankovský et al., 2004) due to disturbances. The analysis of Laarman et al. (2009) reported that the spatial distribution of deadwood, proportion of recent mortality and the causes of mortality seem to be better indicators. Marage & Lemperiere (2005) revealed that the differences between the managed and unmanaged forest stands were only in the category of standing dead trees, as in the managed stands the trees are extracted before they reach their maximum diameter. Hence, deadwood is an appropriate indicator of naturalness only if the additional information about its components, decay stages, etc. is also available (Liira & Sepp, 2009; Rondeux & Sanchez, 2009).

5.4 Geomorphology

Mechanical and physical qualities of large-sized deadwood have a significant influence on the geomorphology of forest soils and small watercourses in forest ecosystems (Stevens, 1997). On slopes, coarse woody debris significantly contributes to slope and soil surface stability. Fallen logs prevent or slow down soil erosion and surface water runoff (Kraigher et al., 2002; Stevens, 1997), and act as barriers for rock fall and avalanches (Kupferschmidt et al., 2003).

6. Factors influencing deadwood pool in forest ecosystems

Deadwood is the result of the influence of various abiotic and biotic factors on individual trees or forest stands. The quantity of deadwood and its decomposition in a particular forest ecosystem depends on many intrinsic and extrinsic factors that drive the input of deadwood and its decomposition process. Intrinsic factors include deadwood type, dimensions, and tree genus that determines basic tree and wood characteristics, while extrinsic factors include climate and site conditions, and disturbances.

Tree species can predetermine the mortality pattern and subsequently the accumulation and decomposition of deadwood. Species with a shallow root system, e.g. Norway spruce, are susceptible to uprooting, while deep-rooted species usually suffer from breakdown. However, under favourable climate and soil conditions, this may not hold, as e.g. in mountain spruce forests of Babia hora Holeksa (2001) detected that the snags were dominant over the uprooted trees, whose proportion was much lower than in other temperate and boreal spruce forests.

The rate of deadwood decay depends on the chemical composition of wood, which is specific for each tree species. Some tree species are decay resistant, for example oak or pine (Radu, 2007). Softwood species, e.g. willow, birch, and poplar, have a much shorter period of decomposition (Radu, 2007). The resistance of deadwood depends on the content of extractives (polyphenols, waxes, oils, resins, gums, tannins) in the heartwood, which are toxic to most decay fungi and some insects, and hence slower the decomposition process.

However, the decay resistance of a particular species may vary greatly depending on the dimensions and site conditions. The length of the decomposition process is positively correlated with deadwood diameter. The turnover of fine dead woody debris is fast (Stevens, 1997), while its decomposition rate increases exponentially with decreasing diameter (Harmon & Sexton, 1996). The differences in decay rate are also between standing and lying deadwood. The decay of snags is slower than the decay of logs because of lower wood moisture (Kupferschmidt et al., 2003). Snag diameter has also a positive influence on the time length the snag stands (Everett et al., 1999; Morrison & Raphael, 1993, as cited in Bütler, 2003).

From site conditions, temperature and moisture seem to be the driving factors. In warm, moist environments decay rates are higher, because such conditions favour microbial and fungal growth (Yin, 1999). This is evident in the analysis of deadwood volume along the elevation gradient. According to MCPFE (2007), the lowest amount of deadwood is in the forests situated at the lowest elevations. As elevation increases, accumulated deadwood volume enlarges. This increasing trend with elevation was also observed in the national analysis in Slovakia (Merganič et al., 2011), when at the lowest elevations the authors reported only 10 $m^3 \cdot ha^{-1}$, while under the timber line the deadwood volume was around 100 $m^3 \cdot ha^{-1}$. Similarly, Kühnel (1999) reported that in mountain forests the amount of deadwood is three times higher than in lowlands.

6.1 Disturbances

In natural forests deadwood originates from tree mortality, which is either the result of inter-tree competition or senescence processes, or it is caused by natural disturbances, which can differ in terms of quality and quantity (Rahman et al., 2008). Disturbances can be driven by abiotic (wind, fire) and/or biotic factors (insect outbreak). Windthrow, icebreak, insect and fungal attacks leave various amounts of deadwood in the forest, while during fire disturbances deadwood is immediately consumed (Hahn & Christensen, 2004). The disturbance factors vary in intensity and scale leading to a patchy distribution of deadwood at the stand and landscape levels (Humphrey et al., 2004). Small-scale disturbances cause the death of individual trees or small groups of trees, while large-scale disturbances affect the whole ecosystem (Korpeľ, 1995).


A) B)

Fig. 5. Large-scale disturbances caused by windthrow (A) and insect outbreak (B).

Small-scale events occur frequently and hence provide a continuous supply of deadwood (Rahman et al., 2008). Due to this, in forests following a so-called small cycle deadwood of different size and decay stages can be found (Korpeľ, 1995; Saniga & Schütz, 2001). On the landscape level, the deadwood pool is relatively stable, and the differences are obvious only on a small scale between the developmental stages. The highest amount of deadwood occurs in breakdown developmental stages, while the lowest amount is in the stage of maturity (Merganičová et al., 2004; Merganičová & Merganič, 2010).

In contrast, large-scale disturbances cause abrupt changes of the whole ecosystem, which result in high deadwood inputs at the time of the event. At this stage, these ecosystems may attain higher amounts of deadwood than the forests developing in a small cycle (Rahman et al., 2008; Šebeň et al., 2009). However, in the following successional stages, deadwood input is minimal, and the total amount of deadwood declines (Rahman et al., 2008).

6.2 Forest management

Apart from the natural factors discussed so far, a man with its activities also affects deadwood in forest ecosystems either directly through forest management or indirectly by e.g. air pollution (Debeljak, 2006). While the first forms of human utilisation of wood, e.g. domestic use of wood, had apparently only a slight influence (Rouvinen et al., 2005), with the increasing human population, human influence has become more intensive and widespread (Björn, 1999, as cited in Rouvinen et al., 2005). Nowadays, it is generally agreed that forest management has a negative effect on deadwood amount and deadwood components (Atici et al., 2008). Dead, damaged and weakened trees are often removed from the forest during harvesting operations (Bütler, 2003). Thinnings reduce deadwood inputs from natural mortality. Short rotation time limits the presence of large dead trees (Bütler, 2003; Debeljak, 2006; Marage & Lemperiere, 2005), because trees are harvested before they reach their maximum diameter (Atici et al., 2008). After natural disturbances, such as windthrow or insect outbreak, dead trees are harvested in salvage logging (Bütler, 2003). The effect of management on deadwood is linked with the accessibility of harvesting areas. Bütler (2003) found a significant negative relationship between road density and deadwood amounts in Switzerland. Pasierbek et al. (2007) detected more deadwood on the sites which were situated far from the settlements.

The current amount of aboveground deadwood in managed forest is very low. According to Nilsson et al. (2002), before human exploitation common deadwood amount in European forests was 130-150 $m^3 \cdot ha^{-1}$, nowadays the values range from 1 to 23 $m^3 \cdot ha^{-1}$ (MCPFE, 2007). Usually, the average amount of aboveground deadwood does not exceed 10 $m^3 \cdot ha^{-1}$ (FAO, 2000; Fridman & Walheim, 2000; Christensen et al., 2005). In some cases, it does not even reach 5 $m^3 \cdot ha^{-1}$ (Albrecht, 1991; Smykala, 1992; Schmitt, 1992; Vallauri et al., 2009). In addition, deadwood in managed forests typically consists of fine woody debris (small twigs and branches) and short stumps (Atici et al., 2008). A large, but often a forgotten part of woody debris in managed stands may be belowground deadwood originating from root systems of cut trees (Debeljak, 2006). This author presented that the proportion of belowground coarse woody debris in managed forests is significantly higher than in virgin forests. However, this type of deadwood is buried, and therefore not available to all saproxylic species, e.g. birds.

Therefore, in the interests of sustainable forestry and biodiversity conservation the efforts are being made to increase the levels of deadwood in managed forests (Atici et al., 2008). There exist a great number of publications that deal with the question how much deadwood should be left in a forest. However, the variation of the recommended values is quite large. Older studies suggest at least 3 $m^3 \cdot ha^{-1}$ (Utschik, 1991) or 5-10 $m^3 \cdot ha^{-1}$ (Ammer, 1991), which is 1-2% of the total volume of the stand. In more recent studies the suggested values are higher and fluctuate between 15 and 30 $m^3 \cdot ha^{-1}$ (Bütler & Schlaepfer, 2004; Colak, 2002; Jankovský et al., 2004), or 5-10% of the total stand volume (Bütler & Schlaepfer, 2004;

Jedicke, 1995; Möller, 1994; Vandekerkhove et al., 2009). According to Vandekerkhove et al. (2009), the minimum amount of deadwood should secure the existence of the whole spectrum of saproxylic species. The works dealing with their populations suggest 40 $m^3 \cdot ha^{-1}$ to be the threshold value, when the diversity of saproxylic communities is comparable with the diversity in virgin forests (Haase et al., 1998; Kirby et al., 1998; Müller & Bussler, 2008). It is clear that very small values are too low to be important for nature conservation (Scherzinger, 1996) or biodiversity. Considering the large variation in the values of deadwood from natural forests, which are references for management, no universal value valid throughout the world exists (Jankovský et al., 2004). The guidelines and recommendations should be given for more homogeneous groups, e.g. individual forest types (Hahn & Christensen, 2004). The consensus should also be found between gains and losses (Atici et al., 2008).

7. Conclusion

Nowadays it is generally accepted that deadwood plays an important role in ecosystem dynamics. In this chapter we presented the synthesis of existing knowledge about deadwood including its assessment, evaluation, and factors influencing deadwood occurrence and dynamics. Although less than one decade ago, the information about the decay rates of deadwood in Europe was almost completely missing, this gap is currently being filled. Addressing the full spectrum of processes within forest ecosystems, in which deadwood occurs, we implied to coherently analyse its importance for sustainable forest management and issues closely coupled, e.g. biodiversity, naturalness. While the importance of deadwood for biodiversity has been thoroughly studied, less information is available about the relationship between deadwood and stand productivity and geomorphology. Future research should focus more on investigating belowground component of deadwood, which is currently usually not accounted for in the inventories. For forest management, more specific guidelines with regard to forest type and/or region would be helpful to maintain sufficient amount of deadwood for biodiversity preservation.

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5

Composition and Stand Structure of Tropical Moist Deciduous Forest of Similipal Biosphere Reserve, Orissa, India

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1. Introduction

Tropical forests are highly productive, structurally complex, genetically rich renewable genetic resources (Roy et al., 2002). The tropical deforestation contributes to increase in atmospheric CO_2 and other gases affecting the climate and biodiversity. Though such type of forests occupy less than 7% of the land surface, there have the higher distinction of harbouring 50% of all plant and animal species (Mayers, 1992). The rate of forest loss due to deforestation as reported by Food and Agriculture Organistion [FAO, (2001)] is 15.2 million hectare per year (Data from 1990-2000). Assessment of the plant diversity of forest ecosystems is one of the fundamental goals of ecological research and is essential for providing information on ecosystem function and stability (World Conservation Monitoring Centre [WCMC], 1992; Tilman 2000; Townsend et. al., 2008). It has attracted attention of ecologists because of the growing awareness of its importance on the one hand and the massive depletion on the other (Singh, 2002; Lewis, 2009). Out of sixteen major forest types of India (Champion and Seth, 1968), tropical forests occupy 38 % of the total forest area in India (Dixit, 1997). However, in Orissa forest ecosystems cover about 37.34% of the State's geographical area and about 7.66% of country's forests. Large population of the state utilizes various components of the forests for both commercial and subsistence purposes. In the past few decades, heavy human pressure has reduced the forested area in the state resulting in degradation and fragmentation of historically contiguous landscapes posing threats to plant diversity (Murthy et al., 2007). It is now high time to conserve the plant diversity and has the task become a major concern for much of the society and for many governments and government agencies at all levels (Tripathi and Singh, 2009).

The Man and Biosphere Programme launched by United Nations Educational Scientific and Cultural Organisation ([UNESCO], 1971 as cited in Parker, 1984) aims at conserving the floral wealth in protected areas established by the Govt. of India in different states. Similipal Biosphere Reserve (SBR), a northern tropical moist deciduous type of forest (Champion and

Seth, 1968) situated in the Mayurbhanj district of Orissa has over the years, played important roles in maintaining the climate and livelihood of local communities (Srivastava and Singh, 1997; Rout et al., 2010). The SBR located in Eastern Ghat has distinctly dissimilar to the forests located in Western Ghats of India and Srilanka (Table-1). Table-2 provides a comparative account of floristic richness of some tropical forests. Genera like *Ficus*, *Diospyros*, *Syzygium*, *Symplocos*, *Dalbergia*, *Glochidion* are prominently represented in all these ecosystems as shown in Table-1.

Name of genera	Number of species		
	Western Ghats	Srilanka	Similipal
Goniothalamus (Annonaceae)	3	5	0
Garcinia (Clusiaceae)	9	6	0
Calophyllum (Clusiaceae)	3	9	0
Mesua (Clusiaceae)	1	3	1
Dipterocarpus (Dipterocarpaceae)	2	4	0
Hopea (Dipterocarpaceae)	8	4	0
Shorea (Dipterocarpaceae)	1	14	1
Stemonoporus (Dipterocarpaceae)	0	22	0
Pterospermum (Sterculiaceae)	6	0	1
Elaeocarpus (Elaeocarpaceae)	6	7	0
Ilex (Aquifoliaceae)	5	3	0
Euonymus (Celastraceae)	5	3	0
Holigarna (Anacardiaceae)	3	0	0
Semecarpus (Anacardiaceae)	2	10	1
Dalbergia (Leguminosae)	4	1	2
Humboldtia (Leguminosae)	5	1	0
Syzygium (Myrtaceae)	29	40	2
Memecylon (Melastomaceae)	9	25	1
Mastixia (Cornaceae)	1	3	0
Canthium (Rubiaceae)	5	4	0
Ixora (Rubiaceae)	6	4	1
Psychotria (Rubiaceae)	14	13	0
Lasianthus (Rubiaceae)	9	9	0
Vernonia (Asteraceae)	4	11	1
Ardisia (Myrsinaceae)	6	6	0
Palaquium (Sapotaceae)	2	9	0
Diospyros (Ebenaceae)	16	22	5
Symplocos (Symplocaceae)	21	12	2
Strobilanthus (Acanthaceae)	9	27	0
Myristica (Myristicaceae)	3	3	0
Cinnamomum (Lauraceae)	6	8	0
Actinodaphne (lauraceae)	5	9	0
Litsea (Lauraceae)	8	12	0
Cleistanthus (Euphorbiaceae)	2	5	1
Drypetes (Euphorbiaceae)	4	1	0
Glochidion (Euphorbiaceae)	10	9	2
Croton (Euphorbiaceae)	6	2	1
Agrostistachys (Euphorbiaceae)	2	3	0
Mallotus (Euphorbiaceae)	5	4	1
Macaranga (Euphorbiaceae)	2	3	1
Aporusa (Euphorbiaceae)	5	3	0
Ficus (Moraceae)	10	8	8

Table 1. Numbers of species in large woody plant genera confined to the Western Ghats, Srilanka and Similipal biosphere reserve (included under Eastern Ghats).

Forest locations	Area (ha)	Number of species	Number of genera	Number of families	Source of information
Jadkal forest	0.5	103	85	46	Vasanthraj et al., 2005
Lowland rain forest, Sabh, Malaysia	8.0	329	128	52	Campbell and Newbery, 1993
Low land dipterocarp forest, Danum Valley, Malaysia	8.0	511	164	59	Newbery et al., 1999
Keranga forest, Sarawak and Brunei	-	637	-	60	Newbery, 1991
Similipal, Orissa, India	3.6	266	204	76	Present study

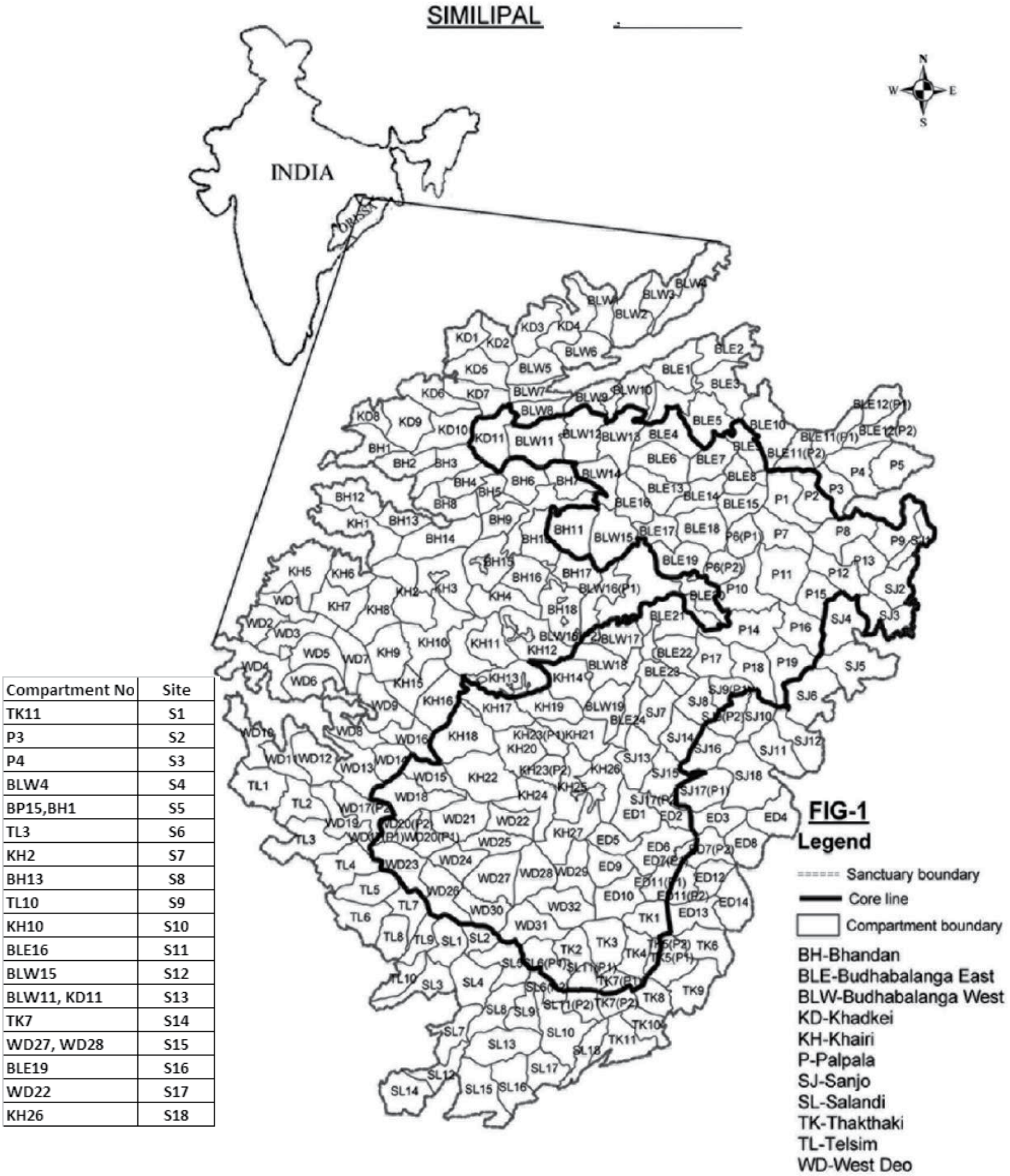
Table 2. A comparative account of floristic richness of some tropical forest locations.

The National forest policy in India stipulates 33% of the total geographical area is to be under forest cover. Large area of fertile forest lands have been converted to other land uses to meet the demand of growing population. In addition opening of the close forests due to deforestation has resulted in increase in soil erosion, landslides, floods and loss of biodiversity and wildlife habitats. At the global level similar situation is reported from Brazil, Malyasia, Indonesia, Africa and Central American countries where loss of wildlife habitat ranges from 40-80% (Puri, 1995). The tropical dry forest of Coasta Rica (Heinrich and Hurka, 2004) is floristically very rich and diverse compared to the dry forests of Puerto Rico (Hare et al., 1997). Compared to other tropical dry deciduous forests of Eastern Ghats of India (Krishnannkutty et al., 2006) which are under various degrees of anthropogenic pressures, the SBR occupies strong ecological position in terms of species number and diversity. SBR is generally believed to be floristically rich, containing many varieties of plant life forms and medicinal plants as well (Saxena and Brahmam, 1989). Carefully compiled and up-to date information on diversity and distribution status of plant resources is however lacking. Though human-induced pressure, mainly through illegal chainsaw logging and access to non-timber forest products (NTFPs) is on the rise (Rout et al., 2009; Rout et al., 2010), a very few sporadic studies of SBR (Mishra et al., 2006, Mishra et al., 2008; Reddy et al., 2007) has so far been conducted to assess the plant diversity status. The conservation status of the biosphere reserve to be known attempting sustainable management, there should be need of proper documentation of diversity status of various plant life forms and their distribution patterns inside the reserve. Knowledge of floristic composition, structure and distribution of angiospermic plants of this biosphere reserve is critical in this direction.

2. Materials and methods

2.1 Study area

Similipal Biosphere Reserve (SBR) located between 21°28′- 22° 08′ N latitude and 86°04′ - 86°37′ E longitude is situated in the Mayurbhanj district of Orissa stretching over an area of 5569 sq. km (Fig.1). The vast patch of forest covers of Similipal is one of the mega-biodiversity zones of the country with a rich population of flora and fauna. The elevation of valley peaks ranges from 80m to 869 m M.S.L. rolling with pockets of grassy meadows in between and traversed by a number of streams and waterfalls.



Compartment No	Site
TK11	S1
P3	S2
P4	S3
BLW4	S4
BP15,BH1	S5
TL3	S6
KH2	S7
BH13	S8
TL10	S9
KH10	S10
BLE16	S11
BLW15	S12
BLW11, KD11	S13
TK7	S14
WD27, WD28	S15
BLE19	S16
WD22	S17
KH26	S18

Fig. 1. Location map of sampling sites in Similipal biosphere reserve.

2.2 Climate

The climate of the reserve is influenced by a monsoon pattern of rainfall. Maximum rainfall occurs from mid June to October accounting for 75-80% of annual rainfall. In spite of high annual rainfall summer and winter are relatively dry generally with <10cm monthly rainfall (Mishra et al., 2006). The amount of average annual rainfall is not correlated with elevation and generally ranges from 28.11 to 344.96 cm. Summer is not unbearable, as the maximum temperature rarely goes above 40 ^{0}C. Winter is severe and the temperature comes down to 4^{0}C in some parts with frosts in valleys (Mishra et al., 2006). Spring is very pleasant. Because of good vegetation and a network of perennial streams Similipal is relatively moist throughout the year. Humidity of Similipal at 0600 hrs is around 40% and at 1800 hrs is around 81% to 93% (Srivastava and Singh, 1997).

2.3 Field methods (vegetation sampling and analysis)

To study the plant diversity status, 18 study sites were selected in East, West, North and South directions inside SBR (Fig.1).The vegetation analysis was conducted during 2005-2008 for all the six layers of the forest i.e. trees, climbers, shrubs, herbs, saplings and seedlings. The species were identified with flora guides (Saxena and Brahmam, 1994-1996; Haines, 1921-25). The tree layer was analyzed by sampling 20 quadrats of 10 m x 10 m size at each site. The size and number of samples were determined using the method of Kershaw (1973) and Mueller-Dombois and Ellenberg (1974). The abundance, density and frequency were calculated for the species. Importance Value Index (IVI) was determined as the sum of the relative frequency, relative density and relative dominance for tree layer only. Raunkiaer's frequency class (1934) analysis was used to assess the rarity or commonness of the tree species (Hewit and Kellman, 2002). In this classification the percentage frequency of the species was classed as A, B, C, D and E; where A represents rare (0–20%), B is low frequency (20–40%), C is intermediate frequency (40–60%), D is moderately high frequency (60–80%) and E is high frequency or common (80–100%). With this classification, the expected distribution of the species is $A>B>C\leq \geq D<E$. The distribution pattern of different species was studied using the ratio of abundance to frequency (Whitford, 1949). Trees were ≥ 30cm cbh (circumference at breast height), saplings were 10-30 cm cbh and seedlings were <10cm cbh (Knight, 1975). The shrub and herb layers were analyzed by randomly placing 20 quadrats of 5m x 5m size and 1m x 1m size, respectively at each site during the post monsoon season. The diversity index at each site was computed by using Shannon- Wiener information function (Shannon-Wiener, 1963) and concentration of dominance by Simpson's index (Simpson, 1949), evenness and richness index following Pielou (1975) and Margalef (1958) (as cited in Tripathi and Singh, 2009), respectively. The presence of climbers on trees affects their growth and development. They have been noted to suppress natural regeneration and delay forest recovery (Babweteera et. al., 2001). The presence or absence of climbers on the trees was scored on a 5-point scale (Alder and Synnott, 1992) whereby 1, 2, 3, 4 and 5 represented trees that were: having bore climbers; trees over grown with climbers; climbers on the stem only; climbers in the crown only and climbers both on the stem and crown, respectively.

3. Results

3.1 Floristic composition and occurrence

A total of 266 species belonging to 204 genera and 76 families were recorded from the study area, out of which 117 were tree species, 17 climber, 31 shrub and 101 herb species. Thus only approximately 24.72% of the estimated flora of Similipal (Saxena and Brahmam, 1989) was covered in the study (Table-3, 4, 5 and 6). A majority of the families were represented by only two or less species. The most common families were Euphorbiaceae and Rubiaceae, each represented by 19 species; followed by Fabaceae (15 species), Mimosaceae = Acanthaceae (12 species each), Asteraceae (11 species), Cyperaceae= Moraceae= Caesalpinaceae = Combretaceae (9 species each), Malvaceae = Melastomataceae = Rutaceae = Poaceae (7 species each), etc. The average number of species per hectare was 74. The number of species per genus was 1.3 and that per family was 3.5. Species in various groups of plant life forms had a wide range of occurrence, ranging in frequency from 5- 72% in herbs, 5-94% in shrubs, and 5- 100% in case of trees, climbers, saplings and seedlings (Table-3, 4, 5, 6, 7 and 8).

Name of the family	Name of the plant species	Density (Plants/ha)	Basal Area (m^2/ha)	Frequency (%)	IVI	A /F
Rubiaceae	*Adina cordifolia* (Roxb.) Hook. f.ex. Brandis	11.94	1.44	77.78	6.54	0.04
Rutaceae	*Aegle marmelos* (L.) Corr.	4.72	0.353	44.44	2.81	0.05
Mimosaceae	*Albizia marginata* (Lam.) Merr.	3.33	0.37	22.22	1.80	0.14
Combretaceae	*Anogeissus latifolia* (Roxb. ex DC.) Wall ex. Guill	45.28	3.36	77.78	13.43	0.15
Bombacaceae	*Bombax ceiba* L.	10.83	1.53	55.56	5.64	0.07
Euphorbiaceae	*Bridelia retusa* (L.) Spreng.	4.72	0.45	38.89	2.73	0.06
Anacardiaceae	*Buchanania lanzan* Spreng.	19.44	0.81	66.67	6.16	0.09
Lecythidaceae	*Careya arborea* Roxb.	6.67	0.36	44.44	3.07	0.07
Flacourtiaceae	*Casearia graveolens* Dalz.	5.28	0.12	55.56	2.98	0.03
Caesalpiniaceae	*Cassia fistula* L.	6.67	0.12	44.44	3.06	0.07
Euphorbiaceae	*Cleistanthus collinus* (Roxb.) Benth. ex Hook.f.	3.33	0.06	11.11	0.94	0.54
Euphorbiaceae	*Croton roxburghii* Balak	6.11	0.21	22.22	1.92	0.25
Mimosaceae	*Dalbergia latifolia* Roxb.	2.78	0.21	22.22	1.41	0.11
Fabaceae	*Desmodium oojeinesis* (Roxb.) Ohashi	5.00	0.58	27.78	2.53	0.13
Dilleniaceae	*Dillenia pentagyna* Roxb.	29.17	2.53	77.78	10.24	0.10
Ebenaceae	*Diospyros embryopteris* Pers.	2.78	0.17	22.22	1.44	0.11
Ebenaceae	*Diospyros melanoxylon* Roxb.	8.61	0.66	44.44	3.73	0.09
Ebenaceae	*Diospyros montana* Roxb.	2.78	0.07	22.22	1.34	0.11
Burseraceae	*Garuga pinata* Roxb.	2.78	0.16	27.78	1.65	0.07
Simaroubaceae	*Gmelina arborea* Roxb.	5.28	0.44	50.00	3.21	0.04
Apocynaceae	*Holarrhena antidysenterica* Wall.ex A.DC.	2.78	0.07	22.22	1.31	0.11
Malvaceae	*Kydia calycina* Roxb.	5.56	0.22	38.89	2.51	0.07
Lythraceae	*Lagerstroemia parviflora* Roxb.	6.39	0.39	33.33	2.65	0.12
Anacardiaceae	*Lannea corromandelica* (Houtt.) Merr.	4.72	0.84	27.78	2.85	0.12

Name of the family	Name of the plant species	Density (Plants/ha)	Basal Area (m^2/ha)	Frequency (%)	IVI	A /F
Sapotaceae	*Madhuca latifolia* Gmel.	12.78	1.074	44.44	4.84	0.13
Anacardiaceae	*Mangifera indica* L.	3.61	1.08	38.89	3.48	0.05
Magnoliaceae	*Michelia champaca* L.	7.78	0.98	11.11	2.78	1.26
Oleaceae	*Nyctanthes arbor- tristis* L.	3.89	0.15	27.78	1.78	0.10
Ochnaceae	*Ochna obtusata* DC.	5.83	0.35	16.67	1.87	0.42
Fabaceae	*Pterocarpus marsupium* Roxb.	12.22	1.24	55.56	5.43	0.08
Euphorbiaceae	*Phyllanthus emblica* L.	4.17	0.2	27.78	1.88	0.11
Burseraceae	*Protium serratum* (Wall. ex Colebr.) Engl.	32.22	1.99	83.33	10.08	0.09
Mimosaceae	*Samanea saman* (Jacq.) Merr.	2.78	0.13	3.13	1.40	0.80
Sapindaceae	*Schleichera oleosa* (Lour.) Oken	13.33	1.48	33.33	5.05	0.24
Euphorbiaceae	*Securinega virosa* (Roxb. ex Willd.) Baill	11.11	1.02	33.33	4.13	0.20
Diptero carpaceae	*Shorea robusta* Gaertn.f.	284.17	27.73	100.00	77.67	0.57
Myrtaceae	*Syzygium cumini* (L.) Skeels	23.06	2.03	83.33	10.19	0.07
Myrtaceae	*Syzygium cerasoides* (Roxb.)Chatt. & Kanjlal	18.06	1.27	66.67	6.64	0.08
Combretaceae	*Terminalia alata* Heyne ex Roth.	50.28	4.37	94.44	16.13	0.11
Combretaceae	*Terminalia bellirica* (Gaertn.) Roxb.	6.67	0.44	44.44	3.49	0.07
Combretaceae	*Terminalia chebula* Retz.	5.56	0.78	61.11	4.29	0.03
Verbenaceae	*Vitex leucoxylon* (L.f.)	5.56	0.21	38.89	2.50	0.07
Rubiaceae	*Wendlandia tinctoria* (Roxb.) DC.	3.61	0.21	27.78	1.82	0.09
Mimosaceae	*Xylia xylocarpa* (Roxb.) Taub.	2.78	0.2	16.67	1.27	0.20
Rhamnaceae	*Ziziphus mauritiana* Lam.	0.28	0.04	5.56	0.31	0.18
Rhamnaceae	*Ziziphus rugosa* Lam.	2.78	0.05	27.78	1.48	0.07
Total		793.67	71.043	-	299.75	-

Table 3. Families, species, density, basal area, frequency, distribution pattern and Importance Value Index (IVI) of trees in Similipal biosphere reserve.

Name of the family	Name of the plant species	Density (Individuals/ha)	Frequency %	Abundance	A/F
Euphorbiaceae	*Antidesma ghaesembila* Gaertn.	97.78	94.44	5.18	0.05
Myrsinaceae	*Ardisia solanacea* Roxb.	45.56	55.56	4.10	0.07
Violaceae	*Bixa orellana* L.	17.78	22.22	4.00	0.18
Rubiaceae	*Catunaregam spinosa* (Thunb.) Tirveng.	12.22	16.67	3.67	0.22
Meliaceae	*Cipadessa baccifera* (Roxb.) Miq.	3.33	5.56	3.00	0.54
Rutaceae	*Citrus medica* L.	48.89	44.44	5.50	0.12
Rutaceae	*Clausena excavata* Burm. f.	3.33	5.56	3.00	0.54
Verbenaceae	*Clerodendrum serratum* (L.) Moon	32.22	22.22	7.25	0.33
Euphorbiaceae	*Croton caudatus* Geisel.	20.00	27.78	3.60	0.13
Rubiaceae	*Gardenia resinifera* Roth	17.78	27.78	3.20	0.12
Euphorbiaceae	*Glochidion* sp.	15.56	22.22	3.50	0.16
Lamiaceae	*Gomphostemma parviflorum* Wall. ex Benth.	21.11	27.78	3.80	0.14
Tiliaceae	*Grewia hirsuta* Vahl.	22.22	27.78	4.00	0.14
Sterculiaceae	*Helicteres isora* L.	17.78	22.22	4.00	0.18
Euphorbiaceae	*Homonoia riparia* Lour.	22.22	44.44	2.50	0.06
Hypericaceae	*Hypericum gaitii* Haines	54.44	22.22	12.25	0.55
Rubiaceae	*Hyptianthera sticta* (Wild.) Wight & Arn.	144.44	66.67	10.83	0.16
Fabaceae	*Indigofera cassioides* Rottel ex DC.	125.56	50.00	12.56	0.25
Oleaceae	*Jasminum arborescens* Roxb.	10.00	27.78	1.80	0.06
Verbenaceae	*Lantana camara* L.	287.78	61.11	23.55	0.39
Vitaceae	*Leea asiatica* (L.) Ridsdale	15.56	22.22	3.50	0.16
Vitaceae	*Leea indica* (Burm. f.) Merr.	34.44	16.67	10.33	0.62
Melastomataceae	*Melastoma malabathricum* L.	122.22	50.00	12.22	0.24
Rubiaceae	*Pavetta tomentosa* Roxb. Ex Sm.	22.22	27.78	4.00	0.14
Lamiaceae	*Pogostemon benghalensis* (Burm. f.) Kuntze	341.11	55.56	30.70	0.55
Fabaceae	*Sesbania bispinosa* (Jacq.) W. F. Wight	18.89	22.22	4.25	0.19
Malvaceae	*Urena lobata* L.	46.67	38.89	6.00	0.15
Asteraceae	*Vernonia anthelmintica* (L.) Willd.	30.00	27.78	5.40	0.19
Lythraceae	*Woodfordia fruticosa* (L.) Kurz	188.89	77.78	12.14	0.16
Rubiaceae	*Gardenia gummifera* L. f.	31.11	22.22	7.00	0.32
Fabaceae	*Flemingia chappar* Buch. – Ham. ex Benth.	73.33	50.00	7.33	0.15
Total		1944.44	-	-	-

Table 4. Families, species, density, frequency, abundance and distribution pattern of shrub layer in Similipal biosphere reserve.

Name of the family	Name of the plant species	Density (Individuals/ha)	Frequency %	Abundance	A/F
Malvaceae	*Abutilon indicum* (L.) Sweet	1944.44	16.67	23.33	1.40
Asteraceae	*Ageratum conyzoides* L.	1527.78	38.89	7.86	0.20
Acanthaceae	*Andrographis paniculata* (Bum.f.) Wall.ex. Nees	833.33	11.11	15.00	1.35
Commelinaceae	*Aneilema ovalifolium* (Wight) Hook.f.ex.	1472.22	11.11	26.50	2.39
Scrophulariaceae	*Bacopa monieri* (L.) Pennell.	2000.00	5.56	72.00	12.96
Capparaceae	*Cleome viscosa* L.	1277.78	11.11	23.00	2.07
Commelinaceae	*Commelina benghalensis* L.	1083.33	11.11	19.50	1.76
Commelinaceae	*Commelina palludosa* Bl.	583.33	5.56	21.00	3.78
Commelinaceae	*Commelina* sp.	611.11	11.11	11.00	0.99
Zingiberaceae	*Costus speciosus* (Koeing) Sm.	1555.56	5.56	56.00	10.08
Hypoxidaceae	*Curculigo orchoides* Gaertn.	6638.89	72.22	18.38	0.25
Zingiberaceae	*Curcuma amada* Roxb.	14138.89	55.56	50.90	0.92
Zingiberaceae	*Curcuma aromaticum* Salisb.	2111.11	27.78	15.20	0.55
Cyperaceae	*Cyperus rotundus* L.	7611.11	11.11	137.00	12.33
Cyperaceae	*Cyperus sp.*	1527.78	11.11	27.50	2.48
Fabaceae	*Desmodium trifolium* (L.) DC.	35888.89	27.78	258.40	9.30
Acanthaceae	*Dicliptera bleupleuroides* Mees.	861.11	11.11	15.50	1.40
Poaceae	*Eragrostis cilliata* (Roxb.) Nees	1805.56	44.44	8.13	0.18
Acanthaceae	*Eranthemum purpurascens* Nees	916.67	22.22	8.25	0.37
Convolvulaceae	*Evolvulus alsinoides* L.	21333.33	27.78	153.60	5.53
Convolvulaceae	*Evolvulus numularis* (L.) L.	14694.44	11.11	264.50	23.81
Cyperaceae	*Fimbristylis aestivalis* (Retz.) Vahl.	3138.89	11.11	56.50	5.09
Rubiaceae	*Knoxia sumatrensis* (Retz.) DC.	3861.11	11.11	69.50	6.26
Lobeliaceae	*Lobelia alsinoides* Lam.	888.89	11.11	16.00	1.44
Cyperaceae	*Mariscos* sp.	1500.00	11.11	27.00	2.43
Sterculiaceae	*Melotia curcurifolia* L.	777.78	5.56	28.00	5.04
Mimosaceae	*Mimosa pudica* L.	611.11	5.56	22.00	3.96
Orobanchaceae	*Orthosiphon rubicundus* (D.Don) Benn.	805.56	11.11	14.50	1.31
Urticaceae	*Pozoulzia pentandra* (Roxb.) Benn.	1111.11	16.67	13.33	0.80
Amaryllidaceae	*Pancratium trifolium* Roxb.	1722.22	22.22	15.50	0.70
Acanthaceae	*Phlogacanthus* sp.	611.11	5.56	22.00	3.96
Arecaceae	*Phoenix acaulis* Buch-Ham.ex Roxb.	888.89	22.22	8.00	0.36
Arecaceae	*Phoenix* sp.	666.67	11.11	12.00	1.08
Euphorbiaceae	*Phyllanthus fraternus*	3416.67	38.89	17.57	0.45
Acanthaceae	*Rungia pectinata* (L.) Nees ex DC.	1750.00	27.78	12.60	0.45
Amaranthaceae	*Celosia argentia* (L.)	583.33	5.56	21.00	3.78
Fabaceae	*Shuteria involucrata* (Wall.) Wt. & Arn.	583.33	27.78	4.20	0.15
Malvaceae	*Sida cordifolia* L.	1111.11	11.11	20.00	1.80

Name of the family	Name of the plant species	Density (Individuals/ha)	Frequency %	Abundance	A/F
Rubiaceae	*Spermococe pusilla* Wall.	1527.78	5.56	55.00	9.90
Acanthaceae	*Strobilanthus auriculatus* Nees	888.89	22.22	8.00	0.36
Fabaceae	*Uraria picta* (Jacq.) Desv. Ex DC.	1138.89	16.67	13.67	0.82
Fabaceae	*Zonia dicola*	1166.67	11.11	21.00	1.89
Rubiaceae	*Hediotys verticillata* (L.) Lam.	861.11	27.78	6.20	0.22
Orchidaceae	*Eulophia nuda* Lindi.	1027.78	33.33	6.17	0.19
Acanthaceae	*Barleria srigosa* (Wild.)	611.11	38.89	3.14	0.08
Cyperaceae	*Cyperus triceps* Endl.	861.11	27.78	6.20	0.22
Others	Others	14083.3	5.56 – 27.78	2 - 18	0.06 – 3.24
Total		1,69,500	-	-	-

Table 5. Families, species, density, frequency, abundance and distribution pattern of herb layer in Similipal biosphere reserve.

Name of the family	Name of the plant species	Density (Individuals/ha)	Frequency %	Abundance	A/F
Liliaceae	*Asparagus racemosus* Willd	9.44	38.89	4.86	0.12
Caesalpinaceae	*Bauhinia vahlii* wight. &Arn	13.33	100.00	2.67	0.03
Fabaceae	*Butea superba* Roxb	3.33	33.33	2.00	0.06
Combretaceae	*Calycopteris floribunda* Lam	3.61	38.89	1.86	0.05
Combretaceae	*Combretum roxburghii* Spreng	5.28	55.56	1.90	0.03
Dioscoreaceae	*Dioscorea bulbifera* L.	8.06	38.89	4.14	0.11
Mimosaceae	*Entada rheedii* Spreng	1.39	16.67	1.67	0.10
Asclepiadaceae	*Hemidesmus indicus* (L.) R.Br.	6.39	44.44	2.88	0.06
Fabaceae	*Millettia extensa* (Benth.) Baker	8.33	27.78	6.00	0.22
Asclepiadaceae	*Pergularia daemia* (Forssk.) Chiov.	13.06	44.44	5.88	0.13
Liliaceae	*Smilax macrophylla* Roxb	8.89	38.89	4.57	0.12
Liliaceae	*Smilax prolifera* Wall ex Roxb.	0.56	5.56	2.00	0.36
Apocynaceae	*Aganosma caryophyllata* (Roxb.ex sims)G.Don	1.94	16.67	2.33	0.14
Euphorbiaceae	*Bridelia stipularis* Bl.	0.83	5.56	3.00	0.54
Lygodiaceae	*Lygodium flexicosum* (L.) Sw	1.39	11.11	2.50	0.23
Araceae	*Pothos scandens* L.	1.94	16.67	2.33	0.14
Oleaceae	*Jasminum flexile* Vahl	0.83	11.11	1.50	0.14
Total		88.6	-	-	-

Table 6. Families, species, density, frequency, abundance and distribution pattern of climber layer in Similipal biosphere reserve.

Name of the family	Name of the plant species	Density (Individuals/ha)	Frequency %	Abundance	A/F
Rubiaceae	*Adina cordifolia* (Roxb.) Hook. f.ex. Brandis	18.89	44.44	2.13	0.05
Rutaceae	*Aegle marmelos* (L.) Corr.	6.67	11.11	3.00	0.27
Mimosaceae	*Albizia marginata* (Lam.) Merr.	12.22	11.11	5.50	0.50
Combretaceae	*Anogeissus latifolia* (Roxb. ex DC.) Wall ex. Guill	85.56	88.89	4.81	0.05
Barringtoniaceae	*Baringtonia acutangula* (L.) Gaertn.	11.11	16.67	3.33	0.20
Caesalpinaceae	*Bauhinia variegata* L.	8.89	16.67	2.67	0.16
Bombacaceae	*Bombax ceiba* L.	6.67	16.67	2.00	0.12
Anacardiaceae	*Buchanania lanzan* Spreng	58.89	55.56	5.30	0.10
Lecythidaceae	*Careya arborea* Roxb.	20.00	44.44	2.25	0.05
Flacourtiaceae	*Casearia graveolens* Dalz.	64.44	83.33	3.87	0.05
Caesalpinaceae	*Cassia fistula* L.	27.78	50.00	2.78	0.06
Cochlospermaceae	*Chochlospermum gossypium* DC.	7.78	5.56	7.00	1.26
Meliaceae	*Cipadessa baccifera* (Roxb.) Miq.	12.22	22.22	2.75	0.12
Euphorbiaceae	*Cleistanthus collinus* (Roxb.) Benth.-ex Hook. f.	18.89	16.67	5.67	0.34
Euphorbiaceae	*Croton roxburghii* Balak	14.44	27.78	2.60	0.09
Fabaceae	*Desmodium oojeinesis* (Roxb.) Ohashi	5.56	11.11	2.50	0.23
Dilleniaceae	*Dillenia pentagyna* Roxb.	50.00	61.11	4.09	0.07
Ebenaceae	*Diospyros malabarica* (Desr.) Kostel.	8.89	11.11	4.00	0.36
Ebenaceae	*Diospyros melanoxylon* Roxb.	21.11	33.33	3.17	0.10
Euphorbiaceae	*Glochidion lanceolarium* (Roxb.) Dalz.Glochidion	8.89	11.11	4.00	0.36
Simaroubaceae	*Gmelina arborea* Roxb.	8.89	22.22	2.00	0.09
Sterculiaceae	*Helicteres isora* L.	10.00	22.22	2.25	0.10
Apocynaceae	*Holarrhena antidysentrica* Wall.ex A.DC.	7.78	16.67	2.33	0.14
Flacourtiaceae	*Homalium nepalens* Benth.	40.00	61.11	3.27	0.05
Malvaceae	*Kydia calycina* Roxb.	6.67	11.11	3.00	0.27
Anacardiaceae	*Nothopegia heyneana* (Hook. f.)	5.56	5.56	5.00	0.90
Lythraceae	*Lagerstroemia parviflora*	17.78	27.78	3.20	0.12

Name of the family	Name of the plant species	Density (Individuals/ha)	Frequency %	Abundance	A/F
	Roxb.				
Sapotaceae	*Madhuca latifolia* Gmel.	13.33	27.78	2.40	0.09
Annonaceae	*Miliusa velutina* (Dunal) Hook.f . & Thomas.	7.78	16.67	2.33	0.14
Rubiaceae	*Mitragyna parviflora* (Roxb.) Korth.	5.56	11.11	2.50	0.23
Oleaceae	*Nyctanthes arber-tristis* L.	36.67	72.22	2.54	0.04
Euphorbiaceae	*Phyllanthus emblica* L.	33.33	61.11	2.73	0.04
Burseraceae	*Protium serratum* (Wall. ex Colebr.) Engl.	35.56	55.56	3.20	0.06
Sapindaceae	*Schleichera oleosa* (Lour.) Oken	45.56	66.67	3.42	0.05
Euphorbiaceae	*Securinega virosa* (Roxb. ex Willd.) Baill	38.89	50.00	3.89	0.08
Dipterocarpaceae	*Shorea robusta* Gaertn.f.	365.56	100.00	18.28	0.18
Sterculiaceae	*Sterculia urens* Roxb.	17.78	16.67	5.33	0.32
Bignoniaceae	*Sterospermum suaveolens* (Roxb.)DC.	13.33	16.67	4.00	0.24
Myrtaceae	*Syzygium cerasoides* (Roxb.)Chatt. & Kanjlal	18.89	33.33	2.83	0.09
Myrtaceae	*Syzgium cumini* (L.) Skeels	30.00	55.56	2.70	0.05
Combretaceae	*Terminalia alta* Heyne ex Roth.	74.44	88.89	4.19	0.05
Combretaceae	*Terminalia bellirica* (Gaertn.) Roxb.	18.89	27.78	3.40	0.12
Combretaceae	*Terminalia chebula* Retz.	11.11	33.33	1.67	0.05
Rubiaceae	*Wendlandia tinctoria* (Roxb.) DC.	20.00	33.33	3.00	0.09
Mimosaceae	*Xylia xylocarpa* (Roxb.) Taub.	15.56	27.78	2.80	0.10
Rhamnaceae	*Ziziphus rugosa* Lam.	7.78	22.22	1.75	0.08
Others		148.74	5.56-16.67	1.00-4.00	0.08-0.72
Total		1524.34	-	-	-

Table 7. Families, species, density, frequency, abundance and distribution pattern of sapling layer in Similipal biosphere reserve.

Name of the family	Name of the plant species	Density (Individuals/ha)	Frequency %	Abundance	A/F
Dipterocarpaceae	*Shorea robusta* Gaertn.f.	27777.78	55.56	100.00	0.56
Euphorbiaceae	*Croton roxburghii* Balak	24250.00	145.50	33.33	4.37
Combretaceae	*Terminalia alata* Heyne ex Roth.	3416.67	9.46	72.22	0.13
Anacardiaceae	*Buchanania lanzan* Spreng.	4944.44	14.83	66.67	0.22
Ebenaceae	*Diospyros melanoxylon* Roxb.	5888.89	26.50	44.44	0.60
Euphorbiaceae	*Cleistanthus collinus* (Roxb.) Benth. Ex Hook.f.	4611.11	23.71	38.89	0.61
Sterculiaceae	*Sterculia urens* Roxb.	1861.11	22.33	16.67	1.34
Flacourtiaceae	*Homalium nepalens* Benth.	1611.11	8.29	38.89	0.21
Euphorbiaceae	*Phyllanthus emblica* L.	2138.89	12.83	33.33	0.39
Combretaceae	*Anogeissus latifolia* (Roxb. Ex DC.) Wall ex. Guill	1500.00	13.50	22.22	0.61
Rutaceae	*Aegle marmelos* (L.) Corr.	972.22	7.00	27.78	0.25
Mimosaceae	*Dalbergia sisoo* Roxb.	500.00	18.00	5.56	3.24
Sapindaceae	*Schleichera oleosa* (Lour.) Oken	805.56	4.14	38.89	0.11
Simaroubaceae	*Ailanthus* sp. Roxb.	805.56	29.00	5.56	5.22
Apocynaceae	*Hollarhaena antidysentrica* Wall.ex A.DC.	1361.11	7.00	38.89	0.18
Oleaceae	*Nyctanthes arbortristis* L.	1527.78	18.33	16.67	1.10
Rhamnaceae	*Ziziphus rugosa* Lam.	916.67	5.50	33.33	0.17
Euphorbiaceae	*Bridelia retusa* (L.) Spreng.	1277.78	11.50	22.22	0.52
Rubiaceae	*Ixora* sp.	722.22	26.00	5.56	4.68
Rubiaceae	*Gardenia gummifera* .L.f.	361.11	4.33	16.67	0.26
Fabaceae	*Pterocarpus marsupium* Roxb.	916.67	5.50	33.33	0.17
Fabaceae	*Desmodium oojeinensis* (Roxb.) Ohashi	1194.44	10.75	22.22	0.48
Myrtaceae	*Syzygium cumini* (L.) Skeels	2472.22	7.42	66.67	0.11
Rubiaceae	*Wendlandia* sp.	2000.00	72.00	5.56	12.96
Sterculiaceae	*Helicteres isora*. L.	972.22	8.75	22.22	0.39
Mimosaceae	*Albizia odoratissima.*	1222.22	22.00	11.11	1.98

Name of the family	Name of the plant species	Density (Individuals/ha)	Frequency %	Abundance	A/F
	(L.f.) Benth.				
Bignoniaceae	*Sterospermum suaveolens* (Roxb.) DC.	638.89	7.67	16.67	0.46
Combretaceae	*Terminalia chebula* Retz.	861.11	5.17	33.33	0.16
Meliaceae	*Trichilia connaroides* (Wight & Arn.) Bentv.	638.89	23.00	5.56	4.14
Euphorbiaceae	*Securinega virosa* (Roxb. Ex Wild.) Baill	500.00	6.00	16.67	0.36
Flacourtiaceae	*Casearia graveolens* Dalz.	1750.00	6.30	55.56	0.11
Dilleniaceae	*Dillenia pentagyna* Roxb.	2194.44	11.29	38.89	0.29
Mimosaceae	*Xylia xylocarpa* (Roxb.) DC.	1583.33	19.00	16.67	1.14
Mimosaceae	*Dalbergia latifolia* Roxb.	805.56	29.00	5.56	5.22
Burseraceae	*Protium serratum* (Wall.ex Colebr.) Engl.	694.44	3.57	38.89	0.09
Mimosaceae	*Albizia marginata* (Lam.) Merr.	861.11	15.50	11.11	1.40
Rubiaceae	*Adina cordifolia* (Roxb.) Hook. F.ex. Brandis	361.11	6.50	11.11	0.59
Anacardiaceae	*Mangifera indica* L.	527.78	4.75	22.22	0.21
Sapotaceae	*Madhuca latifolia* Gmel.	583.33	10.50	11.11	0.95
Lecythidaceae	*Careya arborea* Roxb.	527.78	4.75	22.22	0.21
Euphorbiaceae	*Securinega virosa* (Roxb. Ex Wild.) Baill	583.33	21.00	5.56	3.78
Simaroubaceae	*Gmelina arborea* Roxb.	416.67	5.00	16.67	0.30
Mimosaceae	*Albizia procera* (Roxb.) Benth	388.89	14.00	5.56	2.52
Bombacaceae	Bombax ceiba L.	388.89	7.00	11.11	0.63
Euphorbiaceae	*Mallotus phillipensis* (Lam.) Muell.-Arg.	416.67	15.00	5.56	2.70
Lythraceae	*Lagerostroemia parviflora* Roxb.	333.33	12.00	5.56	2.16
Rubiaceae	*Wendlandia tinctoria* (Roxb.) DC.	416.67	15.00	5.56	2.70
Meliaceae	*Cipadessa baccifera*(Roxb.) Miq	333.33	12.00	5.56	2.16
		1444.44	1.00-9.00	5.56-11.11	0.18-1.62
Total		1,13,416.7	-	-	-

Table 8. Families, species, density, frequency, abundance and distribution pattern of seedling layer in Similipal biosphere reserve.

In most of the plant life forms there were a high number of species that occurred only once. The distribution of the species into Raunkiaer's frequency classes showed that most of the species encountered were rare and very few species were in intermediate and high or common frequency class (Table- 9). Except climbers all other groups of plant life forms do not follow the expected A>B>C ≥ ≤ D<E frequency distribution proposed by Raunkiaer (1934) as the number of species in frequency class D is higher than frequency class E.

Frequency Class	Code	Number of species in vegetation layers						
		Tree	Climber	Shrub	Herb	sapling	seedling	Remark
0-20	A	71 (61)	7 (41)	4 (13)	78 (77)	79 (73)	34 (59)	Rare
21-40	B	27(23)	6 (35)	16 (52)	20 (20)	13 (12)	18 (31)	Low
41-60	C	9 (08)	3 (18)	7 (22)	2 (02)	7 (06)	2 (03)	Intermediate frequency
61-80	D	6 (05)	0 (0)	3 (10)	1 (01)	5 (05)	3 (05)	Moderately high frequency
81-100	E	4 (03)	1 (06)	1 (03)	0 (0)	4 (04)	1 (02)	High frequency (common)

Table 9. Distribution of vegetation layers according to Raunkiaer's classification scheme (Values in parentheses indicate % of species).

3.2 Ecological importance of species

Importance value Index (IVI) is the measurement of ecological amplitude of species (Ludwig and Reynolds, 1988) suggesting the ability of a species to establish over an array of habitats. However, there is no single perfect way of assessing the ecological amplitude of a species. The abundance of a species can be represented by several measures such as relative density, relative frequency and Importance Value Index (IVI). Though frequency and density values are suitable for herbs and shrubs (Airi et al., 2000), IVI is an important information for tree species. On the basis of IVI, *Shorea robusta* was found as the dominant species in the SBR having IVI of 77.67 followed by *Terminalia alata* (16.13) and *Anogeissus latifolia* (13.43). *Wendlandia* sp. had IVI of 0.25 and was considered as the rare species of the reserve. All other tree species showed intermediate range of IVI (Table-3).

3.3 Distribution pattern

The distribution pattern of trees, shrubs, climbers, herbs, saplings and seedlings of the reserve is shown in Table-10. Odum (1971) stated that under natural conditions, a clumped distribution of plants is normal. A higher percentage of random and regular distribution reflects the greater magnitude of disturbance` such as grazing and lopping in natural forest stands. Most of the species of all the vegetational layers of the reserve showed generally clumped type of distribution in the present study. Regular distribution pattern is completely lacking in all the vegetation layers. Both in herb and seedling layers not a single species showed random distribution pattern (Table-10).

Plant group	Number of species in distribution pattern categories			
	Regular	Random	Contiguous	Total number of species
Tree	0	08	109	117
Climber	0	03	14	17
Shrub	0	01	30	31
Herb	0	0	101	101
Sapling	0	06	102	108
Seedling	0	0	58	58

Table 10. Distribution pattern of vegetation layers of Similipal biosphere reserve.

3.4 Distribution of climbers

Out of 794 number of trees per hectare 110 number of trees per hectare affected by 40% bore climbers, 10 % were overgrown with climbers while 15% had climbers restricted to the main stem, 12% had climbers in the crown only and 23% had climbers both the stem and in the crown (Figure. 2).

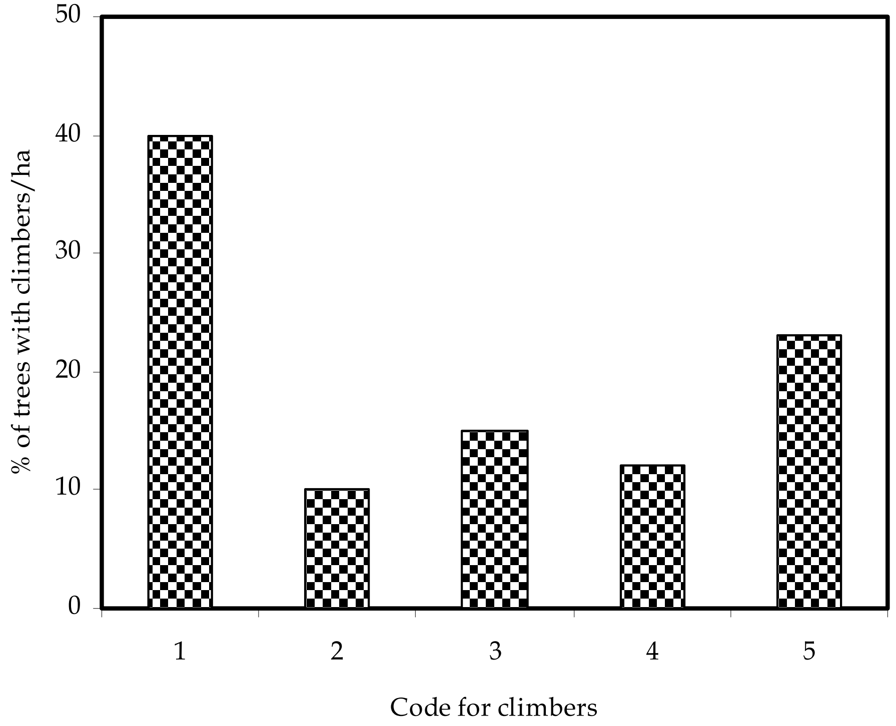


Fig. 2. Percentage distribution of climbers in Similipal biosphere reserve.

3.5 Stand structure

Species wise density of individuals having ≥30cm girth of the reserve ranged from less than one plant per hectare to 284 plants/ha and the total density of the reserve was 794 plants/ha. Maximum density (per hectare of individuals of ≥30cm) was recorded for *Shorea robusta* (284) followed by *Terminalia alata* (50), *Anogeissus latifolia* (45), *Protium serratum* (32) and *Dillenia pentagyna* (29). Density was observed less than or equal to one for many species like *Antidesma acidum, Artocarpus lacuccha, Butea monosperma,, Casearia elliptica, Chionanthus intermedicus, Cochlospermum religiosum, Euonymus glaber*, etc. Some other species showed intermediate range of density per hectare. The densities of climbers in comparison to other vegetation layers of the reserve was too low. However the densities of herbs, seedlings and sapling layers were quite high in comparison to other vegetational layers. Unlike tree layer in herb, shrub and climber layers very few species showed lowest density. *Exacum bicolor* in herb layer, *Cipadesa baccifera* and *Clausena excavata* in shrub layer and, *Jasminum flexile* and *Bridelia stipularis* in climber layers values showed minimum value of density (Table-4, 5, 6, 7 and 8). Total basal area of trees of the reserve was 71.05 m^2/ha in which maximum was experienced by *Shorea robusta*. *Shorea robusta* contributed maximum of 39% to the basal area followed by *Terminalia alata* (6.15%), *Anogeissus latifolia* (4.73%) and *Dillenia pentagyna* (3.57%). The total contribution that resulted from this associated combination of *Shorea-Terminalia-Anogeissus-Dillenia* was 53.45%. A few families contributed most to the total basal area. These included Dipterocarpaceae (39%), Combretaceae (13 %), Myrtaceae (5%), Rubiaceae (4.5 %) and Moraceae (4 %). As a whole the tree density and basal area of 794 plants/ha and 71.05m^2/ha, respectively are well within the reported range of various Indian tropical forests (Visalakshi, 1995; Sapkota et al., 2009).

3.6 Diversity measures

Species diversity, concentration of dominance and some mathematical indices of different vegetational layers of the reserve are given in Table -11. Measurement of biodiversity of specific area (local scale) on the basis of species richness does not provide a complete understanding about the individuals of the species in an ecosystem as it suffers from the

Plant group	Range of diversity indices			
	SD	CD	SR	SE
Tree	1.8 -3.11	0.07 - 0.316	3.36 - 6.59	0.611 - 0.951
Climber	0.63 - 1.86	0.155 - 0.36	0.55 - 2.22	0.8 - 0.931
Shrub	1.76 - 2.37	0.102 - 0.216	1.66 - 2.92	0.76 - 0.96
Herb	1.57 - 2.99	0.053 - 0.323	1.24 - 4.24	0.63 - 0.91
Sapling	2.1 - 3.03	0.061 - 0.194	2.98 - 6.15	0.816 - 0.949
Seedling	1.01 - 2.62	0.129 - 0.397	0.73 - 4.37	0.61 - 0.88

Table 11. Species diversity (SD), Concentration of dominance (CD), species richness (SR) and species evenness (SE) of different forest strata of Similipal biosphere reserve.

lack of evenness or equitability. It was observed that the richness index ranged from 3.36 to 6.59 (tree layer), 0.55 to 2.22 (climber layer), 1.24 to 4.24 (herb layer), 1.66 to 2.92 (shrub layer), 2.98 to 6.15 (sapling layer) and 0.73 to 4.37 (seedling layer). The equitability showed little variation across the vegetational layers which ranged from 0.61 to 0.95 (tree layer), 0.8 to 0.93 (climber layer), 0.63 to 0.91 (herb layer), 0.76 to 0.96 (shrub layer), 0.82 to 0.95 (sapling layer) and 0.61 to 0.88 (seedling layer). Shannon Wiener's index of diversity is one of the popular measures of species diversity. It ranged from 1.80 to 3.11, 0.63 to 1.86, 1.76 to 2.37, 1.57 to 2.99, 1.01 to 2.62 and 2.1 to 3.03 for tree, climber, shrub, herb, seedling and sapling layers, respectively, across all sites. Maximum range of species diversity of 1.8 to 3.11 was experienced by tree layer and the minimum range of 0.63 to 1.86 by climber layer indicating that tree layer of SBR was highly diverse while climber layer was the least (Table-11).

4. Discussion

4.1 Floristic composition

The species richness of a forest ecosystem depends on the number of species per unit area; the more species per unit area, the higher the species richness. A total of 266 species/ 3.6 ha or 74 species/ha in the SBR is more or less similar compared to the number of species reported by several workers in other tropical forest covers of India (Parthasarathy, 1999, 80 to 85 species/ ha in kalakad-MundanthuraiTiger reserve; Parthasarathy and Karthikeyan, 1997, 57 species/ ha in Mylodai- Courtallum reserve forest) and also 70 to 80 species/ha that have been observed in other studies in West African tropical high forests (Lawson, 1985; Vordzogbe et al., 2005). The species richness in neotropical forests showed a wide variation, ranging from 20 species/ha in Varzea forest of Rio Xingu, Brazil (Campbell et al., 1992) to 307 species/ha in the Amazonian Equator (Valenica et al., 1994). In the old world tropics species richness ranged from 26 species/ha in Kolli hills of India (Chittibabu and Parthasarathy, 2000) to 231 species/ha in Brunei Darussalam of South East Asia (Poulsen et al., 1996). In tropical rain forests the range of species count per hectare is about 20 to a maximum of 223. The number of species in SBR was 74 per hectare and this number is at the lower side of the range given in tropical rain forests and neotropical forests. In the study of species richness of the western ghat, south India Sunderpandian and Swamy (2000) stated that pronounced dry season and relatively low annual precipitation factors might be correlated with low species richness.

4.2 Diversity and related measurements

It has become common practice in quantitative descriptive studies to use IVI, which combines the relative frequency, density and dominance into a single measure to analyze a plant community. Though vegetation can be described in terms of a number of parameters including frequency, density and cover, the use of any one of these quantitative parameters could lead to over-simplification or under-estimation of the status of the species (Kigomo et. al., 1990, Oyun et. al., 2009). Except few tree species viz. *Shorea robusta, Terminalia alata* and *Anogeissus latifolia,* low ecological status of most of the tree species in the present investigation, as evidenced by the IVIs, may be attributed to lack of dominance by any one of these species, suggesting positive interactions among the tree species. In other words, resource spaces are shared to minimize negative species interactions and plants can obtain resources with relative ease (Tsingalia, 1990). The low IVIs may also imply that most of the tree species in this forest are rare (Pascal and Pellissier, 1996; Oyun et al., 2009), as confirmed by Raunkiaer's frequency distribution of the tree species (Table- 9). The rarity of species may be attributed to the occurrence of abundant sporadic species with low frequency in the stands (Oyun et al., 2009). The high percentage (>70 %) of rare species observed in various vegetational layers of the reserve confirms the generally acclaimed notion that most of the species in an ecological community are rare, rather than common (Magurran and Henderson, 2003). The range of evenness value and Simpson's diversity index of 0.61-0.96 and 0.053-0.397, respectively in vegetation layers of Similipal implies that most of the species are equitably distributed while very few species showed the degree of dominance (Pascal and Pellissier, 1996). Shannon Wiener species diversity value among vegetational layers of the reserve ranges from 0.63-3.11 indicating that SBR is highly diverse. The species diversity is generally higher for tropical forests, which is reported as 5.06 and 5.40 for young and old stand, respectively (Knight, 1975). For Indian forests the diversity index ranges between 0.83- 4.1 (Visalakshi, 1995). The diversity index of different vegetational layers of SBR is well within the reported range of the forests of Indian sub-continent (Table-11). Higher species diversity index in tropical forests as reported by Knight (1975) in comparison to the present investigation may be due to differences in the area sampled and lack of uniform plot dimensions. On the other hand, the value obtained for the concentration of dominance for vegetation layers of SBR (0.053-0.397) is greater than those recorded in Nelliampathy (0.085; Chandrashekara and Ramakrishnan, 1994) and tropical dry deciduous forests of Western India (0.08- 0.16; Nirmal Kumar et al., 2010). The high dominance value in the present study indicates single species dominance by *Shorea robusta* in tree, sapling and seedling layers of the reserve (Table-3, 7 and 8).

4.3 Distribution pattern of climbers

The distribution of climbers on the trees of the reserve was considerably low, being nearly equal to 14%. This may be due to high canopy coverage, thereby allowing low light to reach the forest floor and not triggering vigorous growth of climbers (Babweteera et al., 2001). The impact of climbers on the vitality of trees is negative (Toledo- Aceves and Swaine, 2008) causing loss of foliage and thereby reducing the surface area available for metabolic processes and reproductive potential as well as impeding or obstructing forest succession (Toledo-Aceves and Swaine, 2008). Notwithstanding their negative impacts, climbers form bridges between the forest canopies, thereby facilitating the movement of arboreal animals across the forest. They also protect weaker trees from strong winds (Schnitzer and Bongers, 2002).

4.4 Stand structure

Stand structure parameters allow predictions of forest biomass and can provide spatial information on potential determinants of plant species distributions (Couteron et al., 2005). In the present study stand structure relates to the basal area of trees, density of trees, and densities of herbs, shrubs, climbers, saplings and seedlings. The tree basal area of 71.05m^2/ha is high and comparable to the reported range of various Indian tropical forests

(Visalakshi, 1995; Sapkota et al., 2009) and slightly higher than the value reported from Monteverde of Costa Rica (62 m^2/ha, Nadkarni et al., 1995). High basal area is a characteristic feature of mature forest stand and serves as a reflection of high performance of the trees. It may also presuppose the development of an extensive root system used efficient nutrient absorption, growth suppressing of subordinate plants as the big trees intercept much of the solar radiation that might otherwise reach the forest floor. Dipterocarpaceae had the highest basal area in the present study, followed by Combretaceae, Myrtaceae, Rubiaceae and Moraceae. These families contain important timber species such as *Shorea robusta*, *Terminalia alata*, *Anogeissus latifolia, Syzygium cumini*, *Syzygium cerasoides*, *Terminalia bellirica*, *Terminalia chebula*, etc. The Barringtoniaceae, Chochlospermaceae, Clusiaceae, Malvaceae, Melastomataceae, Myrsinaceae, Ochnaceae, Rosaceae, Salicaceae, Lauraceae, Rhamnaceae, Sterculiaceae, Symplocaceae, Verbenaceae, Flacourtiaceae, and Rutaceae did not contribute much to the total basal area. In all the stands investigated, Chochlospermaceae, Sapotaceae, Salicaceae, etc. were by one individual each while Barringtoniaceae represented by two individuals and, Clusiaceae and Melastomataceae by three individuals each. This implies that very low contribution of these families to the total basal area may be due to their low numbers. Thus, these families may not be very important in terms of dominance. Species wise density of individuals having ≥30cm girth of the reserve ranged from less than one plant per hectare to 284 plants/ha and the total density of the reserve was 794 plants/ha. Maximum density (per hectare of individuals of ≥30cm) was recorded for *Shorea robusta* (284) followed by *Terminalia alata* (50), *Anogeissus latifolia* (45), *Protium serratum* (32) and *Dillenia pentagyna* (29). Density was observed less than or equal to one for many species like *Antidesma acidum, Artocarpus lacuccha, Butea monosperma,, Casearia elliptica, Chionanthus intermedicus, Cochlospermum religiosum, Euonymus glaber*, etc. Some other species showed intermediate range of density per hectare. The tree density of 794 individuals/ha recorded in the present investigation is lower as compared to densities reported from Saddle Peak of North Andaman Islands and Great Andaman Groups (946-1137 trees/ha, Padalia et al.,2004). However, the tree density of SBR is comparable with other tropical forests e.g. Kalkad Western Ghats (575-855 trees/ha, Parthasarathy, 1999), Brazil (420-777 trees/ha, Campbell et al., 1992), seasonally deciduous forest of Central Brazil (734 trees/ha, Felfili et al., 2007), Semideciduous forest of Piracicaba, Brazil (842 trees/ha, Viana and Tabanez, 1996) and Costa Rica (617 trees/ha, Heaney and Proctor, 1990). There appears to be little literature available to compare the herb, shrub, sapling and seedling densities with at the local level. The reported densities of these vegetation layers of the reserve in the present investigation is well comparable to Mishra et al. (2008). The fewer numbers of saplings recorded in relation to seedlings in this study implies that most of the saplings are transiting into young trees. It could also mean that most of the seedlings probably die due to intense competition (Weidelt, 1988) for available resources before they reach the sapling stage. Nevertheless, the totality of saplings and seedlings is colossal and reflects high regeneration potential of the forest (Mishra et al., 2005; Khumbongmayum et al., 2006).

4.5 Comparative analysis of tree species diversity in various tropical forests

The tree diversity observed in various tropical forests has also been compared with the findings of the present study in SBR (Table-12). The species diversity in SBR can be comparable with other tropical forests. Species richness and density of tree species of the present study (117 species and 794 plants per hectare) is well within the reported range of tropical forests in India and outside India. However, the basal area estimated for tree species in the present investigation is well within the reported range of Indian tropical forests but higher than that of tropical forests found outside India (Table-12). The high basal area of 71 m^2/ha obtained in the present investigation was largely due to the contribution of the dominant tree species of the reserve, maximum by *Shorea robusta* which alone scored 39% (27.73 m^2/ha) of basal area.

Forest and location	No. of species	No. of genera	No. of families	Density (Plants/ha)	Basal area (m2/ha)	Source
Indian tropical forest						
Moist deciduous forest, Similipal	117	87	42	793.67	71.04	Present study
Moist deciduous forest, Andaman	235	153	73	946	28.60	Padalia et al., 2004
Semi evergreen forest, Andaman	231	153	71	1027	33.76	Padalia et al., 2004
Evergreen forest, Andaman	264	176	81	1137	44.28	Padalia et al., 2004
Wet evergreen forest, South western ghat	122	89	41	575-855	61.7-94.64	Parthasarathy, 1999
Tropical forests outside India						
Neotropical cloud forest, Monteverde, Costarica	114	83	47	555	62.0	Nadkarni et al., 1995
Seasonally deciduous forest,Iaciara, Brazil	39	-	-	734	16.73	Felfili et al, 2007
Seasonally deciduous forest, Monte Alegre, Brazil	56	-	-	633	19.36	Nascimento et al., 2004
Semideciduous, Piracicaba, SP, Brazil	101	-	-	842	12.53	Viana and Tabanez, 1996
Evergreen rain forest, Ngovayang (Cameroon)	99-121	-	-	451-634	28.8-42.1	Christelle et al., 2011
Subtropical forest, Bagh district, Kashmir, Pakistan	72	-	31	344	69.31	Saheen et al., 2011
African wet tropical forest	344-494	-	-	371-486	27.8-35.8	Chuyong et al., 2011

Table 12. Tree species diversity in various tropical forests.

5. Conclusion

The overall analysis indicates that species rich communities of the moist deciduous tropical forests are not only being reduced in area but they are also becoming species poor and less diverse due to rapid deforestation and forest fragmentation. The community organization is also changing in response to increased anthropogenic disturbance. The study has shown that SBR is highly rich in plant diversity and is one of the treasure houses of good ecological wealth of Eastern ghat, India. The long history of timber exploitation prior to its conversion into a biosphere reserve has resulted in the alteration of structure of the forest whereby most of the tree species were affected by very few individuals. The ecological importance of most of the tree species was also low, which reflected rarity of most of the species. However, the abundance of small trees coupled with the colossal sum of saplings and seedlings reflects a high regeneration potential of the forest.

The forest management issues of SBR could be addressed by collection and analysis of long term ecological data which requires scientific baseline studies. We have covered extensively structural parameter analysis which is helpful to know the present state of ecological health of the ecosystem. But due to the various forms of anthropogenic pressure the habitat is destroyed with for logging, illegal hunting, and other challenges (mining in periphery, etc.). The conservation efforts have not so far yielded desired result. With continued biotic pressure and consequent change in structure and function of ecosystem, the management methodology also needs to be modified developing a Long Term Research Network. Similipal is a globally recognized ecosystem covered under UNESCO's Biosphere Reserve housing wide range of flora and fauna. We need to carry out Research and education activities to create an institutional platform to academicians, researchers and scientists. This ecosystem is under pressure. Continued destruction of old-growth and pristine forests of Similipal with high biodiversity will have a regional impact on social and ecological sustainability.

The over exploitation of natural resources in tropical world for meting the basic needs of food, fodder and shelter of local population has disturbed the landscapes causing rapid depletion of biodiversity. Our research results may be of some help to develop management schemes for conservation of biodiversity of SBR. Lack of data base and structural and functional characters of the ecosystem at regular intervals will not help to develop a long-term strategy for sustainable development. Thus continuous collection of data as per long-term action plan on successional status of species level up external and local pressures on the ecosystem, soil fertility management and linkage between social and ecological processes is needed. The community participation and use of traditional technologies as tools for natural resource management should be integrated to achieve sustainable resource management and ecological rehabilitation.

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7. References

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6

Vegetation Evolution in the Mountains of Cameroon During the Last 20 000 Years: Pollen Analysis of Lake Bambili Sediments

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1. Introduction

Tropical rainforests are the most biologically diverse ecosystems on the planet (Puig, 2001). In the highlands and mountains of western Cameroon (Central Atlantic Africa), a set of plateaus and mountains that contain large forested areas, this diversity is now subject to significant human pressure due to a large population engaged in agriculture and ranching. Momo Solefack (2009) shows that between 1978 and 2001 deforestation in Oku was 579 ha / year, with a annual rate of 4% increase. In addition to anthropogenic impacts, climate change plays a major role in influencing the distribution and composition of ecosystems (Walther et *al.*, 2002; Thomas et *al.*, 2004; Schröter et *al.*, 2005; Thuiller et *al.*, 2006).

The Bamenda Highlands have a particular forest characterized by the presence of one of the few African gymnosperms, *Podocarpus latifolius*. This species migrated from East to West Africa through Angola and then colonized the high mountains of Cameroon. It is currently restricted to altitudes above 1800 m, in the areas of Mount Oku and Kupé (Letouzey, 1968). Pollen data of Central Atlantic Africa have shown that this *Podocarpus* forest was once significantly more extensive than today during the last climatic cycle, especially during the last ice age (Dupont et *al.*, 2000; Elenga and Vincens, 1990; Maley and Livingstone, 1983). At this time, *Podocarpus* was present at low and mid altitudes mixed with the dense Guineo-Congolian forest. The expansion of *Podocarpus* into these areas did not end until very recently, about 3000 years ago (Vincens et *al.*, 2010). Such a distribution, involving the recent migration of the species to higher altitudes (White, 1993), suggests that such forests are likely refugia. This chapter, based on a sedimentary sequence of 14 m taken at Lake Bambili covering the last 20,000 years, presents the first palynological data from altitude in this region. Preliminary analysis of data from Bambili has been presented by Assi-Kaudjhis et *al.* (2008). The aim of this paper is to study the development and evolution of mountain forest in Cameroon over this interval.

2. Location, climate, and vegetation of bambili

Lake Bambili (05°56'11.9 N, 10°14'31.6 E, 2273 m asl) is a crater lake that lies in the volcanic zone of Cameroon (Figures 2 and 3) in the Bamenda Highlands and Bamboutos Mountains.

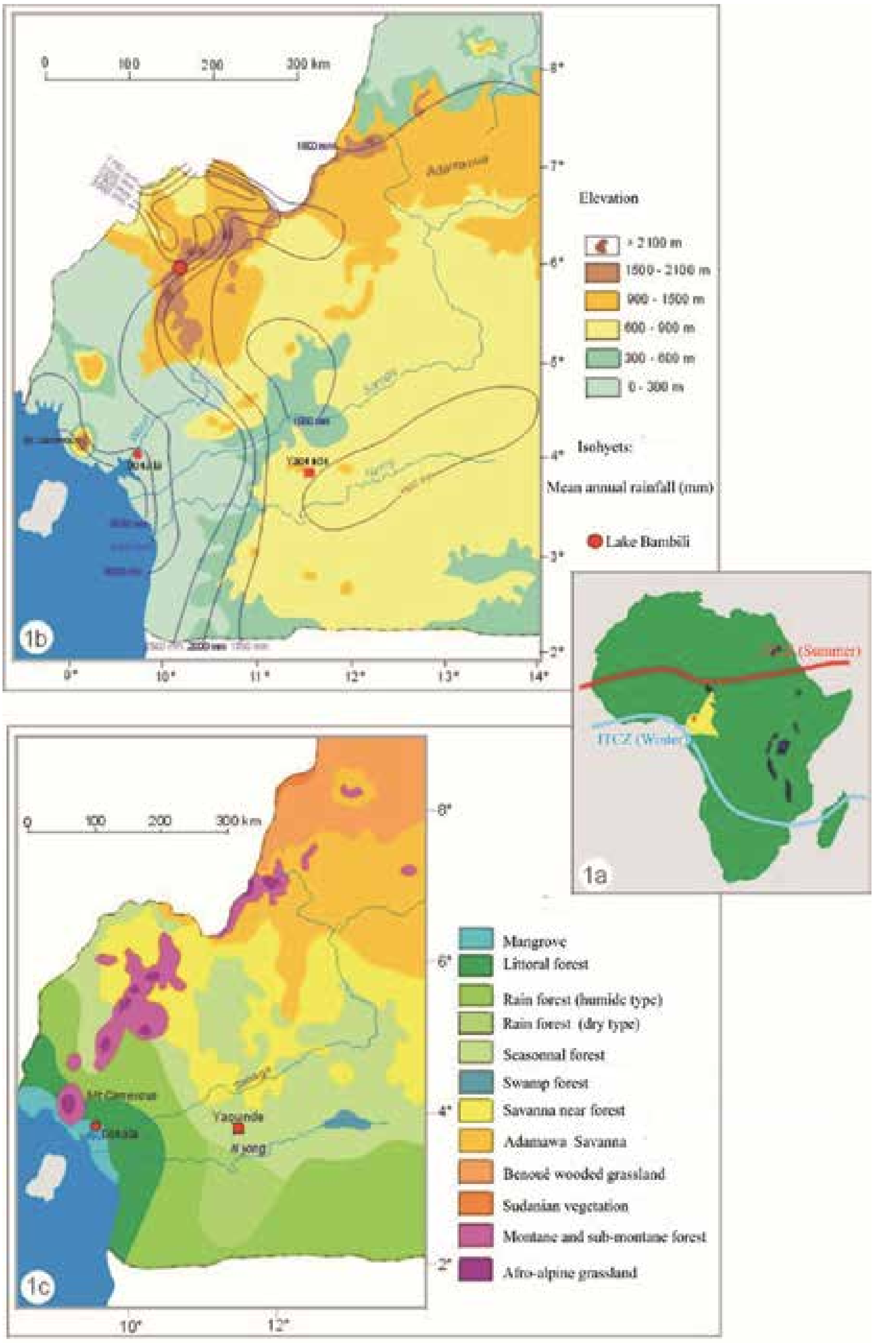

Fig. 1. Presentation of the study site (in Assi-kaudjhis et *al.*, 2008).
1a: Location of Lake Bambili, Cameroon; red line: ITCZ boreal summer; blue line: boreal winter ITCZ.
1b: Topography and rainfall in the study area.
1c: Phytogeography of the study area (Letouzey, 1968).

In northeastern Bambili, Mount Oku rises to 3011 m asl, the second highest peak in the country after Mount Cameroon (4070 m asl). The lake is part of a complex formed by two adjacent craters separated by about 45 m in altitude. The highest crater today is a swamp that discharges water into the crater below. The lower crater contains a lake of about 3 m depth. The lower crater contains a lake of about 3m depth with a single outlet to the northeast. The lake margin is narrow, consisting of a strip of herbaceous sub-aquatic vegetation, such as Cyperaceae and ferns, growing on peat-rich soil.

Fig. 2. The crater lake Bambili (05 ° 56'11.9 N, 10 ° 14'31.6 E, 2273 m asl). The red dot indicates the core location in the lower crater lake and the yellow dot is the second core location in the swamp of the second upper crater.

Centrally located in the Guineo-Congolian region, Cameroon has a relatively humid climate due to the locationof the country to the Gulf of Guinea (Suchel, 1988) which is responsible for the long rainy season over 4 / 5 of the country (western and southern regions) and slightly drier tropical climates in the north of the Adamawa plateaus. The seasonal alternation of southwesterly moisture flux and northerly dry winds, called the Alizé, creates a wet season from March to October and a more variable drier period during the rest of the year. The influence of altitude and distance from the coast result in lower precipitation in Bambili than Douala (2280 mm in Bamenda at 1370 m asl and 2107 mm in Bafoussam at 1411 m asl) and lower average temperatures (19°C to 20°C in Bamenda and Bafoussam against 26°C in Douala). Dry season precipitation from November to February is below 50 mm (Web LocClim, FAO, 2002). During the rainy season, precipitation is as high as 400 mm per month with temperatures fluctuating between 18.1 and 21.2°C.

Cameroon vegetation (Figures 3a and 3b) was described by Letouzey (1968, 1985) and White (1983). It is divided by latitude and altitude. At Bambili, aquatic vegetation grows in bands at the lake margin in the area of permanent open water: after *Nymphaea* sp. (Nymphaeaceae) on the edge of open water is a belt of Cyperaceae, ferns and aquatic plants, then, on the dry ground appear species of Poaceae.

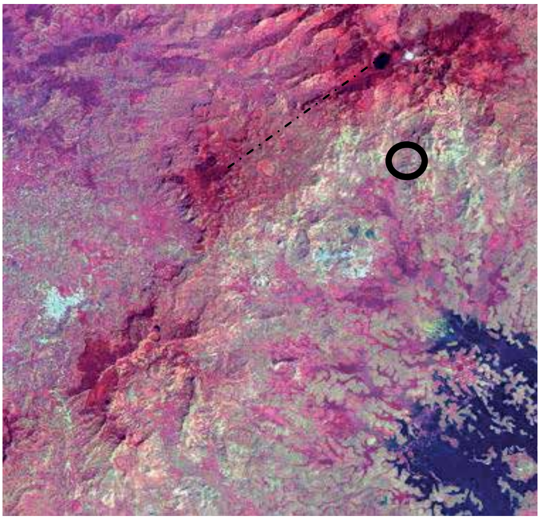

Fig. 3a. Satellite Photo of crater lake Bambili (05°56'11 .9 N, 10°14'31 .6 E, 2273m asl).The dashed line connecting Bambili to Lake Oku is 36.5 km. Dark Red = forest; Light red = mosaic of fallow and degraded forest; Dark Blue = marshland; Black = open water; White = bare soil.

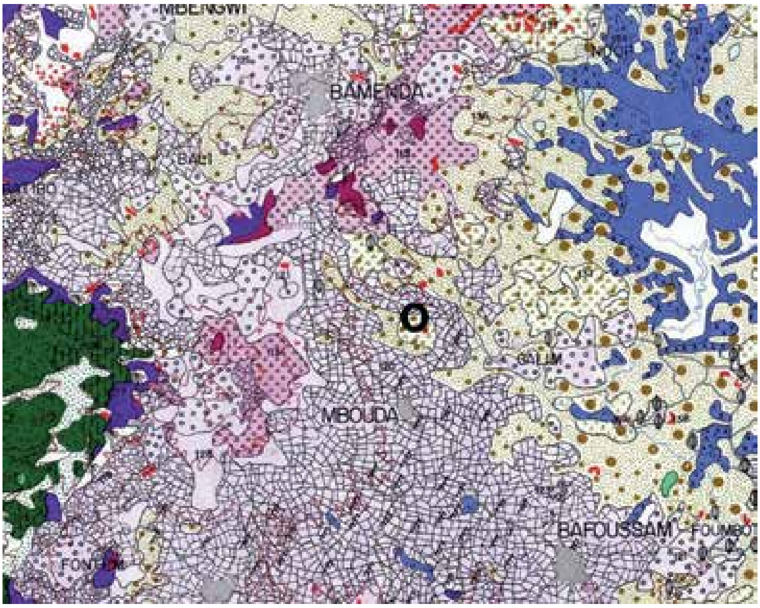

Fig. 3b. Vegetation map of the Bambili region (Letouzey, 1985) Green = moist forests; Light pink = fallow; Red = montane forest; Violet = submontane forest; Blue = marshland; Yellow = edge of the montane forest; Light yellow = savanna. Black circle indicates the location of Lake Bambili.

In general, the distribution of the plant communities of Cameroon at altitude is as follows:

Above 2400 m asl: afro-alpine
Alchemilla fisheri subsp. *camerunensis* (Rosaceae) *Agrostis mannii* (Poaceae) *Veronica mannii* (Asteraceae)...
From 2400 to 1600 m asl: montane forest
Podocarpus latifolius (Podocarpaceae)
Rapanea melanophloeos (Myrsinaceae)
Olea capensis (Oleaceae), Hypericum sp. (Ulmaceae)
Nuxia congestata (Loganiaceae)
Embelia sp. (Myrsinaceae), Celtis (Ulmaceae)
Clematis simensis (Ranunculaceae)
Hypericum sp. (Hypericaceae)
Syzygium staudtii (Myrtaceae)
Gnidia glauca (Thymelaeaceae)
Schefflera abyssinica, S. mannii (Araliaceae)
Arundinaria alpina (Poaceae)
From 1600 to 800 m asl: sub-montane forest (boundary between Guineo-Congolian and Afro-montane regions)
Olea hochstetteri (Oleaceae) *Schefflera abyssinica* (Araliaceae) *Microglossia densiflora* (Asteraceae) *Maytenus undata* (Celastraceae) *Hypericum revolutum* (Hypericaceae) *Prunus africana* (Rosaceae) *Alchemilla fischeri* (Rosaceae)...
Combined with elements of semi-deciduous rain forest
Polyscias fulva (Araliaceae) *Santiria trimera* (Burseraceae) *Bridelia speciosa* (Euphorbiaceae) *Uapaca* sp. (Euphorbiaceae) *Leonardoxa africana* (Caesalpiniaceae) *Celtis africana* (Ulmanceae) *Anthocleista* (Loganiaceae)...
Savannas and herbaceous layer
Annona senegalensis (Annonaceae)
Bridelia ferruginea (Euphorbiaceae)
Cussonia djalonensis (Araliaceae)
Terminalia avicennioides (Combretaceae)
Vernonia turbinata (Compositae)
Hymenocardia acida (Euphorbiaceae)

The organization of vegetation, based on Letouzey's studies (1968). But now, it is a theory, as environmental conditions have deteriorated (Table I). Thus, analysis of satellite images of

1998 and 2003 show that the forest cover around Bambili has deteriorated sharply in recent decades (Assi-Kaudjhis, 2011).

	1988	%	2003	%
Savanna, grassland and crops	3676.17	13.3	11615.65	42.03
Residential areas and bare soil	2196.79	7.95	4 766.18	17.25
Forest	3660.14	13.23	2472.65	8.95
Degraded forest	18086.1	65.40	8754.07	31.66
Lakes	31.81	0.12	29.31	0.11

Table I. Area (ha) of different units of land between 1988 and 2003.

3. Materials and methods

Two cores of 13.5 m and 14.01 m were taken a few meters apart at Lake Bambili in February 2007 and January 2010, respectively (Figure 4). The cores were taken using a Russian manual corer (Jowsey, 1966) in sections of 60 cm in length. The two sedimentary sequences were combined into a single sequence on the basis of benchmark levels identified in each, the depth (mcd) was calculated. The cores were sampled every 5 to 10 cm for pollen analysis.

Fig. 4. Coring on Lake Bambili using the Russian manual corer.

Overall, the sediments are composed of organic material and clay. From 0 to 635 cm, organic rich brown peat dominates becoming more compact and darker towards the base. Between 635 and 657 cm, sediments are mostly organic rich with centimeter-sized nodules of gray-green clay. Finally, 657 cm to the base of the sequence is an organic-rich compact black clay. A charcoal layer is observed at 1355 cm.

Laboratory number	Depth (cm) of the sample	Nature of the sample	Radiocarbon age BP			cal age-	cal age+	Average age (years cal BP)
SacA 8485	199-200	peats	1125	±	30	980	1037	1008.5
SacA 8486	299-300	peats	1745	±	30	1615	1704	1659.5
SacA 8487	399-400	peats	2170	±	30	2124	2301	2212.5
SacA 8488	499-500	peats	2315	±	30	2329	2352	2340.5
SacA 8489	599-600	peats	2485	±	30	2491	2707	2599
SacA 8490	699-700	peats	3175	±	30	3370	3442	3406
SacA 8491	799-800	peats	5515	±	30	6284	6318	6301
SacA 8492	899-900	peats	7255	±	35	8014	8156	8085
SacA 8493	999-1000	peats	8160	±	45	9015	9135	9075
SacA 8494	1099-1100	peats	10050	±	45	11404	11705	11554.5
SacA 8495	1198-1199	peats	11560	±	50	13323	13439	13381
SacA 10870	1248-1249	peats	12550	±	50	14605	14946	14775.5
SacA 10872	1348-1349	peats	14330	±	60	16950	17387	17168.5
Laboratory number	**Depth (cm) of the sample**	**Nature of the sample**	**Radiocarbon age BP**			**cal age-**	**cal age+**	**Average age (years cal BP)**
BB01-2010	1325	peats	14150	±	60	17032	17405	17218.5
BB01-2010	1355	charcoal	15020	±	60	18062	18505	18283.5
BB01-2010	1377	peats	15840	±	70	18840	19258	19049
BB01-2010	1410	peats	16910	±	70	19962	20256	20109

Table II. Radiocarbon dates and age model of the two cores taken in 2007 and 2010 at Bambili.

Seventeen AMS dates were performed, which show a continuous deposition for the last 20,000 years with a sedimentation rate ranging from 0.208 cm per year between 0 and 650 cm and 0.05 cm per year from 650 cm to the base (Table II). Radiocarbon measurements were calibrated using the CALIB software version 5.0. (Stuiver et *al.*, 2005). The samples for pollen analysis were chemically treated with hydrochloric acid (HCl) and hydrofluoric acid (HF) according to the conventional method described by Faegri and Iverson (1975) preceded by a sieving at 250 microns to remove coarse particles. Treatment was terminated by filtration at 5 microns.

A total of 141 samples were analyzed with an average time resolution of 146 years. Counts ranged from 303 to 1500 pollen grains according to the richness of each sample, and 203 pollen taxa were identified. Data are presented as a diagram drawn on the basis of percentages calculated on a sum excluding aquatic plants and ferns.

The CONISS program used in the Tilia program (Grimm, 1987) was employed for the subdivision of the pollen diagram in zones. Analysis of palynological richness (Birks and Line, 1992), in order to estimate biodiversity, was performed with the software PSIMPOLL (http://www.chrono.qub.ac.uk/psimpoll/psimpoll.html).

4. Results

The microflora (Table III) consists of 119 taxa of trees, lianas and palms, together with 36 herbaceous taxa and 32 undifferentiated taxa, which correspond to plants that may be trees or herbs. Finally, 10 taxa correspond to aquatics plants, 4 to ferns and one to a plant parasite.

Family	Taxon	Habit	AA	FM	FSM	FSD	FDH	SAV	STP
LOGANIACEAE	Nuxia-type	A	X	X	X				
POLYGALACEAE	Polygala-type	AL	X	X	X			X	
ROSACEAE	Rubus	AL	X	X	X				
ROSACEAE	Rosaceae undiff.	I	X	X	X				
SOLANACEAE	Solanum-type	I	X	X	X				
URTICACEAE	Urticaceae undiff.	I	X	X	X				
BALSAMINACEAE	Impatiens	N	X	X	X	X			
RANUNCULACEAE	Thalictrum	N	X	X	X				
ERICACEAE	Ericaceae undiff.	A	X	X					
ERICACEAE	Erica-type	A	X	X					
MYRICACEAE	Myrica	A	X	X					
MYRSINACEAE	Rapanea	A	X	X					
RANUNCULACEAE	Ranunculaceae undiff.	A	X	X					
THYMELAEACEAE	Gnidia-type	A	X	X					
MYRSINACEAE	Maesa	AL	X	X				X	
GENTIANACEAE	Gentianaceae undiff.	I	X	X			X		
HYPERICACEAE	Hypericum	I	X	X					
ROSACEAE	Alchemilla	N	X	X					
ACANTHACEAE	Isoglossa	N	X	X					
CRASSULACEAE	Crassula	N	X	X					
DIPSACACEAE	Dipsacaceae undiff.	N	X	X					
LOBELIACEAE	Lobelia	N	X	X					
RUBIACEAE	Galium-type	N	X	X					
POLYGONACEAE	Rumex	N	X		X				
MYRSINACEAE	Myrsine-type africana	A	X						
ASTERACEAE	Artemisia	I	X						X
RUBIACEAE	Anthospermum	I	X						
LAMIACEAE	Leucas-type	N	X					X	
PRIMULACEAE	Anagallis	N	X					X	
EUPHORBIACEAE	Flueggea	A		X	X	X	X	X	
SALICACEAE	Salix	A		X					
ACANTHACEAE	Mellera-type	I		X					
ARALIACEAE	Araliaceae undiff.	A		X	X	X		X	
ARALIACEAE	Polyscias	A		X	X	X		X	

Family	**Taxon**	**Habit**	**FM**	**FSM**	**FSD**	**FDH**	**SAV**	**STP**
BURSERACEAE	Santiria-type	A	X	X	X	X		
COMBRETACEAE	Combretaceae/Melastomataceae undiff.	A	X	X	X	X	X	
HYPERICACEAE	Harungana	A	X	X	X		X	
MELIACEAE	Carapa-type procera	A	X	X	X	X		
MELIACEAE	Entandrophragma-type	A	X	X	X	X		
MELIACEAE	Meliaceae undiff	A	X	X	X	X	X	
MORACEAE	Ficus	A	X	X	X	X	X	
MORACEAE	Trilepisium-type madagascariensis	A	X	X	X	X		
MYRSINACEAE	Embelia-type	A	X	X	X	X		
MYRTACEAE	Syzygium-type	A	X	X	X	X	X	
RUBIACEAE	Pavetta	A	X	X	X			
RUBIACEAE	Psydrax-type	A	X	X	X			
RUTACEAE	Zanthoxylum-type	A	X	X	X	X	X	
SAPINDACEAE	Allophylus	A	X	X	X	X	X	
STERCULIACEAE	Dombeya-type	A	X	X	X			
ULMACEAE	Celtis	A	X	X	X	X	X	
ULMACEAE	Celtis/Trema	A	X	X	X		X	
ARALIACEAE	Schefflera	A	X	X				
HYPERICACEAE	Psorospermum	A	X	X			X	
OLEACEAE	Olea capensis	A	X	X				
RUBIACEAE	Keetia-type cornelia	A	X	X				
SAPOTACEAE	Sapotaceae undiff.	A	X	X			X	
SIMAROUBACEAE	Brucea	A	X	X				
OLEACEAE	Olea europaea-type	A	X	X				
DILLENIACEAE	Tetracera	AL	X	X	X	X	X	
APOCYNACEAE	Landolphia-type	AL	X	X		X		
ACANTHACEAE	Justicia-type	I	X	X	X			
APOCYNACEAE	Apocynaceae undiff.	I	X	X	X	X	X	X
FABACEAE	Dolichos-type	I	X	X	X			
URTICACEAE	Laportea-type	N	X	X	X			
ACANTHACEAE	Hypoestes-type	N	X	X	X		X	
AMARANTHACEAE	Achyranthes-type	N	X	X			X	
RUBIACEAE	Spermacoce-type	N	X	X				
BEGONIACEAE	Begonia	N andNL	X	X	X			
PALMAE	Phoenix	PA	X	X	X			
LORANTHACEAE	Tapinanthus-type	Par	X	X				
ANACARDIACEAE	Lannea-type	A	X		X		X	
CELASTRACEAE	Celastraceae undiff.	A	X		X	X	X	
IRVINGIACEAE	Irvingia-type	A	X		X	X		
RUTACEAE	Clausena anisata	A	X		X		X	
EUPHORBIACEAE	Phyllanthus-type	A	X		X		X	
AQUIFOLIACEAE	Ilex mitis	A	X					

Family	**Taxon**	**Habit**	**FM**	**FSM**	**FSD**	**FDH**	**SAV**	**STP**
CELASTRACEAE	Maytenus	A	X				X	
PODOCARPACEAE	Podocarpus	A	X					
RHAMNACEAE	Rhamnus-type	A	X					
ROSACEAE	Prunus	A	X					
FLACOURTIACEAE	Flacourtia	A	X					
CELASTRACEAE	Cassine	AL	X		X	X		
MIMOSACEAE	Acacia	AL	X				X	X
MENISPERMACEAE	Cissampelos-type	AL	X				X	
FABACEAE	Indigofera	I	X		X		X	
RANUNCULACEAE	Clematis-type	L	X		X			
FABACEAE	Eriosema-type	N	X		X	X	X	
AMARANTHACEAE	Celosia argentea-type	N	X				X	
FABACEAE	Lotus-type	N	X					
GENTIANACEAE	Sebaea	N	X			X		
GENTIANACEAE	Swertia abyssinica-type	N	X					
GESNERIACEAE	Streptocarpus	N	X					
EUPHORBIACEAE	Alchornea	A		X	X	X	X	
EUPHORBIACEAE	Antidesma-type	A		X	X	X	X	
EUPHORBIACEAE	Uapaca	A		X	X	X	X	
LOGANIACEAE	Anthocleista	A		X	X	X	X	
ANACARDIACEAE	Pseudospondias-type	A		X	X			
ANACARDIACEAE	Sorindeia-type	A		X	X		X	
EUPHORBIACEAE	Macaranga-type	A		X	X			
EUPHORBIACEAE	Margaritaria discoidea	A		X	X		X	
MELIANTHACEAE	Bersama	A		X	X		X	
MIMOSACEAE	Entada-type	A		X	X		X	
MORACEAE	Myrianthus-type	A		X	X		X	
RUBIACEAE	Ixora-type	A		X	X			
STERCULIACEAE	Sterculia-type	A		X	X		X	
EUPHORBIACEAE	Croton-type	A		X	X		X	
CAESALPINIACEAE	Leonardoxa-type africana	A		X		X		
EUPHORBIACEAE	Bridelia-type	A		X		X	X	
EUPHORBIACEAE	Erythrococca-type3	A		X			X	
FABACEAE	Baphia-type	AL		X	X	X		
RUBIACEAE	Tarenna-type	AL		X				
CAPPARIDACEAE	Capparidaceae undiff.	I		X	X		X	X
EUPHORBIACEAE	Acalypha	I		X	X			
STERCULIACEAE	Pterygota	N		X	X			
MENISPERMACEAE	Stephania-type abyssinica	NL		X				
OCHNACEAE	Campylospermum	A		X				
MALPIGHIACEAE	Acridocarpus	AL		X				

Family	**Taxon**	**Habit**	**FSD**	**FDH**	**SAV**	**STP**
EUPHORBIACEAE	Drypetes-type	A	X	X		
EUPHORBIACEAE	Tetrorchidium	A	X	X		
MELIACEAE	Khaya-type	A	X	X	X	
MIMOSACEAE	Pentaclethra macrophylla	A	X	X		
MORACEAE	Antiaris-type toxicaria	A	X	X	X	
MYRISTICACEAE	Pycnanthus	A	X	X		
OLACACEAE	Strombosia	A	X	X		
RUBIACEAE	Bertiera	A	X	X		
RUBIACEAE	Pausinystalia-type	A	X	X		
ANACARDIACEAE	Rhus-type	A	X		X	
ARALIACEAE	Cussonia	A	X		X	
BALANITACEAE	Balanites	A	X		X	
CONNARACEAE	Cnestis-type	A	X		X	
DICHAPETALACEAE	Tapura fischeri-type	A	X			
EUPHORBIACEAE	Mallotus-type	A	X			
HYMENO-CARDIACEAE	Hymenocardia	A	X		X	
OCHNACEAE	Lophira	A	X		X	
OLEACEAE	Schrebera	A	X			
RUBIACEAE	Morelia-type senegalensis	A	X		X	
RUTACEAE	Teclea-type	A	X			
SAPINDACEAE	Aphania-type senegalensis	A	X		X	
SAPINDACEAE	Blighia	A	X			
SAPINDACEAE	Lecaniodiscus/Aphania senegalensis	A	X			
ULMACEAE	Holoptelea grandis	A	X		X	
CAESALPINIACEAE	Cassia-type	I	X		X	
TILIACEAE	Triumfetta-type	I	X		X	
SAPINDACEAE	Sapindaceae undiff.	AL	X	X		
OCHNACEAE	Sauvagesia erecta	N	X			
ANISOPHYLLEACEAE	Anopyxis klaineana	A	X			
CAESALPINIACEAE	Crudia-type	A		X		
EUPHORBIACEAE	Klaineanthus gaboniae	A		X		
EUPHORBIACEAE	Thecacoris-type	A		X		
RUBIACEAE	Adenorandia-type kalbreyeri	A		X		
SAPINDACEAE	Aporrhiza	A		X		
OLACACEAE	Olacaceae undiff.	AL		X		
EUPHORBIACEAE	Cyathogyne	N		X		
BURSERACEAE	Commiphora	A			X	X
CAPPARIDACEAE	Crateva adansonii	A			X	X
MENISPERMACEAE	Cocculus	A			X	X
RUBIACEAE	Mitragyna-type inermis	A			X	X
CAPPARIDACEAE	Maerua-type	A			X	
CAPPARIDACEAE	Boscia-type	I			X	X
LAMIACEAE	Basilicum polystachyon/Hoslundia opposita	I			X	

Family	Taxon	Habit	SAV	STP
VERBENACEAE	Lippia-type	I	X	
AMARANTHACEAE/CHENOPODIACEAE	Amaranthaceae/Chenopodiaceae undiff.	N	X	X
RUBIACEAE	Mitracarpus villosus	N	X	X
STERCULIACEAE	Hermannia-type	N	X	X
LAMIACEAE	Leonotis-type	N	X	
AMARANTHACEAE	Aerva-type	N		X
PROTEACEAE	Faurea-type	A	X	
VITACEAE	Cissus	I	X	
COCHLOSPERMACEAE	Cochlospermum	I	X	X
SAPINDACEAE	Pappea capensis	A	X	
CAESALPINIACEAE	Parkinsonia aculeata-type	A	X	
ANACARDIACEAE	Anacardiaceae undiff.	A		
ACANTHACEAE	Acanthaceae undiff	I		
APIACEAE	Apiaceae undiff.	I		
ASTERACEAE	Asteraceae undiff.	I		
ASTERACEAE	Cichoriae undiff.	I		
EUPHORBIACEAE	Euphorbiaceae undiff.	I		
EUPHORBIACEAE	Euphorbia-type	I		
FABACEAE	Fabaceae undiff.	I		
LAMIACEAE	Lamiaceae undiff.	I		
RUBIACEAE	Rubiaceae undiff.	I		
SOLANACEAE	Solanaceae undiff.	I		
MONOCOTYLEDONAE	Monocotyledones	I		
BRASSICACEAE	Brassicaceae undiff.	N		
ASTERACEAE	Centaurea-type	N		
PLANTAGINACEAE	Plantago	N		
POACEAE	Poaceae undiff.	N		
EUPHORBIACEAE	Ricinus communis	N		
CYPERACEAE	Cyperaceae undiff.	Nq		
HALORRHAGACEAE	Laurembergia tetrandra	Nq		
HYDROCHARITACEAE	Ottelia-type	Nq		
NYMPHAEACEAE	Nymphaea	Nq		
ONAGRACEAE	Ludwigia-type	Nq		
ONAGRACEAE	Onagraceae undiff.	Nq		
POLYGONACEAE	Polygonum senegalense-type	Nq		
POTAMOGETONACEAE	Potamogeton	Nq		
TYPHACEAE	Typha	Nq		
XYRIDACEAE	Xyris	Nq		
Monoletes smoothferns		Sp		
Monoletes ferns NL		Sp		
Triletes smooth ferns		Sp		
Triletes ferns NL		Sp		

Table III. List of pollen taxa determined at Bambili. Taxa are ranked according to membership of the corresponding plants to specific vegetation types: AA: Afro-montane;

FM: montane forest; FSM: sub-montane forest; SDF: semi-deciduous forest; FDH: rainforest ; SAV: savannah; STP: steppe. The plant habit is based on definitions of Vincens et *al.* (2007) A: trees; AL: trees and / or lianas; PA: palm; Par: parasites; N: herbs; NL: herbaceous lianas; Nq: aquatic herbs; I: undifferentiated; Sp: fern.

The pollen diagram shows changes in tree taxa percentages between 10.56% (16,593 cal yrs BP) and 95.28% (7032 cal yrs BP) (Figure 4). A number of these taxa belong to the montane forests and mid-altitude dense forest, which are present in almost all samples analyzed. These include *Podocarpus, Schefflera, Alchornea, Celtis, Embelia, Maesa, Macaranga*-type, *Olea capensis, Ficus, Syzygium* and *Rapanea*. However, these percentages are highly variable: from 0.2 to 45.75%. Based on these changes as well as that of the appearance and disappearance of other characteristic taxa (*Aerva, Alchemilla, Artemisia, Farsetia, Hypericum, Ilex mitis, Gnidia*-type and *Myrica*), five pollen zones were distinguished for the sequence:

Zone I: 14.01 to 13.21 mcd (20,109-17,192 cal yrs BP)

This zone is characterized by high percentages of herbaceous plants including Poaceae undiff., which decreases from the base (75.68%) to the top (34.44%), and Asteraceae undiff. (30.29%). The tree percentages do not exceed 26.64%.

This zone also includes many taxa of trees and herbaceous plants that characterize today's open spaces, such as savannas and steppes, including *Lannea* (1.22%), *Commiphora* (0.44%) Capparidaceae undiff. (0.34%) and *Aerva*-type (6.15%). The afro-alpine meadow and tree line are also represented by a number of taxa: *Myrica* (16.99%), Ericaceae undiff. (3.09%), *Artemisia* (1.68%), *Maesa* (1.29%), *Gnidia*-type (0.93%) linked to montane elements, *Nuxia* (9.31%) *Rapanea* (1.25%), *Rubus* (2.37%), and *Carapa procera* (1.82%).The trees of the sub-montane forest and semi-deciduous forest are present in proportions not exceeding 2.5%. These are primarily *Antiaris, Antidesma, Lophira, Pausynistalia, Trilepisium madagascariensis*-type, and Sapindaceae undiff.

Based on the variations of the main taxa of this zone (Asteraceae, *Aerva*-type, *Anthrospermum*, *Myrica*), two sub-areas were identified:

Subzone Ia: 14.01 to 13.63 mcd (20,109-18,589 cal yrs BP)

This subzone is characterized by the maximum percentages of Asteraceae undiff. (30.29%) at 13.495 mcd (19,049 cal yrs BP). The vegetation is dominated by herbaceous taxa and shrubs of the open savanna or forest edges: Amaranthaceae / Chenopodiaceae undiff. (2.30%), Asteraceae undiff. (30.29%), *Aerva*-type (2.63%), Solanaceae undiff. (3.13%), Lamiaceae undiff. (4.15%), *Achyranthes*-type (0.95%), *Lannea* (0.41%) *Boscia* (0.41%), *Crudia* (0.35%) and Urticaceae undiff. (0.74%).

Subzone Ib: 13.63 to 13.21 mcd (18,589-17,192 cal yrs BP)

All trees decreased from 32.89% to 12.84%, while herbaceous taxa increase from 44.40% to 80.41%. This sub-zone is characterized by the successive peaks, between 18,436 and 18,167 cal yrs BP, of herbaceous taxa of the subalpine vegetation type: *Anthospermum* (6.95%), followed at 17,640 cal BP by a first peak of *Olea capensis* (4%) and *Schefflera* (6.22%).

Zone II: 13.21 to 12.295 mcd (17,192-14,320 cal yrs BP)

This area is characterized by high values of Poaceae undiff. (68.58%) associated with *Aerva* at maximum values (6.15%). Asteraceae remains significant throughout the zone.

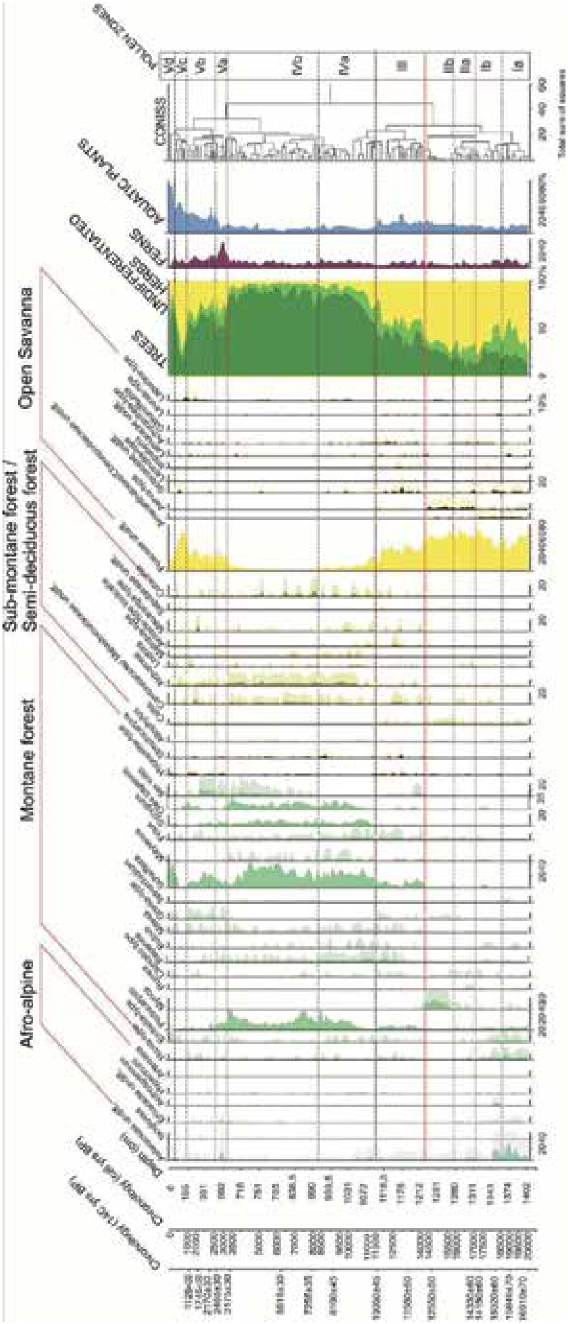

Fig. 4. Pollen diagram of Lake Bambili (Cameroon). This diagram shows, from left to right, radiocarbon ages, calibrated ages, depths, and percentages of major taxa presented in terms of large groups of regional vegetation calculated on a sum excluding aquatic plants and ferns. Poorly represented taxa are exaggerated by a factor of 10 and superimposed on the initial values (in dark). At the far right is a diagram of variations of AP / NAP. Pollen zones were delineated by applying the CONISS software (GRIMM, 1987).

Other savanna and steppe taxa are also present: Amaranthaceae / Chenopodiaceae undiff (1.39%), C*ommiphora* (0.48%), *Mitragyna inermis*-type (0.24%), *Faurea* (0.45%) *Crateva adansonii* (0.23%). Progressions of *Myrica*-type and *Aerva* determine two sub-zones:

Sub-zone IIa: 13.21 to 12.83 mcd (17,192-15,916 cal yrs BP)

In this sub-zone, the montane forest trees and afro-alpine meadow values remain small or decline sharply from the previous zone: *Podocarpus* (3.56%), *Myrica* (2.85), *Schefflera* (2.49%), *Syzygium* (1.85%), *Olea capensis* (1.43%), *Embelia*-type (2.31%) and Ericaceae undiff. (1.1%) while only *Anthospermum* disappears.

Sub-zone IIb: 12.83 to 12.295 mcd (15,916-14,320 cal yrs BP)

This sub-zone is distinguished by very high values of *Myrica* between 15,496 and 14,320 cal yrs BP (16.99%). All trees increase (31.84%); however, this primarily montane taxa (30.94%; *Carapa* type *procea, Clausena anisata, Clematis, Embelia, Ilex mitis,* and *Lannea*), and sub-montane taxa (7.82%; *Macaranga, Bredelia*-type, *Croton*-type, *Erythrococca)*. Most savanna and steppe components disappear, except for *Mitragyna inermis*-type, *Cohlospermum, Commiphora,* and *Crateva adansonii,* with percentages not exceeding 1%.

Zone III: 12.295 to 11.005 mcd (14,320-11,572 cal yrs BP)

This zone is marked by the drastic reduction of Poaceae undiff. percentages by more than 11.13% (minimum at 11,757 cal yrsq BP). The percentages of all trees increase, especially *Schefflera* (19.07%) and *Podocarpus* (7.45%). This zone is also characterized by the final disappearance of *Myrica*, which is replaced by *Ilex mitis* (5.11%).

Between 14,200 and 13,602 cal yrs BP, tree percentages decreased significantly, especially *Schefflera* and *Podocarpus* which represent only 12.03% and 7.45%, respectively.

Zone IV: 11.005 to 6.80 mcd (11,572-3,252 cal yrs BP)

The increase in trees initiated in the previous zone continues in zone IV with percentages reaching the maximum value of 92%. Conversely, Poaceae undiff. disappears along with all elements of non-native steppe and savanna. The changing environment consists of two phases:

Subzone IVa: 11.005 to 9.205 mcd (11,572-8,252 cal yrs BP)

The disappearance of *Ilex mitis* precedes the maximum phase of forest expansion. The general increase of trees results in the appearance and / or expansion of a series of montane forest taxa: *Olea capensis* (15.61%), *Syzygium* (12.62%), *Maytenus* (4.36%), *Ficus* (6%), *Embelia* (3.40%), *Rubus* (5.38%), *Achyranthes*-type (1.38%), *Clematis* (1.84%), *Celtis* (4.34%) *Podocarpus* (32.13%) and *Schefflera* (36%). The sub-montane forest taxa are also increasing: *Alchornea* (7.36%), *Mallotus*-type (3.35%), *Macaranga*-type (3.88 %), *Erythrococca*-type (2.07%), and *Streptocarpus* (4.15%).

Subzone IVb: 9.205 to 6.80 mcd (8,292-3,252 cal yrs BP)

This sub-zone is marked by the re-emergence of *Ilex mitis* (1.74% to 10.15%) and the irregular representation of different forest taxa, all trees ranging from 86.93% to 75.80%. Montane forest taxa, such as Ericaceae undiff. (1.32%), *Isoglossa* (0.23%), *Gnidia* (1.15%), *Maesa* (4.36%), *Rapanea* (3.48%) and *Nuxia*-type (1.75%), have relatively high percentages.

Zone V: 6.80 to 0 mcd (3,252 cal yrs BP-Present)

The pollen spectra of this area reveal a severely depleted forest with percentages of trees that represent only 39% on average. Many taxa completely disappear (*Indigofera*, *Blighia*, Sapindaceae undiff., *Brucea*, *Sauvagesia, Faurea*, *Salix*). Others remain present in significant percentages such as *Podocarpus* (up to 19.43%), *Olea capensis* (12.24%), *Schefflera* (45.25%), *Ilex mitis* (13.27%), Asteraceae undiff. (15.74%), and Ericaceae undiff. (4.45%). In addition, *Achyranthes* (1.53%) and *Laportea*-type (6.33%), both characteristic of degraded environments, along with *Gnidia* (6.08%), *Impatiens* (1.52%) and *Ricinus* (0, 60%) occur and progress in this area. The different variations of the percentages of major taxa suggest four sub-zones:

Subzone Va: 6.80 to 5.805 mcd (3,252-2,549 cal yrs BP)

There is a change in vegetation in this sub-zone marked by the loss of forest as percentages fall to 46% (*Alchornea* (1%), *Allophylus* (0.29%), *Antiaris* (0.30%), *Antidesma*-type (0.81%), *Carapa*-type *procea* (0.34%), *Celtis* (0.40%), *Clausena anisata* (0.67%), Combretaceae undiff. (0.30%), *Cussonia* (0.64%), *Drypetes* (0.29%), *Embelia* (0.30%), Ericaeae undiff. (0.39%), *Erythrococca*-type (0.34%), *Ficus* (0.30%), *Gnidia* (0.31%), *Podocarpus* (5.43%), *Olea capensis* (0.30%), and *Schefflera* (7.66 %)). Poaceae undiff., Asteraceae undiff., and ferns increase dramatically to 36.50%, 5.53% and 15.35%, respectively.

Subzone Vb: 5.805 to 1.905 mcd (2,549 -960 cal yrs BP)

Forest vegetation recovers but is impoverished and deteriorates very quickly at 960 cal yrs BP. This sub-zone also shows the importance of indicators for open environments: *Celtis* (11.84%), *Laportea* (6.33%), Solanaceae undiff. (2.59%), Poaceae undiff (48.95%), *Macaranga* (10.10%), Lamiaceae undiff. (2.17%), *Hypoestes*-type (2.55%), and *Clematis* (2.36%). The majority of the montane taxa cited in the previous sub-zone regress: *Podocarpus* (0.51%). *Maytenus* (0.28%), *Embelia*-type (0.42%), *Syzygium* (1.27%), *Schefflera* (0.84%), *Ilex mitis* (1.68%), *Antiaris* (0.76%), *Rapanea* (0.38%) and *Cussonia* (0.31%).

Subzone Vc: 1.905 to 0.605 mcd (960-266 cal yrs BP)

This subzone marks the minimum representation of trees in the Holocene with a percentage of 18%. Herbaceous plants increase, especially Poaceae undiff. (78%), Asteraceae undiff. (4.11%), Urticaceae (*Laportea*-type) (1%) and Solanaceae undiff. (5.80%). Forest elements such as *Olea capensis* (1.61%), *Podocarpus* (1.36%), *Maytenus* (0.4%), *Syzygium* (1.27%), and *Ficus* (0.34%) as well as afro-alpine elements such as Ericaceae undiff. (0.34%), *Hypericum* (0.40%), and *Isoglossa* (0.80%), are present in very small quantities.

Subzone Vd: 0.605 to 0 mcd (266 cal yrs BP-Present)

The top of this record is differentiated by the extreme poverty of the forest flora dominated by *Schefflera* (45%) and *Embellia* (11%), associated with *Syzygium* (7.07%), *Hypoestes*-type (4.04%), *Clematis* (2.26%), *Celtis* (3.80%), *Ilex mitis* (0.45%), *Cussonia* (3.61%), *Achornea* (4.22%), and *Macaranga*-type (1.1%). Poaceae undiff. remain at a high level and Solanaceae undiff. increases (5.5%).

5. Discussion: The evolution of vegetation cover

5.1 An open and degraded vegetation during the ice age

Forest cover

At Bambili, forest cover was extremely low during the late glacial period (18,000-23,000 cal yrs BP). The vegetation is dominated by herbaceous plants, as is the case in all West African sites regardless of altitude: the swamp Shum Laka (Kadomura, 1994) at 1200 m asl on the Bamenda plateau at Barombi Mbo at the foot of Mount Cameroon (Maley and Brenac, 1998) and Lake Bosumtwi, Ghana (Maley, 1987) located in low and mid altitudes. The pollen studies from the mountains of East Africa also reflect the general degradation of tropical forests during this period (Livingstone, 1967, Coetzee 1967, Hamilton, 1982). Three pollen sites located in southern hemisphere, however, show a different pattern. At Ngamakala, a forest sites in the southern Congo located 400 m asl, the environment, although degraded, remains forest during the glacial period until 13,000 yrs BP (Elenga et *al.*, 1994). At Kisiga Rugaro, a forested part of the Eastern Arc Mountains shows a certain environmental stability during the whole glacial period (Mumbai et *al.* 2008). They note, however, that the herbaceous plants recorded their highest percentages between 19,000 and 14,000 cal yrs BP , which could correspond to drier and colder conditions than even the preceding LGM. Mumbai et *al.* (2008) suggest that the relative stability of ecosystems during the last ice age is due to the influence of the Indian Ocean that would have allowed the maintenance of a rain forest while the regional climate of East Africa was dry. At Lake Masoko (9°20'S, 33°45'E, 840 m asl), Vincens et *al.* (2006) also identify a uninterrupted development phase of semi-deciduous forest from 23,000 - 11,800 cal yrs BP.

The composition of local vegetation

The composition of pollen spectra of the Last Glacial Maximum (LGM) at Bambili shows a mixture of floristic elements representative of distinct stages: the sub-montane forest, the semi-deciduous forest (*Antiaris, Antidesma, Lophira, Pausynistalia, Trilepisium madagascariensis*-type, Sapindaceae undiff.), the montane forest (*Nuxia, Rapanea, Rubus, Carapa procea, Myrica, Gnidia*-type, *Maesa*, Ericaceae undiff.) and Afro-alpine (*Artemisia, Alchemilla, Anthospermum, Hypericum, Rumex, Isoglossa*). Herbaceous taxa dominate open areas or forest edges. Among these are: Poaceae undiff., Cyperaceae undiff., Amaranthaceae / Chenopodiaceae undiff., Asteraceae undiff., Lamiaceae undiff., *Achyranthes*-type and Urticaceae undiff. Among the arboreal taxa, montane forest taxa dominated; however, their percentages are very low.

Distant contributions

The LGM is characterized by the presence of savanna and steppe taxa such as *Aerva*-type, *Boscia*-type, Capparidaceae undiff., *Commiphora, Crataeva adansonii, Crudia*-type, *Lannea*-type and *Maerua*-type that show the importance of long-distance aeolian input, related to an increased flow of trade winds (Sarnthein et *al.*, 1981) and possibly the extension of Sudan-Zambezian vegetation zones due to dry conditions. A layer of charcoal was observed at 1355 cm. Dating of this layer yielded an age of 18 283 cal yrs BP (15 020 ± 60 ^{14}C BP) suggesting the importance of fire at this time in the environment near Lake Bambili.

5.2 The post-glacial forest colonization

Chronology of colonization forest

In the global post-glacial context, recolonization of forest is observed. At Bambili, this occurs in three distinct stages (Figure 5) interrupted by two phases of regression corresponding to the Heinrich event 1 (H1) and the Younger Dryas.

The first phase of colonization starts at 18,400 cal yrs BP with the appearance of *Anthospermum*. This taxon is noted by Livingstone (1967) as an important element of the first stage of colonization of lava fields in the region of the Virunga volcanoes in East Africa. In Cameroon, *Anthospermum camerounensis*, is a dwarf grass found in Afro-alpine vegetation types (Letouzey, 1968). This taxon is followed by a large increase of *Olea capensis* and *Schefflera*, forming a first phase of increase in trees. The increase of trees stops at 17 100 cal yrs BP, with the increase of *Aerva*-type, which indicates the strengthening of the boreal winter northeasterly wind flow from the Sahelian steppes and large fires are indicated by charcoal layers. This increase is contemporaneous with H1, the characteristics of climate on a global scale are drought (Mix et *al.*, 2001; Kageyama et *al.*, 2005; Timmermann and Menvielle, 2009).

Vegetation at Bambili remains relatively stable for about 1900 years when a second stage of forest colonization begins at 14,900 cal yrs BP. This stage is initiated by the appearance of *Myrica*, a fire-tolerant, sun-loving shrub common in clearings of the upper montane forests (Livingstone, 1967). This taxon is followed by another sun-loving species, *Ilex mitis*, and finally by *Olea capensis, Podocarpus* and *Schefflera.* This phase culminates in a very short period between 13,800 and 13,700 cal yrs BP, corresponding to the beginning of the warm Alleröd in high latitudes (Roberts et *al.*, 1993, 2010). This increase of forest cover at Bambili is coeval with the start of the African Humid Period dated to 15,500 cal yrs BP by DeMenocal et *al.* (2000). This period was marked by increased flow of the Niger River (Lézine and Cazet, 2005) and the general rise in lake levels (Gasse, 2000; Shanahan et *al.*, 2006). At Bambili, Stager and Anfang-Sutter (1999) found a positive P / E during this period. The presence of steppe taxa such as *Aerva* up to 11,700 cal yrs BP, however, shows that trade wind flow was still significant over this period. This is in contrast with the termination of Saharan dust transport to the ocean further north noted by DeMenocal et *al.* (2000).

Between 13,000 and 11,700 cal yrs BP, a second phase of forest decline is recorded. This phase does not correspond to the total destruction of the forest. It is characterized instead by a massive regression of *Schefflera*. All trees recorded a large decrease with the exception of *Podocarpus, Rapanea* and *Gnidia*-type. The permanence of steppe elements reflects the importance of continued northeasterly circulation. This phase corresponds to the YD (Younger Dryas) in the high latitudes (Roberts et *al.*, 1993). As mentioned earlier, the YD is generally dry in tropical North Africa, reflected in the general lowering of lake levels (Gasse, 2000). This episode is marked by increased dust transport to the Atlantic recorded from the equator (Lézine et *al.*, 1994) to the Saharan latitudes (DeMenocal et *al.*, 2000). The YD signature on forest vegetation is however not very visible in the Ivory Coast as outlined Lezine and Le Thomas (1995). Despite evidence of increased sedimentological transport by the trade winds, the authors noted no major changes in the forest environment during this episode. The YD seems to be more clearly recorded in the vegetation surrounding lakes Barombi Mbo and Bosumtwi. Data from Barombi Mbo show an increase of spores (2 to over

15%), Poaceae (13 to 17%) and pioneers taxa such as *Trema*, *Macaranga, Mallotus* and *Alchornea* around 12,500 yrs BP (Maley and Brenac, 1998). At the same site, Lebamba et *al.* (2010) show, after ca 14,000 cal yrs BP, the decline of tropical rain forests and seasonal increases in savanna biomes. At Bosumtwi, there is an increase in grasses and sedges, while the tree taxa regress (Maley, 1991). From 11,500 cal yrs BP, *Schefflera* leads a new phase of forest expansion with a forest optimum dated between 10,000 and 8400 cal yrs BP. The development of the forest is gradual between 11,500 and 10,200 cal yrs BP and results in the expansion of montane taxa. Next, *Rubus, Rapanea, Embelia*-type and *Syzygium* appear in turn. The elements of the montane forest, in particular, *Schefflera, Podocarpus, Olea* and *Syzygium* rose steadily over this period. Submontane forest is also present through a number of taxa that appear sporadically, such as *Cussonia, Macaranga*-type, *Antiaris*-type *toxicaria*, and *Allophyllus*.

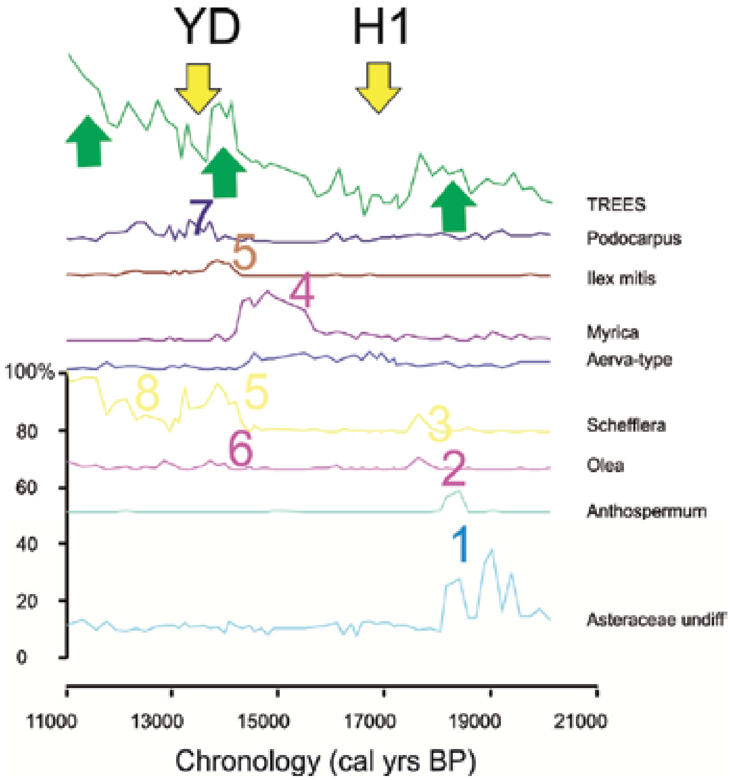

Fig. 5. Colonization of the postglacial forest. The curves are made from percentages of each taxon from 21,000 to 11,000 cal yrs BP. This colonization takes place in three phases forest interrupted by two regressions corresponding to H1 and the YD. It starts at 18,400 cal yrs BP with the appearance of *Anthospermum* (1) followed by *Olea capensis* (2) and *Schefflera* (3). The interruption to 17,100 cal yrs BP, marked by the increase of *Aerva*-type is correlated with H1. A second phase of forest colonization starts at 14,900 cal yrs BP with the appearance of *Myrica* (4) monitoring and *Ilex mitis Schefflera* (5), *Olea capensis* (6) and *Podocarpus* (7). Between 13,000 and 11,700 cal yrs BP, a second phase of regression is observed with decreasing forest trees. Then, from 11,500 cal yrsnBP, *Schefflera* (8) opens the Holocene forest expansion phase.

Example of two major forest taxa: *Olea* and *Podocarpus*

Comparison of pollen data from sites Barombi Mbo, Tilla and Bambili shows that, since 20,000 years BP, some plants have moved from low to high altitudes. This is the case of *Olea* (Figure 6) which shows percentages up to 35%, during the glacial period at Barombi Mbo (Maley and Brenac, 1998), indicating the presence of the plant source at low altitude near the lake. Its percentage decreased drastically from 12,000 cal yrs BP. At this time, *Olea* appears at Tilla, 700 m north of the volcanic line in Cameroon (Salzmann et *al.*, 2000) where it develops until it reaches 14%. It then extends to 2200 m asl at Bambili after 10,800 cal yrs BP where it remained until the end of the Holocene forest. This tree is still present in the mountains at the edge of montane forest and sub-montane, near the village of Oku. *Olea* is known to be a pioneer taxon, which explains its presence at the beginning of the forest recovery at Tilla, before the development of Euphorbiaceae (*Uapaca*) that characterize the forest in the Holocene. The behavior of *Olea* during the glacial-interglacial transition could be related to temperature changes. With rising temperatures after 12,000 years at low altitude, *Olea* migrates toward higher elevations to it current location.

Unlike the previous taxon, *Podocarpus* shows a similar pattern at both sites (Figure 7). It is not represented in the LGM sediments, and pollen percentages that reached Barombi Mbo are so low that it precludes the possibility of its presence at low altitude. At Bambili, it also reduced at this time. *Podocarpus* at Bambili increases from 10,000 cal yrs BP, then develops during two periods centered around 7560 cal yrs BP and 3360 cal yrs BP. It is interesting to note that these two peaks are also found at Barombi Mbo; however, here values are a full order of magnitude lower than at Bambili. This could support the hypothesis of two distinct phases of expansion of *Podocarpus* in altitude during the Holocene.

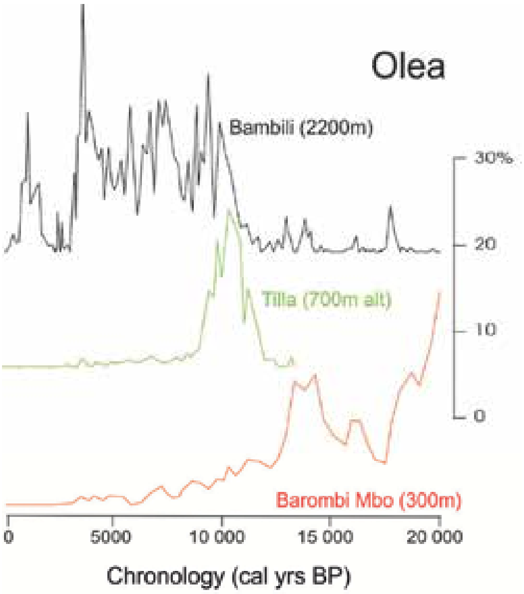

Fig. 6. The evolutionf *Olea*-type at Bambili, Tilla and Barombi Mbo. During the Last Glacial Maximum, *Olea*-type has a significant presence in Barombi Mbo until 12,000 cal yrs BP. The presence is then recorded at Tilla between 12,000 and 11,800 cal yrs BP and at Bambili at 10,800 to 3300 cal yrs BP.

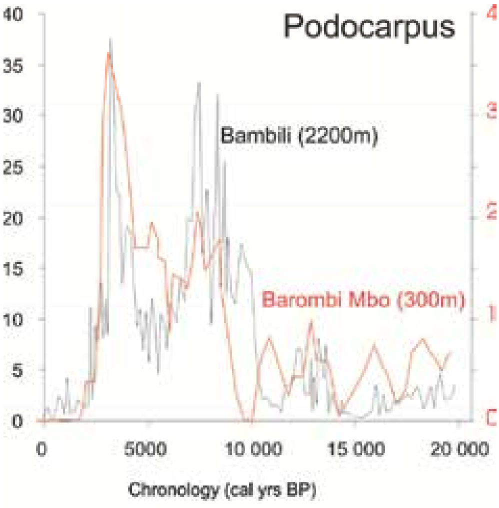

Fig. 7. The evolution of *Podocarpus* at Bambili and Barombi Mbo. The trend in *Podocarpus* expansion is similar between sites; however, the values are often an order of magnitude higher at Bambili.

The expansion of *Podocarpus* during the Holocene is also attested throughout Central Africa from the Atlantic site at 8 m asl at Ossa (Reynaud-Farrera, 1995; Reynaud-Farrera et *al*., 1996), as well as those of Mboandong at 130 m asl (Richards, 1986), Mbalang at 1100 m asl (Vincens et *al*., 2009), Njupi at 1108 m asl (Zogning et *al*., 1997), Bafounda at 1310 m asl (Tamura, 1990), and Shum Laka (W-10) at 1355 m asl (Kadomura, 1994).

5.3 The optimum forest of the early Holocene

The optimum forest at Bambili occurs between 10,000 and 8400 cal yrs BP and is characterized by the dominance of tree taxa at values from 80-92%. Of the 118 total tree taxa determined to Bambili, this period includes more than half (67 taxa), the majority belonging to the montane and semi-deciduous forests. These are mainly *Schefflera*, *Syzygium, Podocarpus, Olea capensis, Rapanea* for the montane forest and *Macaranga*, *Celtis, Cussonia, Antiaris* for semi-deciduous forest. Elements of the open areas have disappeared (*Leonotis, Leucas, Boscia, Aerva*) or decreased (*Impatiens, Achyrantes*, Solanaceae undiff, *Galium / Rubia*).

In tropical Africa during the early Holocene, the percentages of pollen from woody genera are high throughout the region, indicating the expansion of forests into higher latitudes and altitudes (Lézine, 2007). In West Africa, the marine records suggest that the Guineo-congolian forests were not separated by the savanna corridor that exists today in Togo and Benin, the "Dahomey Gap" (Dupont et *al* ., 2000), which is confirmed by the analysis of lake sediments from Sele (Salzmann et *al*., 2000). Tropical plants migrated northwards along the rivers and lakes stretching across the Sahel and the Sahara (Watrin et *al*., 2009). The mangrove taxon *Rhizophora* also occupied many coastal areas northward to around 21°N (Lézine, 1997).

Bonnefille et *al*., (1995) noted also a reduction in forest cover during the LGM and a discontinuous forest colonization at Rusaka Swamp (3°26’S, 29°37’E, 2070 m asl). Many authors link the expansion of Guineo-congolian forest and mangrove with a reinforcement of the Atlantic monsoon at the beginning of the Holocene (Marzin et Braconnot, 2009). Rainfall was significantly higher than today and seasonality was reduced as shown by the high lake levels (Gasse, 2000; Shanahan et *al.*, 2006) and increased fluvial transport (Lézine and Cazet, 2005).

5.4 The destabilization of the forest in the mid-Holocene: The 8.2 event

The forest phase at Bambili is marked by a very short but indicated episode of regression which occurs at the time of the 8.2 event in the high latitudes (Von Grafenstein et *al.*, 1998). It is reflected in the physiognomy of the forest by lower percentages of trees and the more or less pronounced decrease in values of some taxa. The most remarkable decreases are those of *Schefflera, Podocarpus, Rapanea,* and to a lesser extent those of *Olea capensis, Maesa, Syzygium, Ilex mitis, Nuxia,* and *Embelia,* all standard elements of the montane forest as well as those of *Cussonia*, *Alchornea,* and the submontane forest. This degradation could be caused by dry conditions as suggested by the lower lake levels at Lake Bosumtwi (Shanahan et *al.*, 2006) related to the slowdown of the thermohaline circulation in the North Atlantic (Pissart, 2002).

5.5 The end of the Holocene forest at Bambili

After 8400 cal yrs BP, changes in taxa suggest some forest instability. This phase of disruption occurs gradually, leading to the brutal destruction of the forest at 3300 cal yrs BP. At this period, *Podocarpus* opposes *Schefflera, Syzygium* and *Alchornea*. Forest degradation begins at 4500 cal yrs BP, with the decline of *Schefflera* followed by that of *Olea capensis* at 3500 cal yrs BP and *Podocarpus* at 3300 cal yrs BP. The drastic reduction of montane forest elements at 3300 cal yrs BP probably favored soil erosion and sediment supply from the crater rim. The latter was then increased by the return of wet conditions during the early part of this interval after logging dated between 2500 and 1300 cal yrs BP.

At 3300 cal yrs BP, lower montane forest taxa values are partially offset by increases of *Syzygium*, *Maesa* and *Gnidia*-type, indicating the opening of the forest. This opening peaks at 2600 cal yrs BP with the increase of Urticaceae and Poaceae undiff. . The evolution of the vegetation was organized in two stages. Between 2500 and 1300 cal yrs BP, a small forest recovery takes place. Forest vegetation is dominated by *Ilex mitis* associated with *Schefflera* and to a lesser extent *Sygyzium, Rapanea, Maesa, Nuxia*, and *Gnidia*-type. *Podocarpus* and *Olea capensis* are poorly represented. In the later part of this phase, the presence of sub-montane elements successively occurs such as *Macaranga, Celtis,* and *Lophira*. Finally, the Afro-montane elements (Ericaceae undiff., *Hyperycum, Isoglossa)*, with smaller percentages are generally better represented than in the high forest phase. This phase corresponds to wet period as suggested at Bambili by Stager and Anfang-Sutter (1999) who noted a P / E positive. The lake level rose during this period as reflected in the diatom assemblages; however, this could be artificially enhanced by the increased sediment transport from the lake margin. A humid climate is also noted in Ossa between 2700 and 1300 cal yrs BP by Nguetsop et *al.* (2004) confirming its regional character. At 960 cal yrs BP, the deep decline of *Schefflera*, partially offset by higher percentages of *Olea,* illustrates another phase of environmental degradation. The opening in the middle is highlighted by the dominance of Poaceae and Urticaceae. Between 960 cal yrs BP to the present, a marked upturn in forest is observed, with expansion of *Schefflera* (45%). The degradation of forest leads to a generalized fall in the majority of taxa, montane and submontane. The presence of Asteraceae undiff, *Ilex* *mitis*, *Ficus*, *Embelia*-type, *Maesa*, *Rapanea*, *Sygyzium*, *Gnidia*-type, *Clematis*-type, *Nuxia*-type, *Hypoestes*-type, *Alchornea*, Sapotaceae undiff., Solanaceae undiff, however, *Celtis* reveals nature montane forest mixed with the semi-deciduous forest.

5.6 The impact of environmental change on biodiversity

Fluctuations in biodiversity, calculated using the method developed by Birks and Line (1992) (Figure 8), show four phases of maximum biodiversity that correspond to periods of transition or disturbance of the forest. These phases are centered around 18,000 cal yrs BP, 12,000 cal yrs BP, 6500 cal yrs BP and 1500 cal yrs BP. The highest values of the record occur during the post-glacial colonization of forest following the YD (ca 12,000 cal yrs BP) and at the end of the small logging period (ca 1000 cal yrs BP). During these periods, forest biodiversity is increased due to the internal forest dynamics incorporating the gradual disappearance and appearance of certain plants resulting in greater overall species richness. According to Birks and Line (1992), floristic richness is favored during phases of "intermediate" disruption. The ecosystem fragmentation associated with such disruption limits the domination of one single component as long as the disturbance is not sufficient to cause the complete disappearance of the ecosystem on a regional scale.

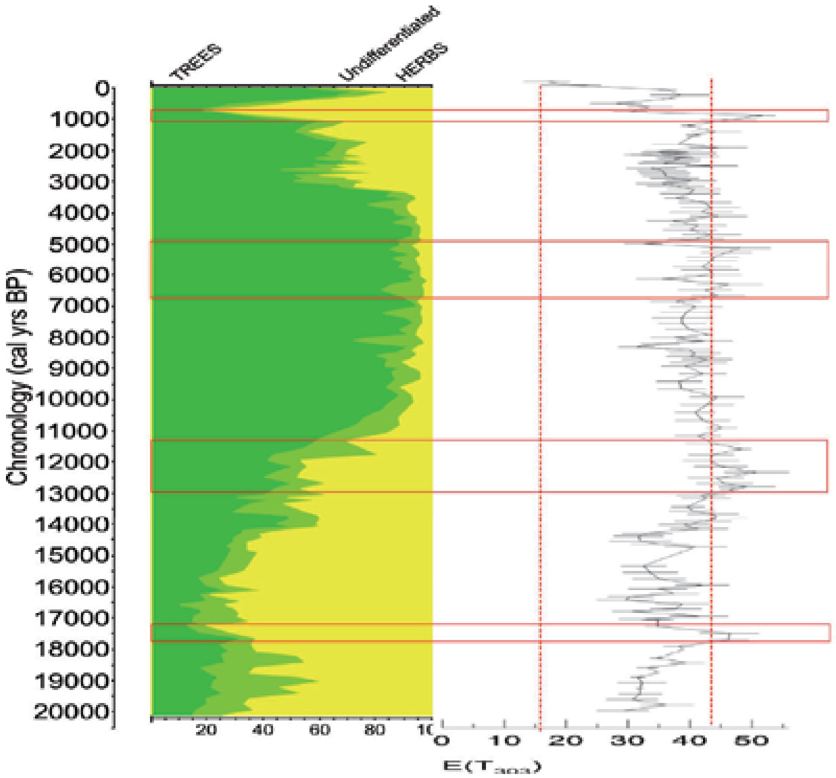

Fig. 8. Physiognomy of the vegetation and changes in biodiversity at Bambili. Left, Bambili diagram synthesis with the percentages of trees, herbs and undifferentiated. Right, rarefaction analysis showing Bambili biodiversity. Biodiversity is very high in the transition phases of the vegetation (red boxes). The dashed lines indicate the minimum of biodiversity (left line) and the value of average biodiversity (right line).

At Bambili, highest biodiversity does not follow forest stabilization, in contrast, biodiversity indices are generally low during these times. As shown in Figure 8, the current biodiversity surrounding Lake Bambili is the lowest in the last 20,000 years. This confirms the considerable impoverishment of the environment related to the recent deterioration of the forest environment undoubtedly amplified by the action of man, as evidenced by the comparative analysis of satellite photos from 1998 and 2003.

6. Conclusion

This palynological study of the paleoenvironments surrounding Bambili reveals the history of montane Central Atlantic Africa over the last 20,000 years. It also provides unique evidence on the response of Cameroon's mountain forests to climate change. During the LGM, a highly degraded forest formation was present around Bambili dominated by light-demanding components suggesting a dry environment. For the Holocene, the proportion of tree pollen shows continuous forest cover between 10,000 and 3300 yrs cal BP. The expansion of forest, very dynamic at the beginning of the Holocene, led to installation of a montane forest dominated by *Schefflera, Podocarpus* and *Olea* which responded individually to climate change. This forest lasted for much of the Holocene, then floristic composition changed. From this period, forest degrades very sharply during three centuries and the forest loses about 40% of its importance.

This is in agreement with the general context of equatorial forest evolution as a result of drier conditions of the end of the Holocene humid period. As emphasized by Birks Line (1992) "floristic richness is maximized by the disruption and fragmentation of the landscape when it reaches a level sufficient to prevent the domination of a single species and insufficient to cause the extinction of all components of the landscape. "The lowest percentages of trees on the top of the Bambili sequence dominated by a single taxon: *Schefflera*, indicates the disturbance of the landscape which reached a maximum level showing considerable impoverishment of the local flora. However, despite the effects of climate, intensified anthropogenic impacts have dramatically reduced forest biodiversity in recent decades. Continuation of such practices, associated largely with agriculture and ranching, in the future will likely lead to the disappearance of this ecosystem.

Palynological studies on other sites of Cameroon during LGM are needed to better assess the extent of *Podocarpus* forest.

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7

Using Remotely Sensed Imagery for Forest Resource Assessment and Inventory

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1. Introduction

Forests are complex ecosystems that develop over centuries through the interactions between organisms and biogeochemical cycles of elements occurring in the soil-atmosphere continuum. The biomass and structure of a forest stand is involved in several ecosystem processes and has been used as an indicator of forest health and productivity. The forest biomass is a key component of the carbon cycle, as forests represent large carbon sources and sinks (Skole & Tucker, 1993). Tree canopy height and area are highly correlated with biomass and are important inputs in forest productivity models (Drake, 2001). The variation of forest biomass production has been related to variations in canopy light absorption since the amount and spatial distribution of vegetation, directly affects light availability in forests. Forest stand factors that determine light absorption include: amount of leaf area, crown and canopy structure, phenology, and leaf optical properties (Jarvis and Leverenz, 1983). The amount of leaf area, measured through the leaf area index (LAI), is considered a key parameter of ecosystem processes (Asner and Wessman, 1997). Several forest ecosystem processes are strongly controlled by LAI including interception of light (Machado & Reich, 1999) and precipitation (Van Dijk & Bruijnzeel, 2001), gross primary productivity (Jarvis & Leverenz, 1983), transpiration (Granier et al., 2000), and soil respiration (Davidson et al., 2002). LAI is also related to other important ecological processes such as evapotranspiration, CO_2 and water exchange with the atmosphere, nutrient cycling and nutrient storage in plants (Dougherty et al. 1995). Therefore, measurements of forest biomass and structure are critical in the study of ecosystems for many applications including management of forest plantations, wildlife and biodiversity, fire modeling, and carbon sequestration among others.

Traditionally, the assessment of forest structure and growth has been done by measuring forest canopy attributes such as tree canopy dimensions, height and LAI in the field using hand-held equipment including leaf area meters, height poles, clinometers and measure tapes. Although field-based methods can be highly accurate, they are typically limited in scope to either mapping at plot scales or sampling sites at the landscape scale. Because of the expense of conducting detailed forest inventories over large areas, considerable research has focused on developing tools to estimate forest canopy attributes using remote sensing techniques. Historical aerial photos have proven useful, but analysis has generally been done manually. With new satellite sensors and improved computing power and analytical software, remote sensing is becoming an important tool for forest cover mapping, environmental monitoring, and ecological process assessments from global, regional, and landscape levels (Plummer, 2000).

This chapter is a review of the remote sensing technologies currently used to achieve more accurate forest resource inventory and assessment at landscape and regional scales. The review had three main objectives. The first objective was to describe remote sensing principles and technology development for forest research worldwide. The second objective was to present practical applications of remote sensing technologies used to characterize forest structure and health at the stand and individual-tree levels. The third objective was to present strategies for effective use of remote sensing technologies to improve management of forests worldwide.

2. Remote sensing technologies for forest research

The basic principle in using remote sensing is based on the selective nature of radiation absorption by vegetation canopies, resulting in unique spectral signatures that describe distinctive patterns of short-wave (visible and infrared) radiation reflectance. The reflectance spectrum of green vegetation is characterized by low reflectance in the red region (0.6 - 0.7 µm), associated with chlorophyll absorption, and strong near infrared (NIR) reflectance (0.7 -1.2 µm) related to internal leaf structure (Jensen, 2000; Roberts et al., 1997). Satellites may be either active or passive and are designed to capture reflectance from various regions of the electromagnetic spectrum as multispectral bands. While active satellite sensors transmit signals which are detected or emitted back at the instrument after hitting the earth surface, passive sensors do not transmit energy signals, but rather only detect reflected energy from earth in the visible and infrared regions. Available multispectral satellite imagery from passive sensors over the last 30 years and improved satellite imaging technologies over the last 10 years have increased the capabilities to describe spatial and temporal dynamics of vegetation characteristics at numerous scales. Multispectral imagery from medium resolution sensors, such as Landsat (30-m pixel resolution) (Curran et al., 1992, Baugh and Groeneveld, 2006; Xu, 2007) and Spot (5-m pixel resolution) (Soudani et al., 2006), have been used to assess vegetation conditions and phenological changes in forested areas at regional and landscape scales. Günlü et al. (2008) integrated the analysis of Landsat imagery with conventional forest inventory measurements and ecological and physiographic information to produce site quality index maps for various temperate forest species in Turkey. However, the spatial resolution of medium resolution satellites does not allow resolving forest stands and individual trees. Fine resolution satellites such as Ikonos, QuickBird, and GeoEye1 have increased pixel resolution down to less than one meter for panchromatic images and 2-4 meters for multispectral images capturing the blue, green, red and NIR spectral regions (Table 1). The analysis of this imagery has provided a way to study large areas by allowing visualization of entire landscapes and regions and identification of individual tree species. Due to high temporal frequency of flights over the same area (3 to 4 days), fine resolution satellites have facilitated assessments of forest structure, condition and health across multiple spatial and temporal scales. Imagery from these satellites has improved the identification and mapping of individual forest species across entire landscapes. While the high spatial resolution allows for delineation of single tree crowns, the multispectral bands allow for determination of variations of canopy greenness within forest stands (Guo et al., 2007). In particular, these satellites have been successfully applied for forest inventory in tropical environments and allowed for the mapping of tree crown sizes (Martinez Morales et al., 2008), tree density, species identification, and assessment of temporal changes in individual tree growth and mortality (Clark et al., 2004; Martinez Morales et al., 2011).

Satellite	Multispectral	Pancromatic
Ikonos	4	1
QuickBird	2.62	0.65
WorldView2	2	0.65
GeoEye1	2	0.5

Table 1. Pixel resolution in meters for common fine resolution satellites.

While high spatial resolution satellite sensors can be used to assess forest structural characteristics, they only collect data on a limited number of spectral bands (blue, green, red, and near-infrared). Hyperspectral remote sensing, or imaging spectroscopy, collects data on hundreds of bands from visible to infrared wavelengths (0.4 to 2.5 µm). Due to higher definition of unique spectral signatures among vegetation types, this kind of data has expanded the potential to identify forest species and assess canopy biochemical and physiological properties such as leaf pigments, carbon and nitrogen content at the species level (Asner et al., 2005; Clark et al., 2005; Pu et al., 2008; Féret and Asner, 2011). Imagery from Hyperion EO-1, a hyperspectral satellite which detects 220 spectral regions at 30-m pixel resolution (eo1.usgs.gov), has been used to map structural vegetation metrics and indices of forest productivity at regional scales (Pu and Gong, 2004; Asner et al., 2005). However, the spatial resolution of this satellite does not allow resolving forest stands and individual trees. The Airborne Visible and Infrared Imaging Spectrometer (AVIRIS) built by NASA (aviris.jpl.nasa.gov) provides 224 contiguous spectral bands with pixel resolution varying from 2 to 20-m depending on flight altitude. These data have improved remotely sensed predictions of forest health, biomass, species identity and variation through a better understanding of spectral responses of forest canopies at the species level (Roberts et al., 1997; Asner and Lobell, 2000). Asner et al., 2008 used AVIRIS data to analyze the reflectance properties of 37 distinct species (7 common native and 24 introduced tree species) in order to spectrally differentiate between native and alien trees in a montane forest in Hawaii. They found that the reflectance signatures of Hawaiian native trees were unique from those of introduced trees. Since the AVIRIS imaging system is costly and frequently unavailable, a number of companies such as Hughes, Lockheed and Surface Optics among others, have developed a variety of visible and infrared imaging spectrometers available in the market. Greg Asner's research team has pioneered the use of airborne hyperspectral sensors to extract detailed biochemical data on plant canopies in Hawaii's forests. Distinct structural or biochemical signatures have been used to map the distribution of native forest species and several tree and shrub invasive species (Asner et al., 2008a; Asner et al., 2008b).

Although passive satellite sensors offer routine and repeated assessments at scales down to 1 meter, this technology has difficulty in capturing reflectance beyond upper canopy layers and is better suited for mapping horizontal structure rather than vertical structure (Weishampel et al., 2000). Active remote sensing technologies offer great potential to spatially map a forest three-dimensional (3D) structure at various scales from landscape, stand and individual tree levels. Active satellite systems based on interferometric synthetic aperture radar (InSAR) can provide measures of horizontal and vertical structure of vegetation at regional scales (Treuhaft & Siqueira, 2000), but this technology does not provide the spatial resolution required in detailed forest studies. However, active airborne laser scanning sensors such as LIDAR (Light Detection and Ranging System) are providing improved capabilities for the estimation of forest canopy dimensions at the individual tree level (Weishampel et al., 2000; Hyde et al., 2005; Chen, 2006). Small foot-print LIDAR systems have provided 3D surveys of forest canopy and have resolved some of the challenges not met by existing techniques for measuring canopy structure (Hetzel et al., 2001; Tickle *et al.*, 2006; Chen et al., 2006). The isolation and extraction of tree structural information from LIDAR imagery has allowed more explicit ecological modeling through the estimation of individual-tree height, crown area, trunk height, biomass and leaf area (Henning, 2005; Chen et al., 2007, Chen, 2010). Chen et al., 2006 isolated trees from small-footprint airborne LIDAR data in deciduous oak woodland in California using a marker-controlled watershed segmentation method and a canopy height model derived from the LIDAR data. In the same site, Chen et al., 2007 proposed a new metric called canopy geometric volume derived from LIDAR data to estimate individual tree height, crown size, LAI, basal area and stem volume at 70 % accuracy. On Hawaii montane forests, Asner et al., 2009 derived canopy vertical profiles from LIDAR imagery in order to quantify 3-D forest structure and above ground biomass (AGB). They found that LIDAR measurements were strong predictors of AGB ($R^2 = 0.78$) across sites and species. Combining or fusing the highly detailed vertical measurements provided by LIDAR and the broad-scale mapping capabilities of passive optical sensors can provide dramatic increases in forest mapping and characterization. Wulder et al., 2004 used texture metrics from Landsat images to improve LIDAR estimates of canopy height. Hyde et al. 2006, combined forest structural information from LIDAR and QuickBird to improve estimates of canopy height and biomass. Asner et al. (2008a) combined airborne LIDAR and hyperspectral imagery to differentiate and map native and alien tree species in Hawaii montane forests, including understory plants like Kahili ginger (*Hedychium gardnerianum*) and strawberry guava. Therefore, airborne systems combining LIDAR with hyperspectral sensors have the highest potential for reliable estimations of individual-tree structure parameters such as canopy size, volume and leaf area.

However, airborne LIDAR imaging systems have disadvantages due to the high cost of flight time and a large number of flights for imaging entire landscapes. Resource Mapping Hawaii Inc (www.remaphawaii.com), developed a system for mapping detailed forest structural and morphological characteristics using ultra high resolution airborne multispectral imagery at 1.5 cm per pixel. The Nature Conservancy of Hawaii is employing such imaging system to map the distribution of Australian tree fern. Geo-referenced locations of individual trees can be obtained from this imagery and uploaded to a handheld GPS, allowing for more efficient eradication efforts (Ambagis et al., 2009). This imaging technology best complements to field inventories, providing detailed information of vegetation in areas that are remote, inaccessible, or rapidly changing.

3. Remote sensing applications in forest research

With the development of advanced image processing techniques, remote sensing technology has rapidly expanded to allow estimation of forest cover in heterogeneous landscapes and estimation of tree density, species identification and assessment of temporal changes in individual tree growth, health and mortality across entire landscapes (Carleer and Wolff, 2004; Carleer and Wolff, 2005; Clark et al., 2004; Chubey et al., 2006; Soudani et al., 2006). Martinez Morales et al., 2011 developed practical methodologies to analyze fine resolution satellite imagery using pixel-based image classification techniques for forest resource assessment. They fused GeoEye1 multispectral and panchromatic bands to conduct landscape-level assessments of koa (*Acacia koa*) forest health across an elevation range of 600–1,000 m asl in the island of Kauai. The goal of the study was to assess the spatial distribution of koa forest dieback patterns across a gradient of temperature and rainfall in order to determine the influence of these environmental factors on dieback patterns. The spectral bands were analyzed using a supervised classification technique to differentiate and classify pixels representing healthy and unhealthy koa stands and other land cover classes existing in the landscape. They classified healthy koa forest stands at 87 % accuracy from areas dominated by introduced tree species and differentiated healthy koa stands from those exhibiting dieback symptoms at 98 % accuracy. A landscape-scale map of healthy koa forest and dieback distribution (Fig. 1) demonstrated larger presence of unhealthy koa stands in areas with lower elevation and precipitation and higher temperature.

While pixel-based image classification involves assigning individual pixels to a vegetation class according to unique reflectance patterns across the spectral bands (spectral signature), object-based methods also include class shape and texture as additional parameters (Jensen 2000). Object-based analysis and image segmentation techniques have been increasingly applied in fine resolution multispectral imagery as an alternative to overcome the difficulties of conventional procedures of spectral image analysis for various forestry applications (Chubey et al., 2006; Herold et al., 2003; Hu et al., 2005). Instead of analyzing a single pixel spectral response, a wide range of spectral values in a group of pixels representing a forest stand is interpreted as a homogeneous object which can be further segmented into even more homogeneous subgroups. Pixel grouping can be controlled by the user through the definition of parameters such as size, homogeneity and shape in order to reduce heterogeneity in the resulting objects (Chubey et al., 2006). Wang et al. (2004) utilized a combination of spectral classification techniques and segmentation methods for tree-top detection and tree classification in a forested area in British Columbia, Canada. They calculated the first principal component from a set of spectral images from the Compact Airborne Spectrographic Imager and applied a Laplacian edge detection method for tree-crown delimitation. They further applied a segmentation technique and tree-top markers in order to differentiate final individual tree crowns at 85% accuracy. In a Belgian forest, Kayitakire et al. (2006) found highly significant relationships between image texture metrics extracted from the IKONOS panchromatic band with several forest productivity indices including tree density, height, crown size and basal area. Since the IKONOS NIR band contains important vegetation information, Herold et al. (2003) used this band to derive various texture and landscape metrics that classified forests at 78 % accuracy along a California coast region. Martinez Morales et al. (2008) analyzed fused Ikonos multispectral and panchromatic bands with spectral and object-based classification methods, to estimate forest cover at 86% accuracy in a Hawaiian dry forest ecosystem. Their comparison between spectral and object-based methods demonstrated superior performance of object-based classification algorithms in delineating tree canopy cover in a highly heterogeneous dry forest environment. The object-based approach allowed for differentiation of tree crowns, tree shades, and their transitional areas from other objects of similar size, shape, or spectral range such as green grass and lava outcrops (Fig. 2). A particular important result was the clear delimitation of individual tree crown areas that can be useful for forest inventory even on high spatial heterogeneity of vegetation conditions.

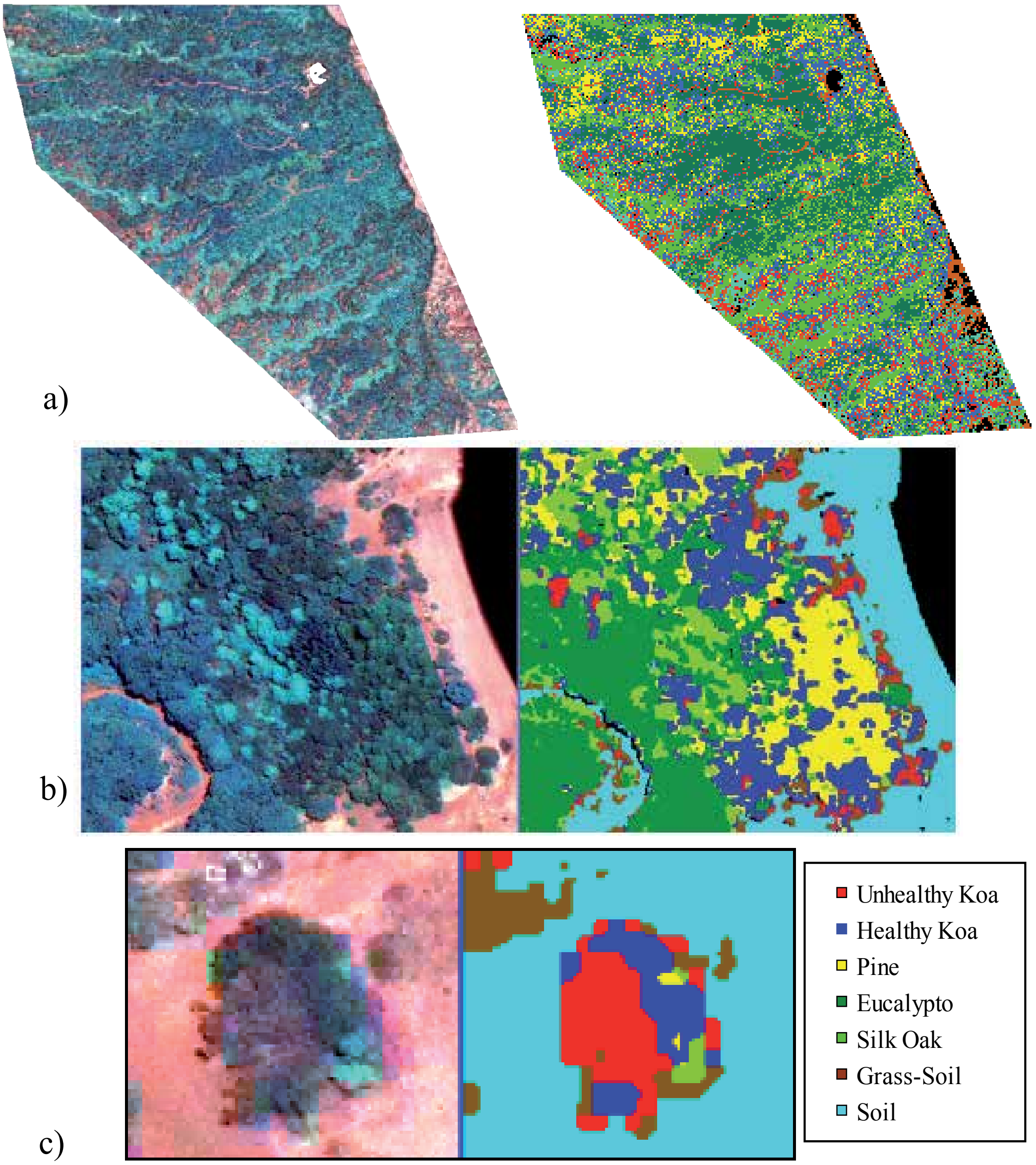

Fig. 1. A montane forest ecosystem from the Island of Kauai as viewed by the GeoEye1 satellite. a) Natural color composite at 0.5-m pixel resolution (left) and its corresponding classification (right); b) Image close-up depicting clear differentiation among tree species; c) Detailed close-up showing classification of diseased from healthy forest stands (Martinez Morales et al., 2011).

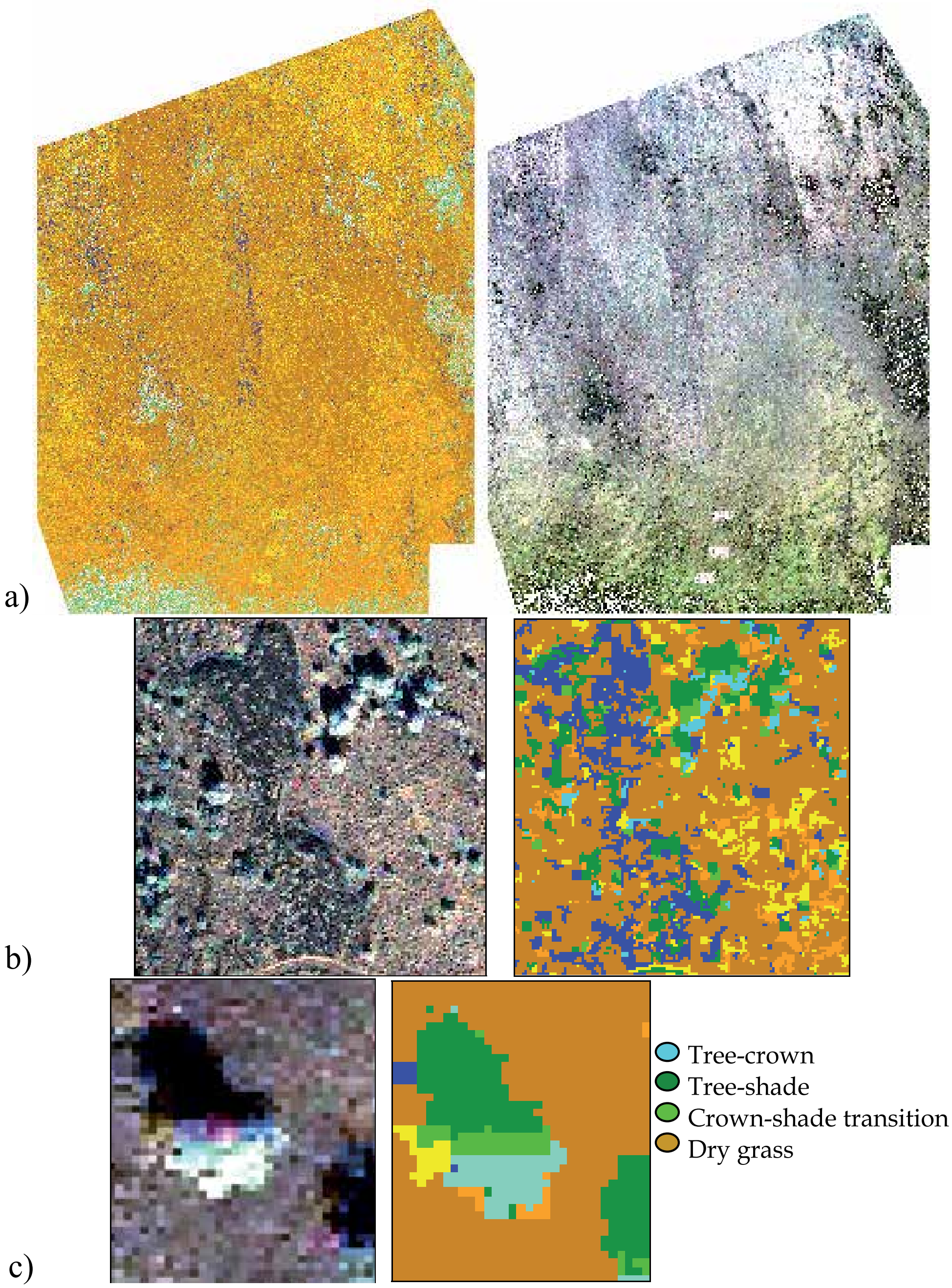

Fig. 2. A dry forest ecosystem from the north Kona region in the Island of Hawaii as viewed by the Ikonos-2 satellite. a) Natural color composite at 1-m pixel resolution (left) and its corresponding classification (right); b) Image close-up depicting differentiation among objects with similar reflectance (tree crowns from shrubs and grasses and tree shades from lava outcrops); c) Detailed close-up showing clear delineation of individual tree crowns and tree shades (Martinez Morales et al., 2008).

Since the reflectance of green vegetation is low in the red region due to chlorophyll absorption, and strong in the NIR due to internal leaf structure, a number of vegetation indices (VIs) (Table 2) have been calculated using these two regions of the reflectance spectrum for assessments of vegetation biomass, chlorophyll abundance and light absorption (Baugh and Groeneveld 2006), phenological changes in forested areas (Loveland et al., 2005) and for detailed identification of forest tree species (Soudani et al. 2006, Martinez Morales et al., 2012). Roberts et al. (1997) successfully used the Normalized Difference Vegetation Index (NDVI) from AVIRIS hyperspectral imagery to estimate LAI and canopy cover at moderate scales in a California forest. Carleer and Wolff (2004) derived NDVI, principal components (PCs) and texture metrics from Ikonos satellite data and used them in the identification of tree species in a forested area in Belgium. Seven tree species, including two different ages, were successfully identified with 86% overall classification accuracy. At various forest stands of tenths of hectares, Soudani et al. (2006) used five different VIs, such

Vegetation index	Formulae Source
1. Simple Ratio	SR = NIR / R (Jordan 1969)
2. Normalized Difference Vegetation Index	NDVI = NIR - R / NIR + R (Rouse et al. 1973)
3. Soil Adjusted Vegetation Index	SAVI = (1 + L) * (NIR - R) / (NIR + R + L) L = 0.5 (canopy background adjustment factor) (Huete 1988)
4. Atmospherically Resistant Vegetation Index	ARVI = (NIR - R) / (NIR + Q_{RB}), Q_{RB} = R - γ (B - R), γ = 1 (calibration factor) (Kaufman and Tanré 1992)
5. Modified Soil Adjusted Vegetation Index	MSAVI = (1 + L) * (NIR - R) / (NIR + R + L) L = 1 - 2a * NDVI * WDVI (Qi et al. 1994)
6. Enhanced Vegetation Index	EVI = G * (NIR - R) / (NIR + C1*R - C2*B + L) with G = 2.5, C1 = 6, C2 = 7.5, L = 1 (Liu and Huete 1995)
7. Modified Simple Ratio	MR = (NIR / R - 1) / ((NIR / R)$^{1/2}$+1) (Chen 1996)

Table 2. Spectral vegetation indices. R, NIR and B are red, near-infrared, and blue bands, respectively. For Modified Soil Adjusted Vegetation Index, WDVI = NIR - aR (a = 0.08, slope of the soil line). For Enhanced Vegetation Index, G, C1, C2 and L are coefficients to correct for aerosol scattering, absorption, and background brightness.

as NDVI, Soil Adjusted Vegetation Index (SAVI), Atmospherically Resistant Vegetation Index (ARVI), Enhanced Vegetation Index (EVI) and Simple Ratio (SR) calculated using data from the IKONOS and SPOT satellites to accurately classify various forest stands in France. They found that ARVI, NDVI and SR had similar and better predictions of LAI compared to SAVI and EVI. Kayitakire et al. (2006), estimated forest productivity at regional and landscape scales by relating VIs with LAI. This relationship has been used as a strong diagnostic tool to make silvicultural management recommendations (Flores 2006). Flores (2006) developed empirical models that were not affected by site, stand structure or time of the year to estimate LAI in broad areas of southern loblolly pine stands in USA using NDVI and SR from Landsat data and airborne hyperspectral data. Asner et al., 2005 found that the canopy water content index (NDWI) calculated from EO-1 data was superior than NDVI in capturing climate driven variations in canopy structure of a Hawaiian forest. In a Hawaiian koa forest, Martinez Morales et al., 2012 used Ikonos multispectral imagery to calculate six VIs (ARVI, EVI, NDVI, SAVI, SR, Modified Soil Adjusted Vegetation Index (MSAVI) and Modified Simple Ratio (MSR)) as a measure of vegetation greenness, and related those to biophysical measures of forest productivity such as tree height, basal area, leaf area index and foliar nutrients for spatial prediction at the landscape scale. This procedure allowed a clear differentiation of koa stands from areas dominated by grasses, shrubs, and bare lava. Vegetation indices allowed differentiation of three koa forest stand classes at upper, intermediate and lower elevations. In agreement with the image classification, analysis of variance of tree height and leaf phosphorus suggested there were also three significantly different groups of koa stands at those elevations.

4. Conclusions

Fine spatial resolution remote sensing allows not only visual interpretations of forest species but also automated classification of forest stands. Since the electromagnetic radiation captured by satellites has interacted with forest canopies through chemical absorption or physical scattering, it contains information about the chemical and physical properties of each vegetation type in the landscape. Therefore, the analysis of spectral data allows distinguishing not only forests species but also forest structural variations based on their unique reflection properties across the electromagnetic spectrum. Based on canopy greenness, analysis of these imagery can also be used to differentiate diseased from healthy forest stands. Such applications should improve forest inventory and collection of forest attributes for productivity assessments among forest scientists, decision-makers, and the general public involved in the ecological restoration, conservation and silviculture of important tree species worldwide.

Although field measurements for forest resource inventory and assessment are more accurate than satellite measurements, satellites collect data across broad areas, sample the full range of variation in forest metrics, capture broad trends and dynamic change in forest stands and help expand our understanding of forests beyond the plot level. As such, satellite data allow for integration across ground measurements, extending them across landscapes and regions and allowing detection of spatial and temporal changes in forests that we could not measure using conventional survey methods. Therefore, the analysis of satellite imagery has become a practical necessity to measure and manage forests at landscape and regional scales. The greatest strengths of satellite imagery are their monthly to daily frequency and view of entire regions, which could improve monitoring and verification of forest management for sustainable harvest and carbon sequestration. Aerial photos have proven useful, but the technology is costly and limited to small areas. The advent of high spatial resolution satellites such as Ikonos, Quickbird and GeoEye1 has changed the cost and availability of high-resolution imagery. If available for an area, archived imagery from these satellites can be acquired for one third of the original cost. With current technology, fine resolution remote sensing is suited to differentiate among forest species with classification accuracy usually decreasing with an increasing number of forest classes. It is also difficult to distinguish forests of different ages or composition, and primary forests from tree plantations and older secondary forests. However, remote sensing is rapidly developing by technological advancements in data gathering and processing. The GeoEye2 satellite at 0.25 m pixel resolution will be launched in 2012 and it is expected to revolutionize the management of forest ecosystems worldwide since it will allow more accurate assessment of the small-scale forest variability across environmental gradients. Improved characterizations and delimitations of forest species, stands types and growth stages along environmental gradients will allow development of more efficient silvicultural management practices according to site-specific ecological requirements.

The integrated analysis of environmental data with remote sensing imagery in a Geographical Information System (GIS) framework, allows inferences on how environmental factors influence forest ecosystem functioning. The increasing integration of GIS and remote sensing has facilitated display and communication of satellite imagery between scientists and the general public, as witnessed by the explosive growth in mapping using tools like Google Earth. Overall, remote sensing technologies are proving to be powerful research and management tools for the inventory and assessment of forests around the world. We are now at the point where both satellite and airborne sensing systems can provide reliable and detailed information at the individual-tree level. These technologies will become increasingly important for assessment and management of forests worldwide as we continue to face the challenges of land use pressures, invasive species, and climate change.

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Part 2

Forest Function – Energy, Mass and Biological Fluxes

8

Ecohydrology and Biogeochemistry in a Temperate Forest Catchment

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South Korea

1. Introduction

The assimilated carbon stored in terrestrial ecosystems is exported with water movement in both organic and inorganic forms, which are defined as particulate organic carbon (POC), dissolved organic carbon (DOC), and dissolved inorganic carbon (DIC). The transport of terrestrial carbon into streams, rivers and eventually the oceans is an important link in the global carbon cycle (Ludwig et al., 1996; Warnken and Santschi, 2004). The Committee on Flux of Carbon to the Ocean estimated that of the organic carbon entering rivers globally, around 50% is transported to the ocean, 25% is oxidized within the system and 25% stored as POC in the system as sediment (Hope et al. 1994). As compared to the terrestrial carbon sinks (1.9 Gt-C/yr; Prentice et al., 2001), the organic carbon transport from terrestrial ecosystems to oceans is 0.4–0.9 Gt-C/yr (Meybeck, 1982; Hope et al., 1994; Prentice et al., 2001), representing a substantial component of the ecosystem carbon balance.

The water and carbon cycles in forest catchments are important elements for understanding the impact of global environmental changes on terrestrial ecosystems. Various theories have been suggested to better understand water discharge (Horton, 1933; Betson, 1964; Kirkby, 1978; Anderson and Burt, 1991; Kim et al., 2003) and its effect on carbon efflux processes from forest catchments (McGlynn and McDonnell, 2003; Kawasaki et al., 2005; Schulze, 2006; Kim et al., 2007b; Kim et al., 2010). Most of the results indicated that the hydrological flowpaths are important in carbon dynamics within the forest catchments.

Data from major results show export of organic carbon to be highly correlated with annual river discharge and watershed size (Table 1; Fig. 1). Hydrological processes strongly affect organic carbon discharge from terrestrial ecosystems, especially in monsoon climate zone of East Asia, and 60-80% of annual organic carbon export to the ocean during summer rainy season (Tao, 1998; Liu et al., 2003; Kawasaki et al., 2005; Zhang et al., 2009; Kim et al., 2010).

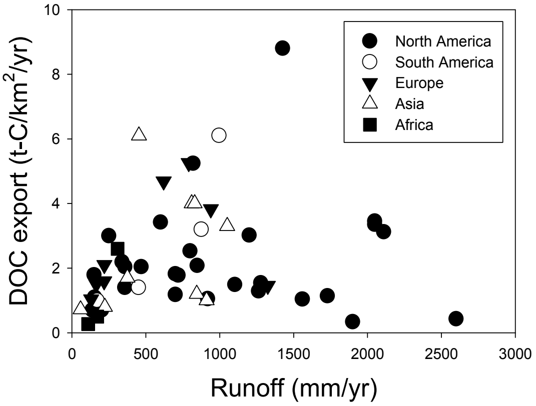

Fig. 1. Annual DOC export by rivers from watersheds (modified from Ittekkot and Laane (1991), Hope et al. (1994), and Table 1)

Ecosystem type, location	Annual precipitation (mm)	Annual runoff (mm)	Watershed size (km^2)	Loss of organic carbon DOC (t-C/ha/yr)	Loss of organic carbon POC (t-C/ha/yr)	Reference
Huanghe, Semi-arid area, Central China	-	59	745,000	0.007	-	Gan et al. (1983)
Yichun, Humid temperate area, North-eastern China	500-650	-	2500	0.03	-	Tao (1998)
Luodingjiang River, Subtropical mountainous, Southern China	1534	844	3164	0.012	0.011	Zhang et al. (2009)
Guandaushi, Subtropical forest, Taiwan	2300-2700	-	0.47	0.025	-	Liu et al. (2003)
Tomakomai, Cool temperate mixed forest, Northern Japan	1200	-	9.4	0.0052	0.0076	Shibata et al. (2005)
Kiryu, Temperate conifer, Central Japan	1645	911	0.006	0.01	-	Kawasaki et al. (2005)
Gwangneung, Temperate deciduous, Central Korea	1332	809	0.22	0.04	0.05	Kim et al. (2010)
Han River, Temperate area, Central Korea	1244	-	26,018	0.04	0.02	Kim et al. (2007a)

Table 1. Export of organic carbon East Asian watersheds

Forests are the major terrestrial biome, in which soils and vegetation are the primary sources of DOC and POC in streamwater. Within the forest soil profile, concentrations of DOC typically are highest in the interstitial waters of the organic-rich upper soil horizons (McDowell and Likens, 1988; Richter et al., 1994; Dosskey and Bertsch, 1997). Both column experiments and field observations have indicated that significant transport of DOC occurs by preferential flow, given that the state of adsorption equilibrium cannot be reached, owing to the reduction of the contact time between DOC and the soil surface (Jardine et al., 1989; Hagedorn et al., 1999). Understanding the flow paths of DOC discharge from forested catchments to streams is important because DOC provides a source of energy to microorganisms in water systems (Stewart and Wetzel, 1982) and carbon fixation in the soil (Neff and Asner 2001; Kawasaki et al., 2005).

Since the 1970s 2.3 million hectares of land have been planted with coniferous species such as *Pinus Koraiensis*, *Abies holophylla* and *Larix leptolepis* in South Korea. Because coniferous forests lose and consume water resources much more than deciduous forests due to higher leaf area index (LAI) and year-round transpiration, theses planted coniferous forests may deteriorate the physical properties of the topsoil owing to the water repellence of the soil surface and decrease the availability of water resources by high evapotranspiration rates. To conserve soil and water resources, densely planted coniferous forests must be managed using silvicultural techniques (e.g. pruning, thinning) that could influence water quantity and quality. In South Korea, various studies have shown that forest management practices in coniferous forests decreased the amount of interception loss and increased discharges during the dry season. Clear cutting resulted in catastrophic augmentation of runoff and soil loss. The water quality of stream headwaters improved after thinning and pruning because these techniques tended to ameliorate soil physical properties and increase soil ion exchange capacity.

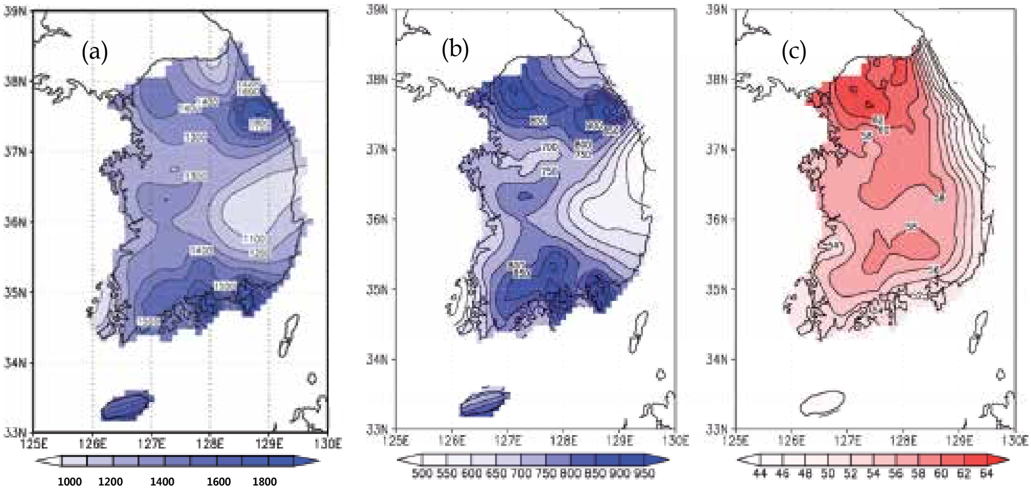

Fig. 2. Accumulated climatological precipitation (mm) at 60 stations for (a) annual total precipitation, (b) summer (from June to August) in South Korea. (c) Percentage (%) of accumulated climatological precipitation with respect to annual total precipitation summer. (Seo et al., 2011)

Hydrological circumstances in South Korea are unfavourable to manage water resources. Temporal and spatial variations of rainfall are very large (Fig. 2). Annual rainfall ranges from 754 to 1,683 mm. In South Korea, more than 50% of the annual precipitation falls in the summer monsoon season (Fig. 2(b, c)), which quickly discharges to the ocean due to the steep slopes and short river lengths (<500 km). Therefore, the water regime in the catchment undergoes drastic changes with recurring wet and dry seasons, which makes it difficult to interpret and predict hydrological processes and subsequently their effect on nutrients cycling (Kim et al., 2009).

The amount of water storage capacity in a forest stand increases with the forest aging, when a forest stand grows, the amount of litter falls and roots also increases. The mineral soils and humus materials tend to aggregate into their structure. The aggregation may change the distribution of pore sizes and often increase the total porosity of soil. Forests have been called 'Green Dam' or 'Reservoir' because of its function of controlling the flood and drought through a litter layer and topsoil like a sponge filter. Net infiltration rate of a well-developed forest soil has been estimated 76 mm/hr in comparison with 8mm/hr of a bare land (Brooks et. al. 1991). Generally, infiltration capacity of soil in a deciduous forest is higher than that in a coniferous forest because the litter fall of the former is easily decomposed and incorporated with mineral particles compared to that of the latter. Most of stream water in South Korea comes from mountain headwaters as mountains occupy 65% of the total area. Stream in forested headwaters yields clean water. Forest soils hold the water like sponge, which is 3.3 times more than the soil in a bare land. Water holding capacity of forest soil in Korea is estimated about 18 billion tons, as shown in Table 2 (Ministry of Science and Technology, 1992).

Bed rock	Igneous	Metanorphic	Basalt	Sedimentary		Lime	Total
				I	II		
Maximum storage	A 34.3	40.1	32.4	36.1	33.9	39.8	
capacity(%)	B 39.5	44.4	35.1	39.0	35.5	41.1	
Total storage	A 15.2	20.0	5.0	4.0	1.5	2.1	
(0.1 billion tons)	B 36.5	60.3	8.5	14.2	4.6	7.9	
Sub-total	51.7	80.3	13.5	18.2	6.1	10.0	179.8

Table 2. Water holding capacity of forest soils depending on bed rock in South Korea (Ministry of Science and Technology, 1992)

Despite decades of dedicated scientific efforts on these fundamental questions, it is still difficult to find a robust interpretation even for some basic hydrological processes such as discharge and runoff. The up to date results showed that the geophysical and meteorological conditions greatly affect the hydrological processes (Hooper et al., 1990; Elsenber et al., 1995; Katsuyama et al., 2001; McGlynn and McDonnell, 2003; Kim et al., 2010).

In this chapter, we have implemented a comprehensive ecohydrological measurement system at the temperate forest catchment in South Korea. Most importantly, high quality long-term data of hydrological and meteorological conditions have been collected, which may be also important in monitoring global environmental changes and their effects. The study was also designed based on a nested watershed concept (smaller catchments are nested in successively larger catchments) to investigate how catchment processes change as scale varies. In this chapter, we introduce the concepts and techniques that were implemented to investigate the movement of water and carbon in a forest catchment. We also briefly discuss preliminary results and their implications for the interactions between hydrological and biogeochemical processes in a temperate forest catchment.

2. Hydrological cycle of forested catchments in South Korea

2.1 Interception loss and evapotranspiration

The differences in the amount and process of interception loss and evapotranspiration depend on the factors of the forest structure and local climate. The forest structure includes the forest type, age and density. Generally, coniferous forests intercept rain and snowfall more than deciduous because the former has higher LAI and longer leaf-period than the latter.

The first research on interception loss by tree canopy and stem in Korea had conducted in 1935 for determining the total and net precipitation at the forest stand in Korea Forest Research Institute (Kim and Jo, 1937). The experiment was conducted during 23 months on the natural 50-year-old red pine (*Pinus densiflora*) with the tree height of 12 m and DBH of 18 cm. It showed that the annual total and net rainfall were 1,194.2 mm and 1,066.3 mm, respectively. The percentage of interception loss from the total rainfall varied from less than 10% in the season to more than 26% in the growing dormant season.

To clarify the effects of forest types on interception, three types of forest were chosen in Gwangnung experiment station during the period of 1982 to 1988, namely natural matured-deciduous, planted young-coniferous and rehabilitated mixed forest. The results of the research are shown in Table 3 (Lee et al. 1989). Among the three forest types, the planted young-coniferous forest showed the most interception loss of 32.6%, compared to 29.1% in natural matured-deciduous and 18.5% in rehabilitated mixed forest. Even though the naturally matured deciduous has the largest forest structure of 80 years old, its amount of interception loss resulted in less percentage compared with the planted young-coniferous for the cause mentioned above.

Forest type	Precipitation (mm)	Intensity (mm/hr)	Throughfall (mm)	Steamflow (mm)	Interception (mm)	Interception (%)
Mixed	1733.2	6.7	1312.6 (75.8)	99.2 (5.7)	321.4	18.5
Coniferous	1477.3	6.0	945.2 (64.0)	50.4 (3.4)	481.5	32.6
Deciduous	1172.4	6.2	758.7 (64.7)	72.2 (6.2)	341.5	29.1

( ) means % for precipitation

Table 3. The amount of interception loss by three forest types in South Korea

In other results, the young coniferous forest of 26-year-old *Pinus rigitaeda* and deciduous forest of 16-year-old *Quercus mongolica* intercepted 17.4 and 13.9% of the total rainfall, respectively, during the period of July 1986 to September 1987 in Seoul National University's Gwanak arboretum (Kim and Woo 1988a, b).

It is difficult to measure the exact amount of interception loss due to the large variations of forests and climate factors. Several forest hydrologists have tried to predict the amount by using an interception model. There are three kinds of interception model for the estimation of the processes and amount of interception; the dynamic, analytical and regression-methods. The dynamic-interception model was developed using the forest stand structure and Penman-Monteith model to predict the amount of evaporation under saturation condition (Kim and Woo 1997).

Another loss component of hydrological cycle in forested catchment is evapotanspiration from tree canopy during a period of no rainfall. The amount of evapotranspiration can be estimated by using the water budget method in a short term or a calculating method like penman or Thornthwaite method. The amount of evapotanspiration estimated by Thornthwaite method in three forest types is shown in Table 4 (Kim 1987).

(unit: ton/day/ha)

Month Type	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Yangju[a]	0.0	0.0	2.7	15.7	31.0	38.4	48.5	47.7	31.2	15.2	3.6	0.0
Mixed[b]	3.5	4.1	8.7	11.5	16.3	18.4	25.7	26.1	20.6	10.5	10.7	7.3
Gwangnung[a]	0.0	0.0	3.2	17.8	31.4	40.3	50.6	49.9	32.4	17.0	4.0	0.2
Coniferous[b]	6.3	6.6	15.7	14.0	33.3	34.0	44.4	56.4	40.3	17.8	12.0	8.2
Deciduous[b]	6.0	4.2	11.5	10.8	20.9	35.7	17.9	29.3	24.6	17.8	10.7	8.2

[a] means the amount of evaportranspiration by Thornthwaite method.

[b] means the amount of evaportranspiration by short-term water budget method.

Table 4. Monthly evaportranspiration determined by means of Thornthwaite and short-term water budget methods.

2.2 Discharge and soil loss variations depending on land cover

In the 1960s and 70s, the main theme on forest hydrology was to evaluate soil and water conservation at the different land cover types. Because in those periods, most of the lands in South Korea were completely devastated all over the country, development of techniques on the erosion control was urgent, especially in the fields (Fig. 3).

Lee et al. (1967) clarified that land cover type influence discharge in the small plot. They concluded that the coniferous plot produces the least discharge (26%) while bare land produces most (76%). They also found that the discharge in the bare land plot started at the rainfall of 10 mm and increased radically at the rainfall more than 80 mm, whereas in the coniferous plot started at the rainfall of 30 mm.

Kim (1987) estimated effects of floods, direct flow reduction and long-term yields on forest by utilizing the measured rainfall-runoff data from the three above-mentioned experimental catchments. He found that the flood peak discharge of the young coniferous and mature deciduous stands were 49% and 36% of the devastated-mixed stand respectively. Also, the direct flow dropped to 53% in the young coniferous stand and to 55% in the mature deciduous stand, compared to that of the devastated-mixed catchment.

Lee et al. (1989) analyzed the runoff rate and soil at the the natural deciduous, the planted coniferous and the rehabilitated mixed forests, using the data from 1980 to 1988. The runoff rates of the three forest types in an order above were 61.9%, 48.5% and 71.3%, respectively. They concluded that the natural deciduous forest mitigated the peak of flow during the rainy season while it discharged more of low-flow during the dry season, in comparison with the rehabilitated mixed forest. The amount of soil loss during the rainy season was the highest in the rehabilitated mixed forest (2.2 ton/ha/yr) and the least in the deciduous one (0.7 ton/ha/yr).

Fig. 3. Before and after the construction of a hillside planting work in South Korea

Several techniques for analyzing the discharge components include surface runoff, interflow and groundwater, for different forest types in a long-term. The recession coefficient represents the rate of runoff that is released from a soil and streamside. If the recession coefficient of an independent event in the hydrograph changes statistically with the lapse of time, the hydrological characteristics of the forested catchment would be changed. Korea Forest Research Institute (1998) studied the hydrological variation of discharge, soil loss and recession coefficient in three small, forested catchments, using a long-term hydrological data from 1983 to 1992. This study included the naturally matured deciduous, planted coniferous and erosion-controlled mixed forest. The amount of discharge and soil loss varied with the rainfall and forest type. Fig. 4 (up left) shows the variation of the recession coefficient of surface runoff ($\alpha1$) for 10 years. $\alpha1$ gradually decreases in the coniferous forest while it does not show the tendency in the others. This may be caused by the change of the forest structure in the coniferous forest after the planting. The amount of the initial loss by the interception and transpiration has been greatly increased since 1976 as the coniferous trees grow. However, the forest structures in others have not much changed since 1983.

The recession coefficient of interflow ($\alpha2$) decreased in the coniferous and mixed forests with time Fig. 4 (up right). This can be interpreted by an increase in the soil storage capacity after the planting and erosion control work. As the amount of evapotranspiration increases, the storage opportunity of rainfall in the soil improves. Increment of the storage capacity may result in delaying the releasing time of interflow from the soil.

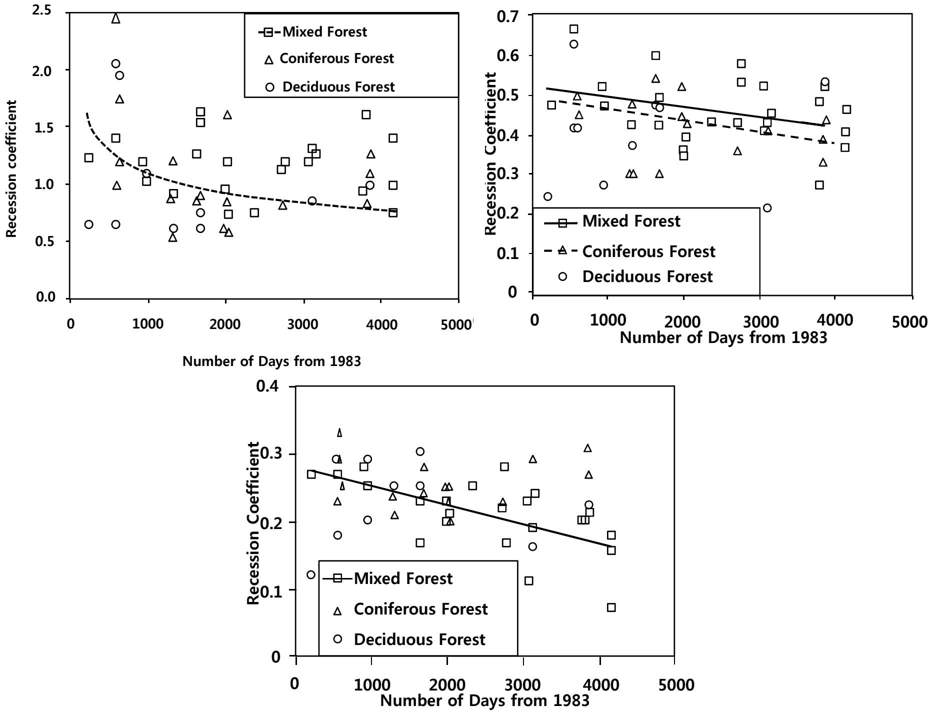

Fig. 4. Variation of the recession coefficient of surface runoff (up left), interflow (up right), and groundwater (down) for 10 years

In the case of the recession coefficient of groundwater (α3), only mixed forest showed a gradual reduction for 10 years (Fig. 4. down). The mixed forest has been a devastated land until erosion control work had finished in 1974. After the work, the soil layer rapidly formed and the soil's physical properties improved.

2.3 Residence time of water in a forest catchment

Various radioactive tracers have provided valuable information regarding hydrological processes, such as mean residence time of water, flowpaths during storm events, groundwater movement, and biogeochemical reactions occurring along the flowpaths (Michel and Naftz, 1995; Shanley et al., 1998; Sueker et al., 1999). For example, ^{3}H and ^{14}C have been widely used for determination of time scale of hydrological processes (Matsutani et al., 1993). However, these tracers are inadequate for studying hydrological processes in small and headwater catchments with expected time scales of a year or less because of their long half lives (decadesto thousands of years). In this study, we will introduce a short-lived cosmogenic radioactive isotope of ^{35}S (half life = 87 days) for measuring the mean residence time of water in the Gwangneung catchment.

The measured activity of ^{35}S in water can be expressed as an equation:

$$C = C_o e^{-\lambda t} \tag{1}$$

where C_o is the initial ^{35}S activity, λ is the decay constant (0.0079655), t is the number of days from the start of decay, and C is the measured ^{35}S activity. The ^{35}S activity in water provided information of the residence time of atmospherically deposited sulfate. Biogeochemical reactions such as adsorption/desorption in soil and groundwater are also important in affecting the calculated residence time of water in a forested catchment. Assuming a conservative response of sulfate in streamwater, the mean residence time of water was < 40 days during the summer monsoon period in the natural deciduous forest catchment. However, the mean residence time of water increased to around 100 days in the dry season with increasing contribution of the base flow to the stream water (Fig. 5). These results demonstrate that ^{35}S is useful in estimating the age of water exiting a small catchment where the time scales of hydrologic processes are on the order of 1 year or less.

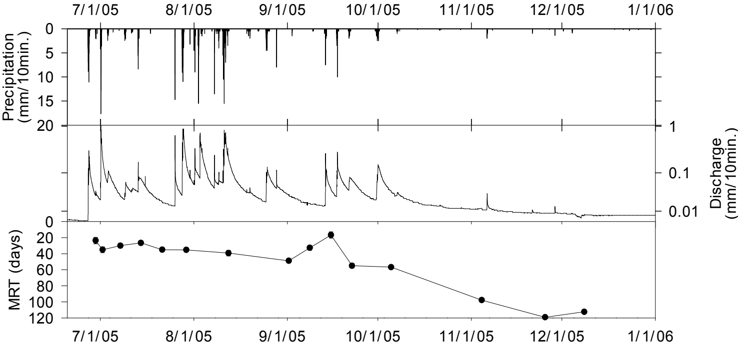

Fig. 5. Temporal variation in mean residence time (MRT) calculated from ^{35}S based method along with the precipitation and stream discharge (Kim et al., 2009)

From this MRT estimate, the existence of substantial, long-term subsurface water storage is not supported in the studied catchment. The assumed rapid turnover of water in the catchment indicates that the hydrological conditions will respond to the change in precipitation directly and immediately. Therefore, surplus (flooding) and shortage (drought) of water supply may alternate at a relatively short time scale (even within a year) depending on the seasonal distribution of precipitation. A secure water resource planning in catchments of this type will require a reliable prediction and efficient management of precipitation and surface water bodies (Kim et al., 2009).

2.4 Flow paths of water during storm events

The identification of flow paths in forested catchments has been elusive because of difficulties in measuring subsurface flow. Forested catchments are spatially complex and subsurface flow is invisible. Hence, one can only infer the movement and mixing of water from the natural tracer elements that the water carries (Pinder and Jones, 1969). Using various tracers, the end-member mixing analysis (EMMA) has been used to elucidate flow paths and hydrological processes in several catchments (e.g. Hooper et al., 1990; Christophersen et al., 1990; Elsenbeer et al., 1995; Katsuyama et al., 2001). Numerous conceptual models have adopted the flow path dynamics proposed by Anderson et al. (1997), i.e., both pre-event soil water and bedrock groundwater contribute to the formation of a saturated zone in the area adjacent to the stream (e.g., McGlynn et al., 1999; Bowden et al., 2001; Uchida et al., 2002).

The EMMA can be applied for individual storm events to quantitatively evaluate the contribution of each solutions component. The source waters are called 'end members'. The tracer concentrations of end members are more extreme than stream water since streamwater is a mixture of these sources (Fig. 6). In order to apply EMMA, (1) tracers should be conservative, (2) sources should be significantly different in tracer concentrations, (3) unmeasured sources must have same concentration with known sources or don't contribute significantly, and (4) the sources should maintain a constant concentration. Typical source waters are those from organic rich soil horizon, hillslope groundwater, valley bottom groundwater, throughfall, and precipitation.

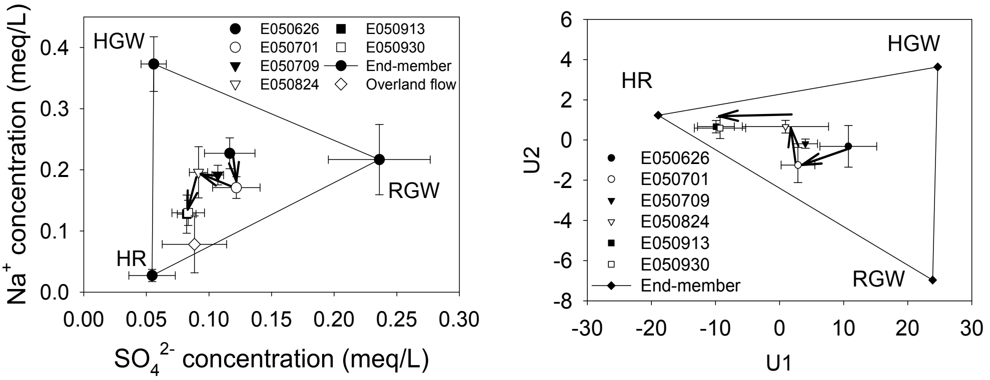

Fig. 6. Three-component mixing diagram for each storm event (left) and mixing diagram showing stream water evolution and end-member composition in U space during six storm events (right)

The hydrological characteristics of the six storm events observed during the summer of 2005 are summarized in Table 5. The maxima of precipitation intensity and discharge intensity were observed on 1 July 2005, which were 17.7 mm/10min. and 1.0 mm/10min., respectively. Stream discharge as a proportion of total precipitation ranged from 15 to 60% with an average of 30%. The maximum discharge rate also was observed in E050701, but associated with 5 days' antecedent precipitation.

The end-member mixing analysis (EMMA) with principal components analysis (PCA) was applied to each storm event to evaluate quantitatively the contribution of each water component (Christophersen and Hooper, 1992; Burns et al., 2001). Three-component mixing diagrams are shown in Fig. 6. Stormflow in E050626 lay near the groundwater end-member, and moved to soil water in E050701. Stormflow were also closer to that of groundwater through E050709 and E050824. After moving near groundwater, stormflow were closer to that of throughfall in E050913 and E050930. Stormflow solutes in E050913 and E050930 were not significantly different from overland flow.

In E050913 and E050930, the values of water-filled porosity in the surface layer (0–0.1 m) was about 5% higher than the maximum observed during the previous storm events. This higher water-filled porosity (as compared to prior storm events) led to a low water infiltration rate and an increase in the contribution of surface discharge. Previous studies suggested that a maintained precipitation expands the saturation zone and increases macropore flows in the forested catchment (e.g., McDonnell, 1990). Such macropore flows deliver new water in which dissolved ion concentrations are low because of the short contact time with soil and bedrock (Burns et al., 1998). The calculated mean residence time of water based on the ^{35}S analysis varied with changing water regime in the study area, ranging from 20 to 40 days during the summer monsoon period (Kim et al., 2009). Especially, for the stream water sample taken on 15 September when the surface runoff increased due to the storm event, the mean residence time of water also decreased abruptly (Kim et al., 2009; Fig. 5).

	E050626	E050701	E050709	E050824	E050913	E050930
Observed period	26–28, Jun.	1–3, Jul.	9–10, Jul.	24–26, Aug.	13–15, Sep.	30, Sep.–2, Oct.
Total precipitation (mm)	160.5	104.0	40.5	83.5	85.5	87.0
Max. precipitation intensity (mm/10min)	11.1	17.7	2.5	4.5	7.5	2.5
Total discharge (mm)	23.6	61.5	11.5	22.8	18.1	29.1
Max. discharge intensity (mm/10min)	0.32	1.05	0.06	0.14	0.28	0.16
Total discharge / Total precipitation (%)	15	60	28	27	21	33
Antecedent precipitation (5 days)	0.0	161.9	1.3	1.5	7.0	1.0
Antecedent precipitation (10 days)	1.3	161.9	154.3	19.5	7.0	43.5

Table 5. Hydrological characteristic of storm events in 2005

3. Dynamics of water and dissolved materials in forest soils

The dynamics of water in the soil layer are important for the understanding of water storage and dissolved material fluxes in a forest catchment. In the field measurement, an intensive monitoring is useful using a precise multiplex Time Domain Reflectometry system to capture and characterize variation patterns of soil moisture on a steep hillslope. Here, we introduce the methods for estimating the water and dissolved material flux in soils with tensiometer and water table fluctuations.

3.1 Estimation of soil water and dissolved material flux using a tensiometer

Tensiometer consists of a pressure transducer which measures the pressure (when saturated) or tension (when unsaturated) that the soil moisture exerts on a column of water, a porous cup which is in contact with the soil water at the measurement level, and a water body with a PVC pipe. According to Kim (2003), the one-dimensional, vertical water flow equation for unsaturated soil in a compartment can be written as:

$$Q_{in} = Q_{out} - E + \Delta W \tag{2}$$

where Q_{in} and Q_{out} are input and output of water to and from the compartment, respectively, E is the evapotranspiration, and ΔW is the change of water content in the compartment during the period. For example, Q_{in} in the 0-10 m soil compartment can be obtained from the throughfall measurement, and ΔW, E by direct observations. The calculated Q_{out}, in turn, becomes Q_{in} for the 0.1-0.2 m soil compartment. Therefore, the equation can be used to calculate the water flux through a series of compartments up to 1.0 m soil depth.

E can be calculated from temporal variations of evapotranspiration (Suzuki, 1980).

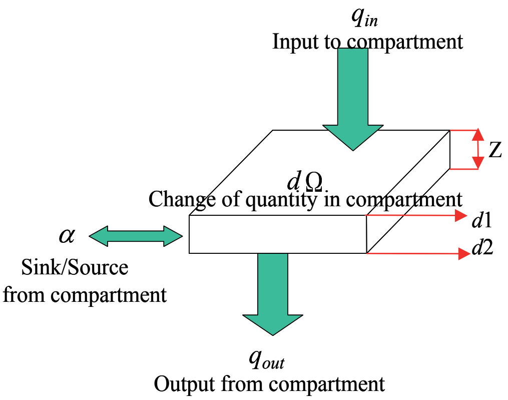

Fig. 7. Calculation of dissolved material flux in soil compartment (Kim, 2003)

$$E_{d1\text{-}d2} = cE \tag{3}$$

where $E_{d1\text{-}d2}$ is evapotranspiration in soil depth from $d1$ to $d2$, E is the total evapotranspiration from the entire soil column, and c is the proportion of $E_{d1\text{-}d2}$ to E. For example, c in the 0-0.1 m soil compartment (if the total soil depth is 1.0 m) during time t is calculated from the change of water content by using equation (4).

$$c = \frac{\left(\theta_{0-10}^{t+\Delta t} - \theta_{0-10}^{t}\right)}{\left(\theta_{0-10}^{t+\Delta t} - \theta_{0-10}^{t}\right) + \left(\theta_{10-20}^{t+\Delta t} - \theta_{10-20}^{t}\right) + \left(\theta_{20-30}^{t+\Delta t} - \theta_{20-30}^{t}\right) + \left(\theta_{30-50}^{t+\Delta t} - \theta_{30-50}^{t}\right) + \left(\theta_{50-100}^{t+\Delta t} - \theta_{50-100}^{t}\right)} \tag{4}$$

ΔW can be calculated from the change of water content, which is derived from the relationship between θ and ψ (Kosugi, 1994; Kosugi, 1996).

$$\Delta \mathrm{W} = \left(\theta_{(d1+d2)/2}^{t+\Delta t} - \theta_{(d1+d2)/2}^{t}\right) \cdot \mathrm{Z} \tag{5}$$

where θ_d^t is water content during time t at soil depth $(d1+d2)/2$, and Z is soil thickness.

Dissolved ions and compounds in soils move with water infiltration processes. Therefore, dissolved material flux is calculated by multiplying dissolved material concentration with the water flux. The calculation method of dissolved material flux is described in Fig. 7. The dissolved material flux is calculated from the change of quantity in a compartment. The sink/source (a) property of the compartment can be estimated from q_{in}, q_{out} and the change of quantity in the compartment ($d\Omega$), such as:

$$a = d\Omega - (q_{in} - q_{out}) \tag{6}$$

where $d\Omega$ is calculated from the concentration of dissolved materials and water content.

$$d\Omega = \left(\theta^{t+\Delta t}_{(d1+d2)/2} \cdot S^{t+\Delta t}_{(d1+d2)/2} - \theta^{t}_{(d1+d2)/2} \cdot S^{t}_{(d1+d2)/2}\right) / Z \tag{7}$$

where $S^{t}_{(d1+d2)/2}$ is the dissolved material concentration during time t at soil depth $(d1+d2)/2$. The equation (7) indicates the change of dissolved material budget in the soil compartment during time t. Moreover, q_{in} and q_{out} at depth d can be described as:

$$q_{in} = \left(f^{t}_{d1} + f^{t+\Delta t}_{d1}\right) / 2 \cdot \Delta t \tag{8}$$

$$q_{out} = \left(f^{t}_{d2} + f^{t+\Delta t}_{d2}\right) / 2 \cdot \Delta t \tag{9}$$

where f^{t}_{d1} is dissolved material flux at soil depth $d1$ during time t.

3.2 Estimation of water infiltration rate using a water table fluctuation

The water infiltration rate can be calculated indirectly from the groundwater recharge rate. To estimate the water infiltration rate, the groundwater recharge rate from the water table fluctuation can be calculated as follows (Moon et al., 2004):

$$\alpha = \frac{\Delta h}{\sum P} \times S_y \tag{10}$$

where α is the recharge rate, h is the change of groundwater level, P is precipitation, and S_y is the specific yield. On specific conditions, groundwater recharge rate may practically represent the infiltration rate. We can also estimate the dissolved material flux, such as dissolved organic carbon (DOC) by multiplying groundwater recharge rate with the measured concentration. This technique has been applied to the headwater region in the Gwangneung catchment, and its reliability has been critically evaluated by comparing with other methodologies. The uncertainty of this technique is largely due to the measurement error of specific yield (S_y) caused by the heterogeneity of geologic materials, and other factors influencing the water table fluctuation such as changes in atmospheric pressures, air entrapment during the infiltration of water, irrigation, and pumping (Choi et al., 2007).

According to the results from the water infiltration rates, 0.44 t-C ha^{-1} DOC was infiltrated into the soil from late June to early October in 2005, which represented approximately 8% of the stored carbon in the forest floor (5.6 t-C ha^{-1}; Lim et al., 2003) and 30 to 50% of NEE (-0.84 to 1.56 t-C ha^{-1} yr^{-1}; Kwon et al., 2010) (Fig. 8). These results indicate that a considerable amount of decomposed organic matter is stored in the soil through water movement processes. If most of the infiltrated DOC were to accumulate as soil organic carbon in the shallow soil and to be decomposed in the deep soil, then 0.5% of the soil carbon (92.0 t-C ha^{-1}; Lim et al., 2003) would be retained from DOC during the summer monsoon (Fig. 8).

While these values seem to be relatively small, soil organic carbon can be accumulated in the mineral soil for an extended period (e.g., Michalzik et al., 2003); potentially making the 0.5% of soil carbon retained from DOC during the summer monsoon an important component of the forest carbon budget to consider (e.g., Battin et al., 2009).

Based on these estimates of NPP ranging from 4.3 to 5.8 t C ha^{-1} yr^{-1}, the observed amount of total DOC and POC effluxes is roughly 2% of the annual NPP – a small but non-negligible amount in terms of net ecosystem carbon exchange (NEE). Considering the averaged NEE of -0.84 t C ha^{-1} yr^{-1} (negative sign indicates net uptake of carbon by the forest; Kwon et al., 2010), approximately 10% of NEE would escape from this forest catchment as DOC and POC (Fig. 8). Our results further indicate that 50 and 80% of the respective annual DOC and POC effluxes were transported out of this forest catchment during the summer monsoon period.

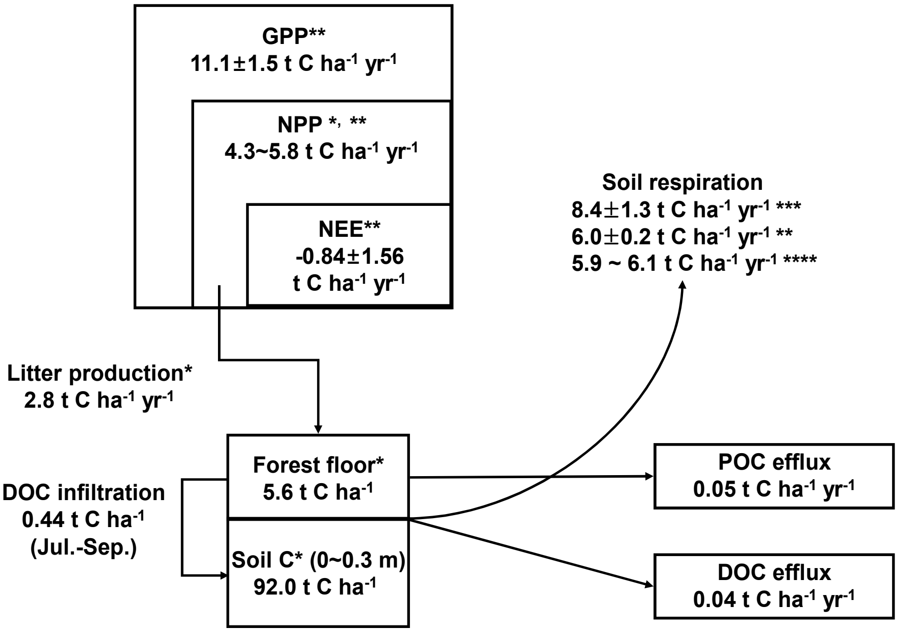

Fig. 8. The contribution of DOC and POC to the carbon budget in the Gwangneung deciduous forest catchment. * Lim et al. (2003; observation periods 1998 to 1999), ** Kwon et al. (2010; observation periods 2006 to 2008), *** Chae (2008; observation periods 2001 to 2004). The difference of soil respiration is due to difference of observation periods and methods. Modified from Kim et al., 2010.

3.3 Adsorption of DOC in forest soil

Many field studies have shown that the concentration of DOC in soil water significantly decreases with increasing soil depth (Fig. 9). It is generally assumed that adsorption of DOC to the surface of mineral soil is important than decomposition in reducing DOC concentrations. Various sorption mechanisms have been reported, including anion exchange, cation bridging, physical adsorption, etc. (Jardine et al., 1989; Gu et al., 1994; Edwards et al., 1996; Kaiser and Zech, 1998a; Kaiser and Zech, 1998b). These DOC sorptions are irreversible under natural soil conditions (Gu et al., 1994). Because Fe and Al oxides are the most important sources of variable charge in soils (Jardine et al., 1989; Moore et al., 1992; Kaiser and Zech, 1998a), DOC adsorption can be related quantitatively to the Fe and Al oxide contents of soils (Moore et al., 1992). The proportion of clay in mineral soil is also an important factor for DOC adsorption. DOC concentrations in catchment runoff are negatively correlated with the clay contents of soils in the catchment. The adsorption process is relatively rapid, which completed within 2 to 12 hours (Kaiser and Zech, 1998b). The effect of pH on the adsorption of DOC in forest soil is also important. Tipping and Woof (1990) calculated that an increase in soil pH by 0.5 units would lead to an increase by about 50% in the amount of mobilized organic matter. Nodvin et al. (1986) also calculated the reactive soil pool of DOC under various pH conditions.

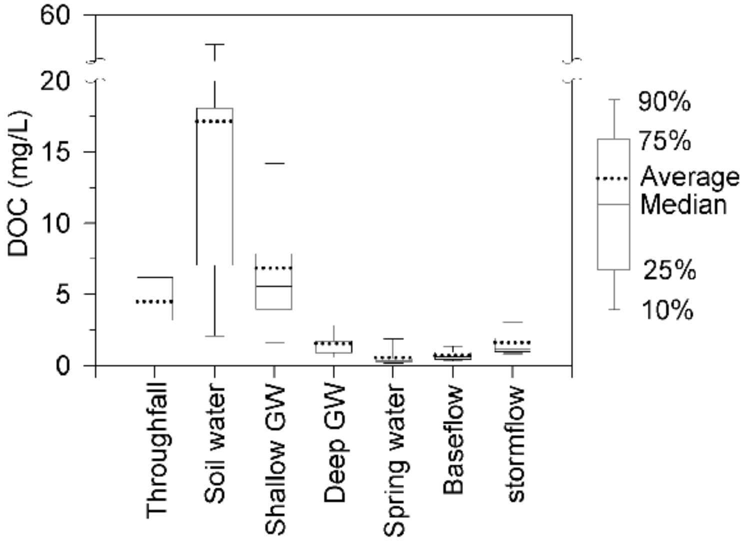

Fig. 9. Spatial variations in the concentrations of DOC of throughfall, soil water, shallow groundwater (0.5 m), deep groundwater (0.8-1.0 m), spring water, and baseflow, with respect to and stormflow (Kim et al., 2007b)

3.4 Temporal and seasonal change of DOC export from temperate forest catchment

Typical temporal variations in DOC concentrations during storm events are shown in Fig. 10. With the onset of heavy precipitation, DOC concentration in streamwater increases significantly, and after the precipitation ceased, DOC concentrations returned to pre-storm levels. The results from the hydrograph separation during storm events indicated that a large amount of water discharged through surface and subsurface soil layers (Fig. 6). DOC concentration in the surface soil is higher than the deep soil and the groundwater (Fig. 9). The Storm event leads to the increase in the surface runoff with a high DOC concentration. During the baseflow period, most stream waters flow out from the groundwater with a low DOC concentration (Fig. 11). These results indicate that hydrological processes strongly affect the DOC export and thereby the carbon budget in the catchment.

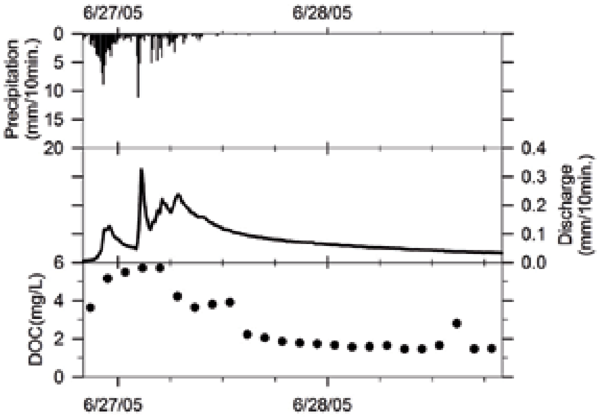

Fig. 10. Precipitation, stream discharge and temporal variations of DOC concentration in streamwater during storm event (Kim et al., 2007b)

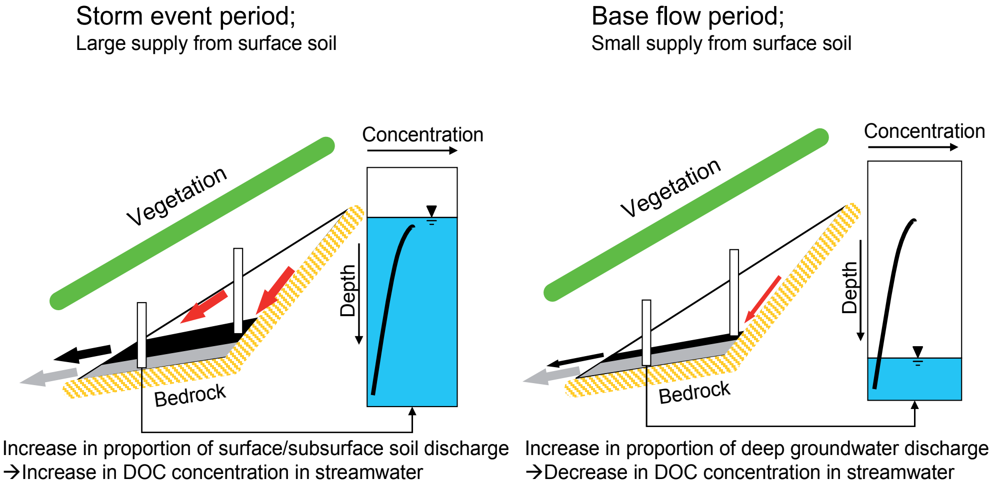

Fig. 11. Precipitation, stream discharge and temporal variations of DOC concentration in streamwater during storm event (Kim et al., 2007b)

Forest treatments		Throughfall (mm)	Stemflow (mm)	Interception loss (mm)	Interception loss (%)	Rainfall (mm)
Pinus Koraiensis	Not practice	85.8	6.5	74.0	44.6	166.0
	Practiced	100.2	7.5	58.3	35.1	
Abie holophylla	Not practice	90.1	7.8	68.1	41.0	
	Practiced	104.8	8.2	53.0	31.9	
	Deciduous forest	118.6	33.9	12.0	7.3	
	Mixed forest	115.3	17.6	33.1	19.9	

Table 6. Percentage of interception loss by forest practices and vegetation types

4. Effects of forest managements on water cycle and quality

Change of the forest stand structure causes the modification of the hydrological characteristics because the components of water loss by interception and evapotranspiration change immediately, owing to the reduction of LAI. Moreover, physical and chemical properties of forest soil change in a long term.

Kim et al. (1993) conducted a research on the effects of site conditions in headwater stream on water storage of reservoirs on small-forested watersheds. The result shows that the water storage of the reservoirs during the dry season is positively correlated with the tree height, DBH, stand ages and crown closure, but negatively with understory coverage and drainage density.

The first change in hydrological components after forest practices is the interception loss from the tree canopy surface during rainfall. The amount of interception loss decreases after thinning and cutting. The rate of reduction for interception loss is correlated positively with the percentage of thinning and cutting of forest types. Table 6 represents the effects of forest practices and types on the percentage of interception loss. In the coniferous stand, the percentage of interception loss decreased to about 10% after forest practices. The mixed forest intercepted the rainfall in about half the amount of the coniferous, whereas the deciduous stand did in about one-sixths of that. Forest treatments increase not only interception loss but also discharge due to the reduction of loss components such as evapotranspiration. The amount of discharge after the forest practices during the dry season was increased by two and three-tenths of that, respectively, before the treatments.

Generally, forest soil has a filtering property like sponge and conserves soil and water resources. If forests, regardless of the types, are cut clearly, catastrophic amounts of soil and water are produced. Fig. 12 explains the effects of clear cutting on the peak flow in a small-forested catchment. The amount of peak flow in the clear-cut site increased to 78.3 mm compared to the controlled site during the rainfall of 400 mm.

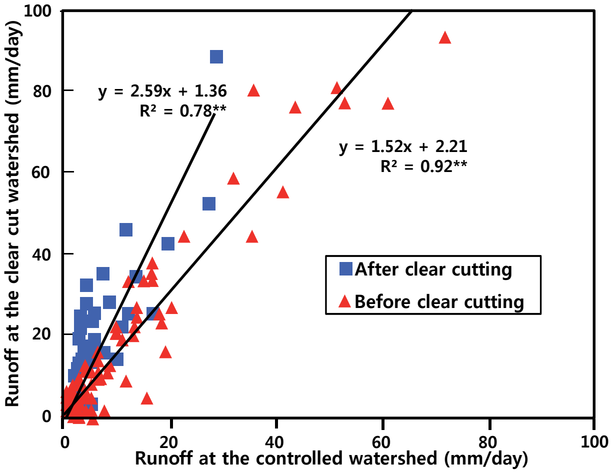

Fig. 12. Change of peak flow after clear cutting

Jeong et al. (1997) analyzed the influential factors on the electrical conductivity of stream and soil water in a small-forested watershed. They concluded that the electrical conductivity was correlated with the total amount of a cation and an anion in stream and soil water. Their results proposed that the amounts of NO_3- and Na^+ in the stream have a statistical significance for the electrical conductivity in streams and the amounts of K^+ and Ca^{2+} and pH in soil water for the electrical conductivity in soil water.

Jeong et al.(1999a, b) further clarified the effect of forest management practices (thinning and pruning) on soil physical properties and water quality to obtain fundamental information on the facility of purifying water quality after forestry practices. They investigated the water quality of rainfall, throughfall, stemflow, and soil and stream water at the coniferous stands that consisted of *Abies holophylla* and *Pinus koraiensis*. The seasonal variation of water qualities of throughfall, stemflow and soil water were decreased after practices. Some researches supported the mesopore ratio on pore geometry of surface soil to be used as an index of the water retention capacity of forestlands.

Jeong et al. (2001a) investigated 23 parameters, including site conditions and soil properties to analyze the influencing factors of mesopore ratio on pore geometry of surface soil in coniferous stands. They found that the factors influencing the mesopore ratio (pF2.7) on the surface soil were macropore ratio (pF 1.6), slope, crown-cover rates, and thickness of F-layer, organic matter contents, and the growing stock. They concluded that crown-cover rates of stands should be controlled to be less than 80% for enhancing the water resource retention capacity in coniferous stands.

Jeong et al. (2001b) investigated fifteen factors, including site conditions and soil properties to analyze the influencing factors of mesopore ratio on a pore geometry of surface soil in deciduous stands. The factors influencing the mesopore ratio (pF2.7) on the surface soil were found to be the tree height, under vegetation coverage and organic matter contents of soil in deciduous stands. Hence, they concluded that the water resource retention capacity would be improved when under vegetation coverage was increased from 30 to 80%.

5. Upscaling of observation data through hydrological modeling

The rainfall-runoff process, which is an important component of the hydrological system, is very complex considering the large number of factors involved and their temporal and spatial distribution. Hydrological modelling is a suitable technique to represent the rainfall-runoff process in various symbolic or mathematical forms using known or assumed functions expressing the various components of a rainfall-runoff response (Ndiritu and Daniell, 1999). In the last half-century there have been hundreds of hydrological response models, each with their own attributes and shortcomings, developed by many different researchers. Furthermore, with the current rapid developments within computer technology and hydrology, the application of computer based hydrologic models is only likely to increase in the near future (Loague and Van der Kwaak, 2004).

The distributed hydrological models aim to better represent the spatio-temporal variability of hydrological characteristics governing the rainfall-runoff response at the catchment scale. One of the distributed hydrological models used commonly is TOPMODEL, which is a quasi-physically based semi-distributed hydrological model (Beven and Kirby, 1979; Beven et al., 1995; Beven, 1997; Beven, 2001; Beven and Freer, 2001a, b).

Most physically based distributed models have parameters which are effective at the scale of the computational elements. In order for a rainfall-runoff model to have practical utility or be useful for hypothesis testing, it is necessary to select appropriate values for the model parameters. Unfortunately, it is not normally possible to estimate the effective values of parameters by either prior estimation or measurement, even given intensive series of measurements of parameter values. Therefore, parameter values must be calibrated for individual applications (Refsgaard and Knudsen, 1996; Refsgaard, 1997; Freer, 1998; Beven, 2001).

In general, the process of parameter calibration has involved some form of determination of a parameter set that gives a simulation that adequately matches the observation. However, many calibration studies in the past have revealed that while one optimum parameter set could often be found, there would usually be a multitude of quite different parameter sets that can produce almost equally good simulation results. Recognition of multiple acceptance parameter sets results in the concept of equifinality of parameter sets (Beven and Freer, 2001b; Beven, 2002; Freer et al., 2003). In addition, in the general case for rainfall-runoff modelling with multiple storm sequences, it might be difficult to assess model performance using a single likelihood measure, because the form of the distribution of uncertain predictions varies markedly over the range of streamflow and the appropriate error structure might vary with both of type of data and the model parameter set (Freer et al., 2003). It may often be the case that the available data are not adequate to allow identification of complex models and/or that a single performance measure (objective function) is not adequate to properly take into account the simulation of all the characteristics of a system used. Thus, the multi-criteria or multi-objective methods using multiple objective functions or other data in addition to rainfall-runoff data may allow more robust analyses of models, and aid hypothesis testing of competing model structures (Gupta et al., 1999; Beven, 2001; Madsen et al., 2002; Freer et al., 2003).

The multi-criteria performance measures based on the concept of equifinality of behavioral model simulations were used for calibration of the rainfall-runoff model, TOPMODEL at natural deciduous forest in South Korea. Totally 100,000 parameter sets uniformly sampled by Monte Carlo Simulations from the ranges for each TOPMODEL parameters, and hourly stream flow and rainfall data observed from April to October, 2005 i n the deciduous forest catchment located in the Gwangnung experimental forests were used for model calibration.

The performance of each parameter set was evaluated and identified with 6 different performance measures against behavioral acceptance thresholds defined for each performance measure, and the results were analyzed focused on the variability and relationship between the behavioral parameter distributions according to the definitions of performance measures.

The results demonstrate that there are many acceptable parameter sets scattered throughout the parameter space, all of which are consistent in some sense with the calibration data, and the range of model behavior for each parameter varied considerably between the different performance measures. Sensitivity was very high in some parameters, and varied depending on the kind of performance measure (Fig. 13). Compatibilities of behavioral parameter sets between different performance measures also varied, and a very small minority of parameter sets could produce reliable predictions regardless of the kind of performance measures (at least, for the performance measures used in this paper).

Especially, the results indicate that using a single performance measure for the calibration of a hydrological model may lead to an increase in model uncertainty. Therefore, careful consideration should be given to the choice of performance measure appropriate to the characteristics of used model and data and the purpose of study.

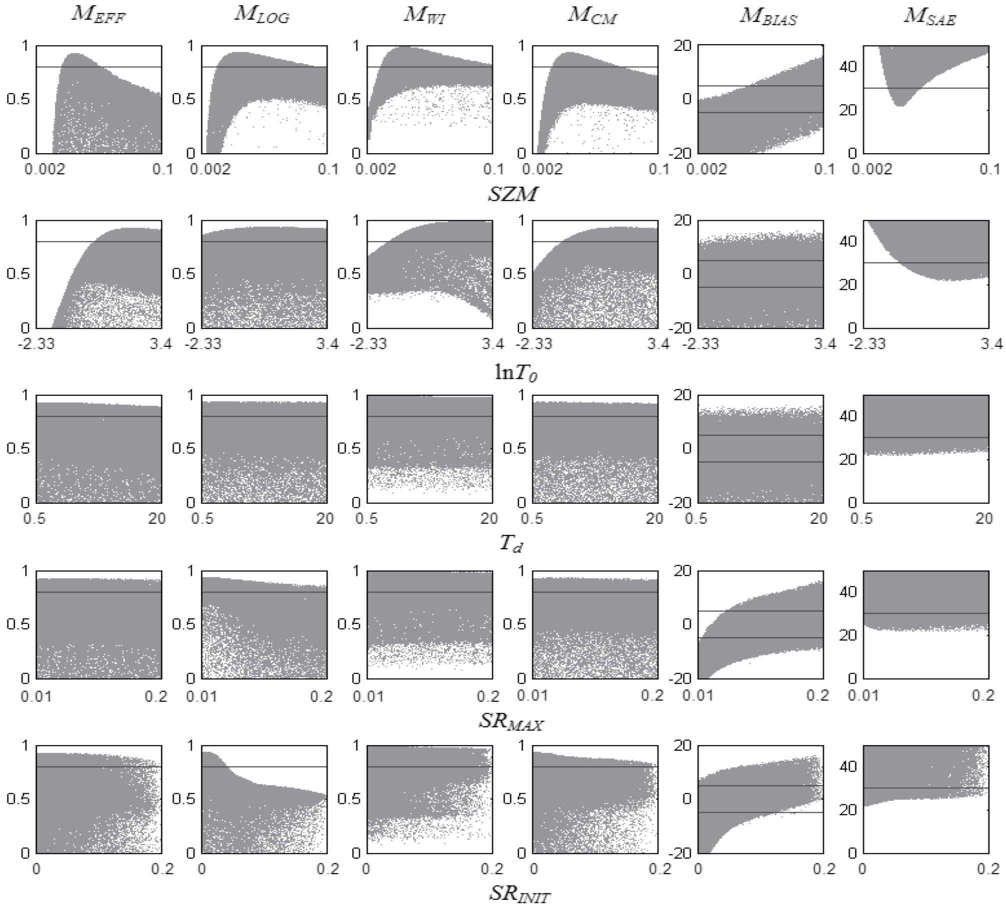

Fig. 13. Scatter plots of likelihood values for TOPMODEL parameters from Monte Carlo simulations of the deciduous forest catchment conditioned on the 2005 discharge period using six performance measures. Each dot represents one simulation with a likelihood weight calculated by a given performance measure, and horizontal lines mean thresholds identifying behavioural parameter sets for each performance measure; dots over the line (in cases of M_{EFF}, M_{LOG}, M_{WI} *and* M_{CM}), dots between both lines(in case of M_{BIAS}) and dots below the line (in case of M_{SAE}) are classified as behavioural simulations.

Differences in the behavioral parameter distributions according to the performance measures may be directly caused by the definitions of performance measures. However, it also should be considered that the effects of model nonlinearity, covariation of parameter values and errors in model structure, input data or observed variables may be taken into account in the nonlinearity of the response of acceptable model.

The performance of the parameter set can be used to produce the likelihood-weighted marginal parameter distributions for individual parameters, and the likelihood weighted model simulations can be used to estimate prediction quantiles in a way that allows that different models may contribute to the ensemble prediction interval at different time steps and that the distributional form of the predictions may change from time to time step (Fig. 14).

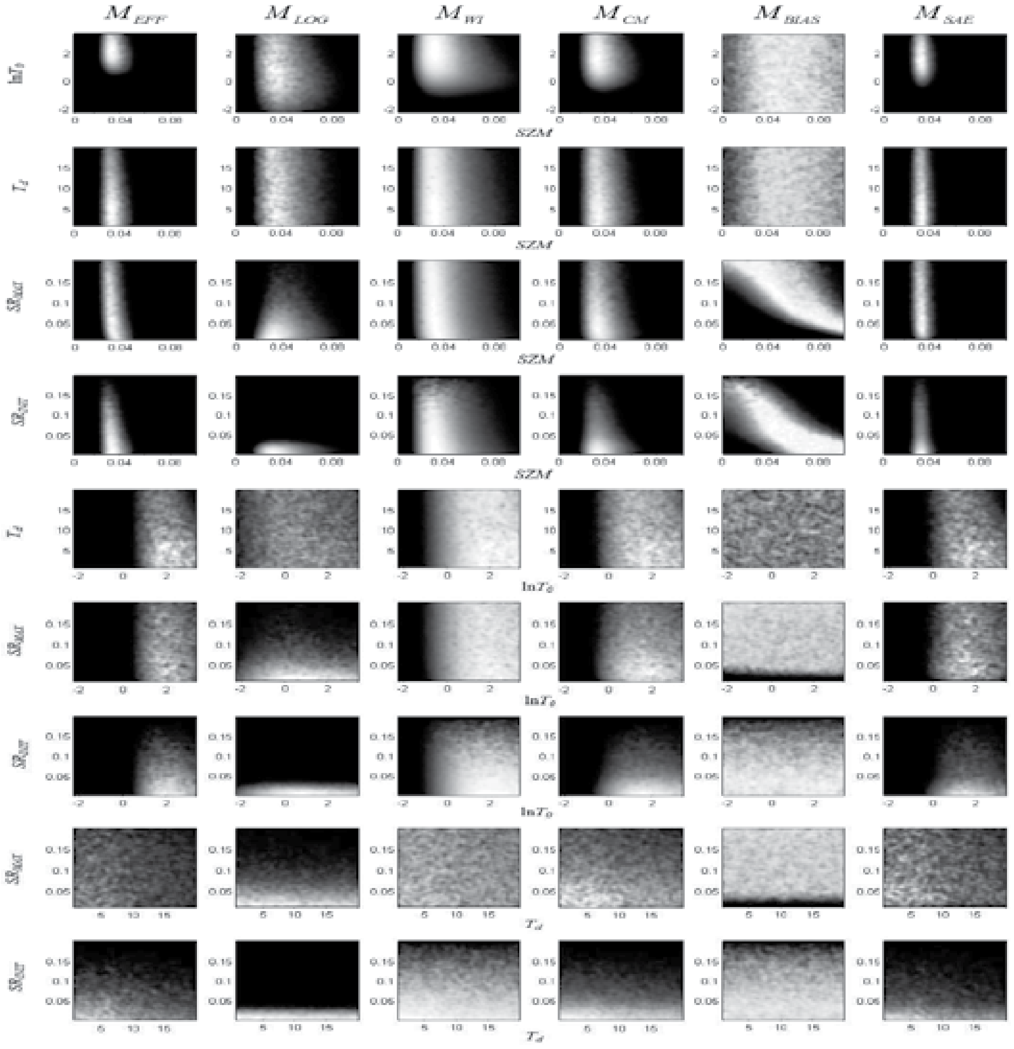

Fig. 14. Likelihood response surfaces between the major parameters of TOPMODEL, conditioned on the 2005 discharge period of the deciduous forest catchment (Behavioural parameter sets with higher model performance are in the white zone.)

6. Conclusions

The ecohydrological and biogeochemical studies have proposed a major scientific question: What is the role of hydrology in the carbon budget of complex forest catchment and how will it change in the hydrologic cycle in monsoon Asia and influence the forest carbon budget? (Kim et al., 2006) To properly answer this question, some of the most fundamental aspects in catchment hydrology need to be clarified i.e., (1) How much water is stored in the catchments? (2) What flowpaths does water take to the stream? (3) How long does water reside in catchments? (4) How can we scale or transfer our observations to other catchments? Despite decades of dedicated scientific efforts on these fundamental questions, it is still difficult to find a robust interpretation even for some basic hydrological processes such as discharge and runoff. The up to date results showed that the geophysical and meteorological conditions greatly affect the hydrological processes (Hooper et al., 1990; Elsenber et al., 1995; Katsuyama et al., 2001; McGlynn and McDonnell, 2003; Kim et al., 2010).

To understand carbon cycling in this catchment better, it is necessary to estimate the annual accumulation and movement of water and DOC in the soil. The organic carbon has been continuously discharged from terrestrial ecosystems of river basin. This organic carbon will contribute for an important sink for carbon through burial in coastal sea sediments or floor. These missing values have to consider for estimation of carbon budget in terrestrial ecosystems. Our results suggest that storm events during summer monsoon (including the typhoon season) are important to estimate flow paths of water and carbon budget in a Korean forested catchment and East Asia. The seasonally concentrated precipitation increases the surface runoff, when the infiltration capacity of the soil decreases during summer monsoon. The outbreak of surface runoff reduced the mean residence time of water in the catchment, and increased DOC export from the surface soil layer. The precipitation also plays an important role in infiltration processes of dissolved material. The precipitation patterns and hydrological processes strongly affect the carbon cycling in the Korean temperate forest during summer monsoon. The increasing occasions of heavy precipitation may not lead to the simultaneous increase of available water resources in the catchment due to the shortening of the water residence time. However, the heavy precipitation will clearly increase material discharge such as DOC. Therefore, the effect of monsoon climate on water and carbon cycling in forest catchment should be critically evaluated on the basis of improved understanding of catchment hydrological and biogeochemical processes.

Our understandings in water and carbon cycling obtained from the hydro-biogeochemical approaches are limited due to the prescribed spatial scale of the measurements. The scaling issues are implicitly built into our field measurements and model representations (Kim et al., 2006). The information provided in this chapter should be carefully considered in modelling formulations at the hydrologic catchment and grid scales of ecohydrological/biogeoche-mical models and satellite image analyses. Such efforts should provide insights as to how various information is transferred across scales, and hence on how to simplify and aggregate measurements, models and satellite products. Future research must be focused on how to make measurements at scales that are appropriate for parameterization and model validation, and how to make the scales of modeling and satellite algorithm converge with those of field measurements (Kim et al., 2006).

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9

Carbon Cycling in Teak Plantations in Comparison with Seasonally Dry Tropical Forests in Thailand

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1. Introduction

Tropical deforestation has become a significant source of increased atmospheric CO_2 concentration, hence efforts to promote several actions for reducing emissions from deforestation and forest degradation (REDD) in the international society, one important example of which is afforestation in deforested areas (Gibbs et al., 2007). Recently, Pan et al. (2011) estimated that the global average of the gross emission rate of tropical deforestation was 2.9 petagrams of carbon (Pg C y^{-1}) from 1990 to 2007 and that tropical regrowth forests were partially compensated for by a carbon sink of 1.6 Pg C y^{-1} within an area of 557 Mha. In contrast, the carbon sink from intact forests, not substantially affected by direct human activities, was 1.19 Pg C y^{-1} within an area of 1392 Mha, suggesting that tropical plantations acted as strong carbon sinks due to rapid biomass accumulation.

Teak (*Tectona grandis*), as a tall tree species indigenous to India, Myanmar and Thailand and growing in seasonal dry tropical areas in Asia (Bunyavejchewin, 1983), is highly rated among hardwood plantations due to its durability, mellow color, and long straight cylindrical bole. Although natural teak is distributed in relation to productive soils, derived from e.g. limestone (Tanaka et al., 1998), teak is planted over many tropical countries, such as Nigeria, the Côte d'Ivoire, and Sierra Leone in Africa, and Costa Rica, Panama, Colombia, Trinidad and Tobago and Venezuela in central America, as well as Asian countries (Kashio & White, 1998; Pandey & Brown, 2000). By the year 2000, global teak plantation area reached 5.7 million hectares (FAO, 2001) and is still growing for investment by small landholders in agroforestry management as well as industrial wood supply (ITTO, 2004). However, the expansion of teak plantation has been propounding discussion from environmental perspectives, such as reduced biodiversity by mono-cultural plantations involving the clearing of undergrowth vegetation; soil erosion by fire treatment and litter raking; nutrient losses during harvesting; the spread of pests such as defoliators, the bee hole borer, skeletonizer; and the effects of water cycling (Niskanen, 1998; Pandey & Brown, 2000; Hallett et al., 2011).

Nowadays, one of the incentives for planting teak is to meet the demand in terms of carbon sequestration by indigenous tree species, at least in Indochina, with high economical return (Pibumrung et al., 2008; Jayaraman et al., 2010). However, despite several studies on carbon and biomass distribution in teak plantation in many countries, the carbon cycling of teak plantation has rarely been reported (Khanduri et al., 2008; Kraenzel et al., 2003; Viriyabuncha et al., 2002; Pande, 2005). Teak plantation production varies widely among countries and depending on soil conditions (Enters, 2000; Kaosa-ard, 1998). For example, the mean annual increment ranged from 2.0 m^3 ha^{-1} y^{-1} in poor sites in India to 17.6 m^3 ha^{-1} y^{-1} in prime sites in Indonesia with 50 year rotation periods (Pandey & Brown, 2000). Thus, the quantative illustration of carbon cycling in teak plantations is useful for understanding the key carbon sequestration channels, which may serve as the basis for improving forest management.

In this study, we estimated carbon stocks and fluxes of teak plantations in western Thailand, where productive soil was formed by underlying limestone and sandstone geological series (Suksawang et al., 1995). According to carbon allocation and carbon dynamic models (Richter et al., 1999; De Deyn et al., 2008), site productivity usually enhances carbon accumulation in soil by returning litter above and below ground to the soil. To understand the effects of forestry plantation on the carbon sequestration potential, carbon dynamics in adjacent natural forests were compared.

2. Materials and methods

2.1 Study sites, vegetation and soil

The study site was located in the Mae Klong Watershed Research Station (14˚35'N, 98˚52'E, Fig. 1), Lintin, Thong Pha Phum, Kanchanaburi Province, western Thailand (Takahashi et al., 2009). The annual mean air temperature at the station is about 25°C, ranging from 9.3 to 42.2°C, and the annual mean precipitation is 1,650 mm, most of which falls during the rainy season from April to October (Suksawang et al., 1995). Altitudes at the study sites ranged from 150 to 350 m a.s.l. In the watershed, the CO_2 and water exchange of the forest were monitored by a flux tower (Fisher et al., 2009; Saigusa et al., 2008).

Fig. 1. The location of the Mae Klong Watershed Research Station in Thailand.

Two plots were established in the teak plantation: young aged stand (T1, planted in 1992) and middle aged and gmelina (*Gmelina arborea*) mixed stand (T2, planted in 1977). The T1 plot had 530 trees ha^{-1} and its basal area at a height of 1.3 m was 6.0 m^{2} ha^{-1} in 1996 (Photo 1.). In T2, the tree density and the basal area of teak were 384 trees ha^{-1} and 17.4 m^{2} ha^{-1}, respectively, while those of gmelina were 181 trees ha^{-1} and 12.3 m^{2} ha^{-1}, respectively, in

Photo 1. Photographs of the study sites. Top left: 3-year-old teak (T1), top right: 7-year-old teak (T1), middle left: 16-year-old teak (T2), middle right: natural forest (MDF), bottom left: bamboo undergrowth in the natural forest, and bottom right: aerial photo of the Mae Klong watershed research area (back hills).

1996. The teak plantation was mainly distributed over a lower slope area, which was formerly cultivated land e.g. for upland rice.

The adjacent natural forest was of the mixed deciduous forest (MDF) (Rundel & Boonpragob, 1995). Detailed descriptions of the vegetation were given by Marod et al. (1999). The dominant tree species were *Shorea siamensis*, *Vitex peduncularis*, *Dillenia parviflora* var. *Keruii*, and *Xylia xylocarpa* var. *Keruii*, while four bamboo species were mixed as undergrowth vegetation (Takahashi et al., 2007). The forest was spread on a hill behind the teak plantation. Despite being so-called natural forest, it is still thought to have been historically affected by human disturbances such as hunting and collecting forest products, forest fires, and logging, as the other tropical dry forest (Murphy & Lugo, 1986), as well as natural disturbances by winds and storms (Baker et al., 2005).

Soil with a relatively high pH and rich in exchangeable calcium is classified as Alfisols (Soil Survey Staff, 2010) and derived from sedimentary rock, gneiss and limestone. Concisely, the soil pH (H_2O) is 5.7 - 7.1; exchangeable cations (cmol kg^{-1}) are 5.8 - 17.9 for Ca, 1.4 - 3.0 for Mg and 0.5 - 1.3 for K respectively; the cation exchangeable capacity is 10.3 - 16.2 cmol kg^{-1} and the base saturation is 75 – 127%. Soil texture is classified into sandy loam, loam, or clay loam and the soil is well drained. The chemical and physical properties of the soil in the study sites were also reported elsewhere (Takahashi et al., 2009, 2011).

2.2 Tree enumeration, litterfall, and fine root mass

Plots for tree enumeration were 40 × 60 m for T1 and 30 × 60 m for T2 in the teak plantation. In the watershed, plantation trees were planted at a spacing of 4 × 4 m. For the natural forest, enumeration was performed within an area 200 × 200 m on the slope (Marod et al., 1999). Diameter at the breast height (DBH, 1.3 m above the ground) was measured every year in the plantation and every two years in the natural forest.

The litterfall was measured using 10 litter traps with 1 × 1 m openings in the teak-gmelina plantation (T2), but not in the young teak plantation (T1). For the natural forest, 100 traps were installed in grids at 20 m intervals. Litter was collected once or twice a month and the oven dry mass was weighed (70 °C). The conversion factor to carbon mass used was 0.47.

Fine and small root biomass (< 2 cm in diameter) was measured by a soil column with an area 15 × 15 cm and a depth of 15 or 30 cm. The sampling was performed in triplicate in November 1998, the beginning of the dry season. Dead roots were eliminated and bamboo roots were separated by visible inspection. Root diameters (mm) were classified into <1, 1 – 3, 3 – 5, 5 – 10, and 10 – 20 and the oven dry weight was determined. The carbon concentration was assumed to be 0.45 gC g^{-1}.

2.3 Carbon stocks in ecosystem compartments

To calculate the carbon stock in living biomass, biomass conversion equations from basal areas (Kiyono et al., 2010) were used for estimating carbon in leaves, branches, stems, and roots. The wood density of tree species, carbon contents of leaves and woody materials were all collected from the IPCC report (IPCC, 2006).

Soil carbon stocks were determined at the representative soil profile in the plots. For the natural forest, soil pits were set on a slope at different topographical positions: ridge, upper and lower slope positions and a soil sample was taken from each soil horizon described in the soil survey. The soil carbon concentration was analyzed using the dry combustion method (NC analyzer, Shimadzu Co., Kyoto, Japan), while the soil bulk density was measured using a 4 × 100 cm^2 cylinder core. The soil carbon stock was calculated by multiplying the carbon concentration by the soil bulk density of the soil layer and cumulating to a certain depth. The litter (forest floor) was collected using a 0.5 × 0.5 m frame with four replications.

2.4 Soil respiration rate

The soil respiration rate was measured using the closed chamber method (Takahashi et al., 2009). The steel chamber used was 30 cm in both diameter and height. About 20 min after the cover had been sealed, the CO_2 concentration in the chamber headspace was determined by an infrared gas analyzer (ZFP5, Fuji Electronics Co., Ltd., Japan), while the soil respiration rate was calculated using a linear model of increasing CO_2 concentration with temperature correction. In this measurement, we manipulated trenching around the chamber and litter removal to separate the respiration sources of the roots, organic layer, and soil. Detailed results were reported elsewhere (Takahashi et al., 2009, 2011).

3. Results and discussion

3.1 Stock and growth of trees

In the teak plantation, plots T1 and T2 showed constant accumulation of carbon in the biomass. The teak biomass was 3.8 MgC ha^{-1} at 3 years, increasing to 28.6 MgC ha^{-1} at 6 years in T1 (Fig. 2). Biomass in T2, where one third of the planted trees were gmelina, was 56 MgC ha^{-1} for teak, 37.5 MgC ha^{-1} for 15-year-old gmelina, increasing to 86.9 MgC ha^{-1} for teak and 59.8 MgC ha^{-1} for gmelina at 20 years. Although plot T2 was a mixed stand and the stand age differed from plot T1, the T1 and T2 growth rates were comparable. Combining these stands, the growth rate of these plantations was estimated as 9.3 MgC ha^{-1} y^{-1} by linear regression ($r = 0.999$, $p < 0.01$). Total biomass consisted of 1.9% for leaves, 14.8% for branches, 69.2% for stems and 14.1% for roots aged 20 years at plot T2.

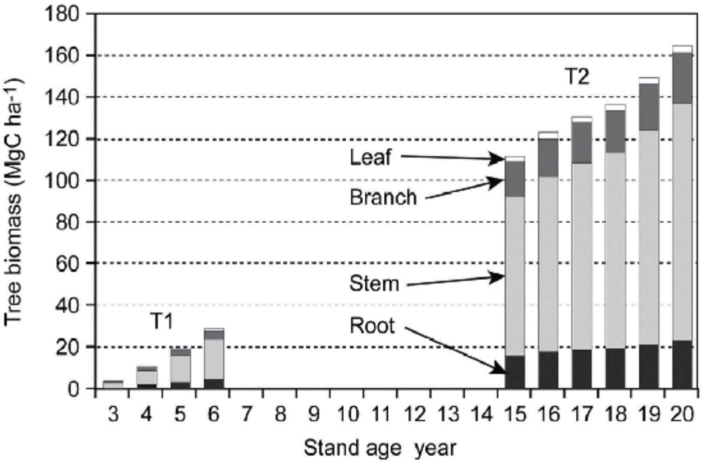

Fig. 2. Leaf, branch, stem and root biomass in teak plantations. Plots T1 and T2 are shown in the same figure according to the stand age.

Previous reports on carbon stocks in teak plantations in several countries were summarized in Table 1. Among the reference data, the site productivity of the teak in this watershed was the highest value. The increase rate of carbon stock of 9.3 MgC ha^{-1} y^{-1} was almost equivalent to 24 m^3 ha^{-1} y^{-1} for the stem volume increment, which would almost represent the upper limit of the mean annual increment of teak plantations under short rotation (< 20 years) system (Enters, 2000; Kiyono et al., 2007). This is probably due to the soil properties: well drained, rich in calcium, and high soil pH (Takahashi et al., 2009), namely ideal soil conditions for teak growth (Kaosa-ard, 1998; Tanaka et al., 1998).

Country, region	AG†	BG‡	Litter	Soil§	Stand age	Tree density	Soil pH	Ref.¶
		(MgC ha^{-1})			(y)	(ha^{-1})		
Panama, Boquerón	91.8	13.8	3.6	225 (200cm)	20	586	6.6	1)
Panama, Peňas Blancas	122.2	18.4	3.3		20	566	6.2	
Panama, Tranquilla	117.1	17.6	3.2		20	621	5.9	
Panama, Agua Claras	86.8	13.1	3.5		20	723	6.1	
Nigeria, Oyo	21.2		0.8		5	1184		2)
	57.2		2.2		8	1088		
	57.0		1.4		11	1100		
	67.1		1.5		14	988		
India, Chhindwara	17.8	4.9			16	2500	7.9	3)
India, Kerala	78.7				20	217	5.03	4)
	92.2				20	250	5.36	
	96.0				20	300	5.74	
	70.9				15	233	5.05	
	56.1				15	217	5.36	
	82.5				15	333	5.81	
Thailand, Prachuap Khiri Khan	43.7	13.8		56.77 (50cm)	15			5)
Thailand, Lampang	35.6	9.1		221 (50 cm)	17	844		6)
	41.2	8.2		137 (50 cm)	22	544		
Thailand, Kanchanaburi	24.1	4.4		108 (100cm)	6	530	7.1	7)
	141.0	23.2	2.5	123 (100cm)	20	565	6.2	

†: Aboveground biomass, ‡: Belowground biomass, §: cumulative soil depth in parentheses, ¶:Reference 1) Kraenzel et al., 2003; 2) Mbaekwe & Mackenzie, 2008; 3) Pande, 2005; 4) Chandrashekara, 1996; 5) Meunpong et al., 2010; 6) Hiratsuka et al., 2005; 7) This study.

Note: Dry mass was converted to carbon mass by a factor of 0.5.

Table 1. Comparison of carbon stocks in teak plantations in the seasonally dry tropics.

In the natural forest, the density of trees above 5 cm in DHB was almost stable with slight fluctuation during the 8 years of monitoring, ranging from 174 to 199 trees ha^{-1} and 16.9 to 17.7 m^2 ha^{-1} for basal areas (Fig. 3). However, the tree density was rather low, compared to the forest in Huai Kha Khaeng, about 120 km north of Mae Klong, where 438 trees (> 10 cm in DBH) ha^{-1} (Bunyavejchewin et al., 2001), suggesting a history of high disturbance in this area (Baker et al., 2005). Total tree biomass in 2000 was 139 MgC ha^{-1}, consisting of 1.5 MgC ha^{-1} for leaves, 19.3 MgC ha^{-1} for branches, 101 MgC ha^{-1} for stems, and 17.8 MgC ha^{-1} for roots. Because carbon densities in the Thai forests vary with forest type (Ogawa et al., 1961, 1965), our comparison was limited to the aboveground biomass of trees of the MDF (mixed deciduous forest) type. Similarly, low carbon densities were reported such as 48.14 MgC ha^{-1} in Pong Phu Ron station (Terakunpisut et al., 2007) and 24.79 and 50.58 MgC ha^{-1} for secondary and primary MDF in Phetchabun province (Kaewkron et al. 2011). As for MDF comparable forests from the early ecological study in Thailand, Ogawa et al. (1965) showed an aboveground dry mass of 157 Mg ha^{-1} (77 MgC ha^{-1}) for a forest classified as monsoon forest-savanna ecotone in Chiang Mai province and that of 103 Mg ha^{-1} (51 MgC ha^{-1}) for a mixed savanna forest in Tak province. Although carbon accumulation in MDF varies widely, our result seems typical of this forest type.

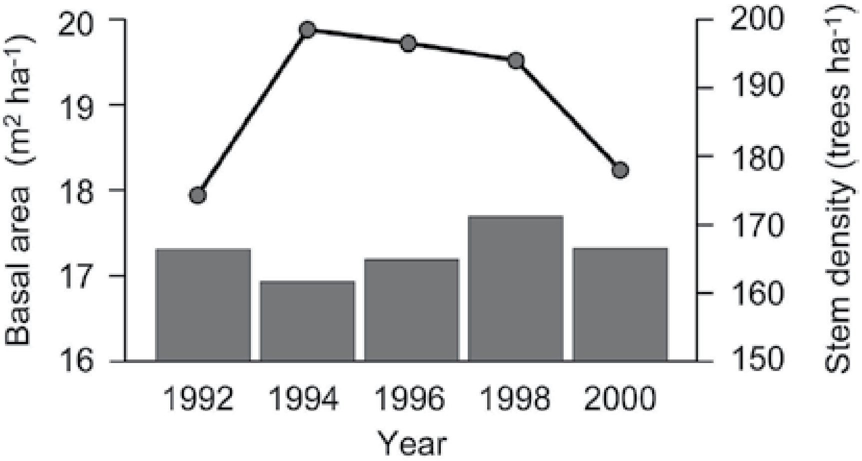

Fig. 3. Changes in stem density (DBH > 5 cm, dots and lines) and basal area (bars) in the natural forest.

Despite the low tree density, no apparent increment of carbon accumulation was detected in the natural forest studied. The natural forest nearby the teak plantation seemed static or in balance with the sequestration of carbon in the forest biomass. Our observation confirmed that most individual trees had increased steadily but some were dead with broken stems and standing dead, probably due to competition during the 8-year monitoring period (Marod et al., 1999 and unpublished data by Marod). In terms of the recruitment of trees, forest fires and drought stress would control the survival rates of tree seedlings and seed germination as well (Marod et al., 2002). In addition, shading by bamboo leaves during the rainy season influences the survival rate of seedlings (Marod et al., 2004). Similar findings showing that abundance in terms of seedlings and species had declined under bamboo in the MDF were reported in the Loei province of Thailand (Larpkern et al., 2011).

3.2 Litterfall

Annual litterfall in the teak-gmelina stand (T2) was 2.22 Mg ha^{-1} y^{-1} on average, consisting of 89.3% for leaf, 2.5% for fruit, and 8.2% for others such as bark. Of the leaf litter, 52.8% was counted for teak, 29.0% for gmelina, and 18.2% for other leaves (Fig. 4). The litterfall in the natural forest was 2.38 Mg ha^{-1} y^{-1}, on average, consisting of 61.5% leaves, 2.3% flowers, 7.7% fruit and 28.5% for others such as branches and bark (Fig. 5). About half the leaf litter (51.7%) was bamboo leaves. The litterfall tended to peak during January to March in both the natural forest and teak plantation: during this quarter, 46% of the litterfall fell in the natural forest and 56% in the teak plantation.

Seasonal patterns of litterfall were reported in several seasonal tropical forests with seasonal drought (e.g. Martínez-Yrízar & Sarukhán, 1990; Bunyavejchewin, 1997), usually as a dry matter basis. For teak plantations, 9.0 Mg ha^{-1} of annual litterfall, 90% of which was leaf litter and 70% or so of which fell during the dry season in Nigeria (Egunjobi, 1974). In India, total litterfall in teak plantations ranged from 3.3 to 4.5 Mg ha^{-1} (Pande et al., 2002). In the natural forests of Thailand, levels of 6.8 Mg ha^{-1} in *Shorea henryana* and 6.4 Mg ha^{-1} in a *Hopea ferrea* were observed (Bunyavejchewin, 1997). Mixed deciduous forest with teak showed total litterfall of 7.98 Mg ha^{-1} (Thaiutsa et al., 1978). The annual litterfall and proportion of the same in this study were comparable to previous studies of seasonal dry tropical forests (Martínez-Yrízar, 1995).

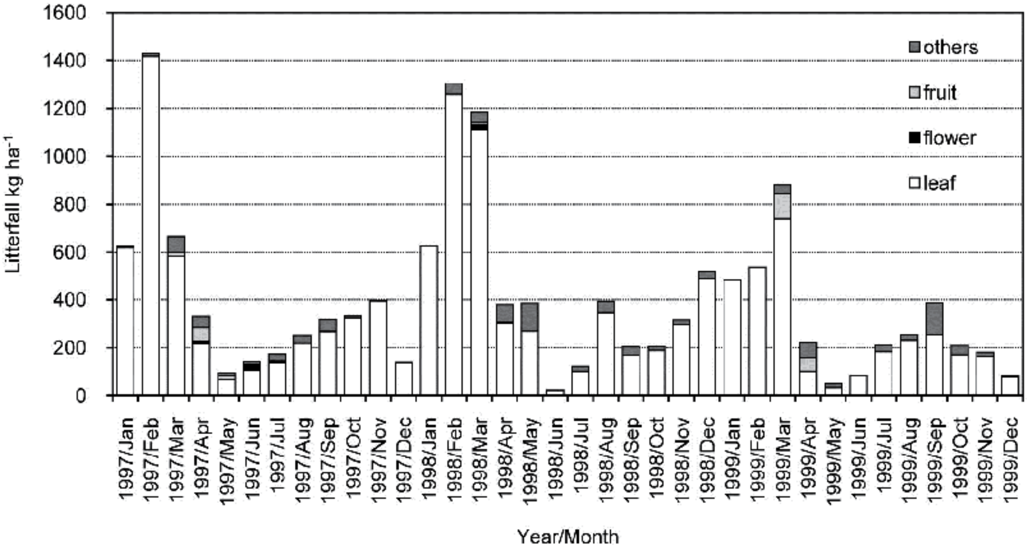

Fig. 4. Dry weight of monthly litterfall in the teak-gmelina plantation (plot T2).

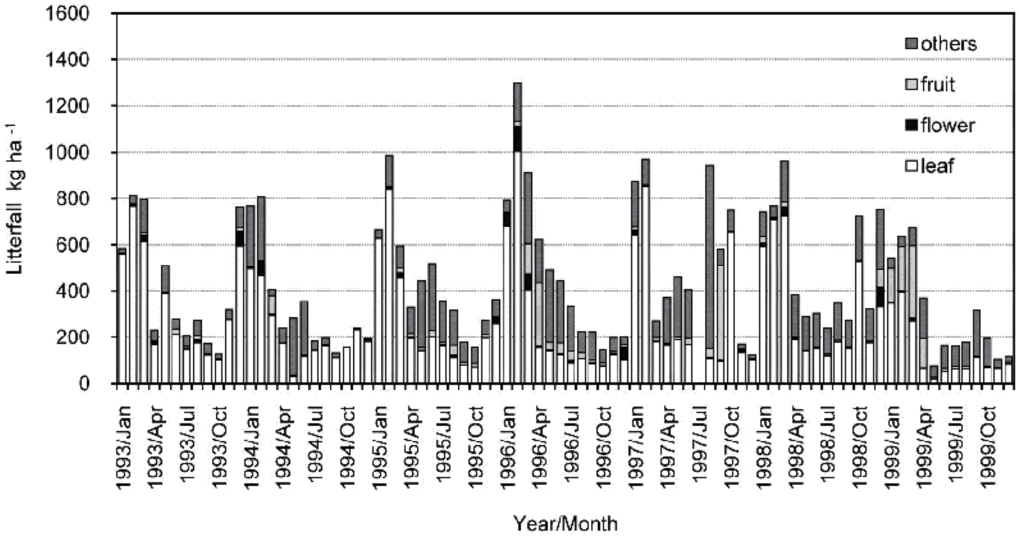

Fig. 5. Dry weight of monthly litterfall in the natural forest.

3.3 Root distribution and biomass

Fine root biomass (< 1 and 1 - 3 mm) was concentrated in the surface soil layer (0 - 15 cm) in all the plots studied (Fig. 6). The teak plantation had a sparse rooting system: fine roots (< 3 mm) with density in the 0 - 15 cm soil layer of 392 and 219 g m^{-3} for T2 and T1 respectively, compared to those in the natural forest (1144 g m^{-3} on average). In the 0 – 30 cm soil layer, fine root biomass (< 3 mm) was 0.47 and 0.32 MgC ha^{-1} for T2 and T1. Total fine and small root biomass (< 2 cm) at depths of 30 cm and 1 m was 2.3 and 2.7 MgC ha^{-1}, respectively, for plot T2 and 0.4 and 1.6 MgC ha^{-1} for plot T1. In the natural forest, the bamboo roots were mostly fine roots (< 3mm) at the surface (725 g m^{-3}), while the fine root biomass (<3 mm) of the 0 – 30 cm layer was 2.8 MgC ha^{-1} on average. Total root biomass (< 2 cm) was 4.0 MgC ha^{-1} at a depth of 30 cm and 8.8 MgC ha^{-1} at a depth of 1 m. These data are included in the root biomass estimated by the allometric equations above.

Although limited data is available for root biomass estimation in seasonal tropical forests, previous research revealed that fine root growth and density in seasonal tropical forests were highly controlled by soil hydrological regime (Cuevas, 1995). Our root biomass measurement, conducted at the beginning of the dry season, was probably lower than that in the rainy season. According to the review data by Cuevas (1995), the root mass in the wet season was about 1.5 times larger than that in the dry season. Singh & Srivastava (1985) found that the dynamics of root tip development, indicating growth and activity of fine roots, occurred mostly in the top 20 cm soil layer in teak plantations and that the highest root tips were observed in the mid rainy season. Similar fluctuations were found in both natural and Mexican dry forests (Kummerow et al., 1990; Kavanagh & Kellman, 1992). We could not clarify the fine root dynamics from the one-time measurement. However, the relative proportion of root biomass between the teak plantation and natural forest would be reasonable because the differences in root respiration as a proportion of total soil respiration between the teak plantation (15%) and the natural forest (19.4 – 33.6%) were comparable to the difference in root biomass of the same (Takahashi et al., 2011). These findings suggest that carbon flux by root necromass and exudates from fine root to mineral soil may be higher in natural forest than teak plantations, although high carbon accumulation by a developing living root system occurred at a rate of 1.3 MgC ha^{-1} y^{-1}; as calculated by total biomass increment and the root biomass proportion of these forests.

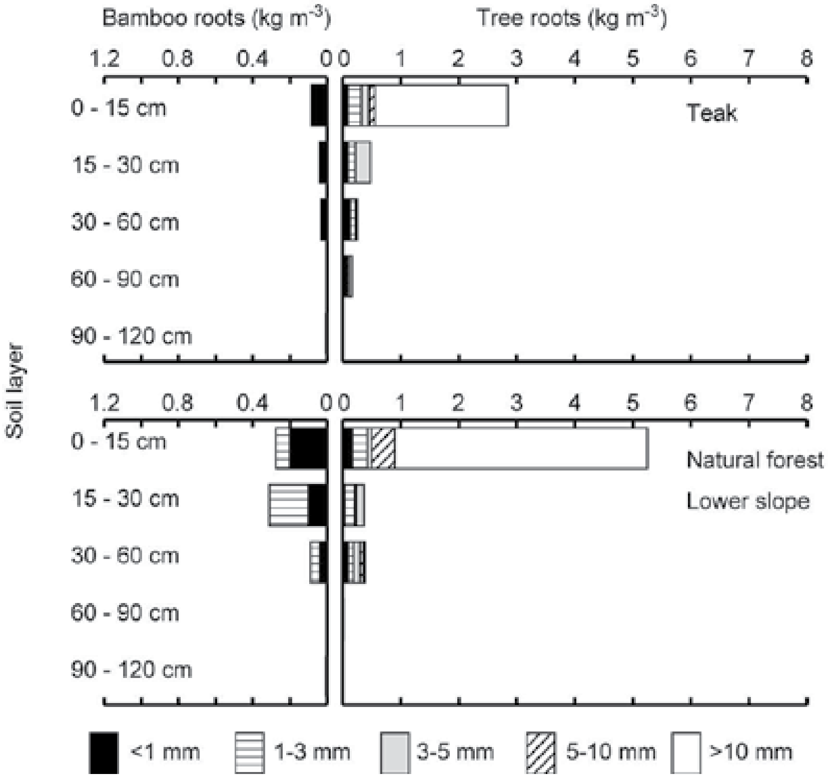

Fig. 6. Vertical distribution of fine and small roots density (< 20 mm) in the teak plantation (T1) and the natural forest (lower slope position). Bamboo roots are shown in the left-hand side and tree and other roots are in the right-hand side.

3.4 Soil carbon stock

In the teak plantation, soil carbon stocks at a depth of 1 m were 108 and 124 MgC ha^{-1} for plots T1 and T2 respectively (Fig. 7). The surface layer 0 – 15 cm had 34 MgC ha^{-1} in both plots T1 and T2. In the natural forest, carbon stocks in soil at a depth of 1 m varied with slope position and tended to have a larger ascribing slope, ranging from 113 to 178 MgC ha^{-1} (Takahashi et al., 2011, and unpublished data by Takahashi). The soil carbon stock in the soil layer of 0 - 15 cm was 32 and 38 MgC ha^{-1} in the lower and middle slope positions respectively.

Tangsinmankong et al. (2007) reported that soil carbon stocks up to 1 m depth under teak plantations of varying age ranged from 78.8 to 157 MgC ha^{-1} and that those in the 0 – 15 cm layer had 26.7 to 37.2 MgC ha^{-1} in the same district of this study. In peninsular Thailand, soil carbon in the 0 – 50 cm layer was 56.8 MgC ha^{-1} in a 15 year-old teak plantation with tree biomass of 57.5 MgC ha^{-1} (Meunpong et al., 2010). Soil carbon in the 0 – 50 cm soil layer under a teak plantation in Colombia was 54.9 MgC ha^{-1} (Usuga et al., 2010). These values are comparable to our results. In north Thailand, however, Hiratsuka et al. (2005) reported very high carbon stock in soils in 0 – 50 cm layers, 211 MgC ha^{-1} in 17 year-old stand, with 2 × 4 m spacing, by accumulating high organic carbon in the top soil layer, and 137 MgC ha^{-1} in the 22 year-old stand with 4 × 4 m spacing. In Panama, 225 MgC ha^{-1} was stocked up to the bottom of the soil profile, almost 2 m in depth, under 20 year-old teak plantation (Kraenzel et al., 2003). In MDF of Thailand, the soil carbon stocks at depths of 15 cm and 1 m were 26.7 and 71.0 MgC ha^{-1} (Tangsinmankong et al., 2007). Soil carbon at a depth of 0 – 30 cm (MgC ha^{-1}) on the sandstone and conglomerate was 27.6 while that on the limestone was 74.9 under MDF in Thailand (summarized by Toriyama et al., 2011).

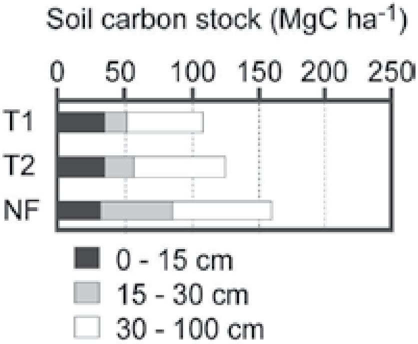

Fig. 7. Vertical distributions of soil carbon stocks in the teak plantations (plots T1 and T2) and natural forest (NF).

It is difficult to compare the results of soil carbon stock between different cumulating depths and different soil groups, which are not identified in some reports. Usuga et al. (2010) pointed out the importance of land-use history for analyzing soil carbon stocks, while Sakai et al. (2010) reported that the accumulation of carbon stock after conversion from arable land to forest plantation was only evident in the organic layer and the surface soil layer with 0 – 5 cm in the Japanese cedar and cypress stands younger than 25 years-old.. With reference to fine root distribution in the top 0 – 15 cm soil layer and litter on the forest floor, comparison of soil carbon stocks should be limited to the upper soil horizons, where the active component of soil organic carbon is concentrated. In addition, Toriyama et al. (2011) showed the importance of parent materials for soil carbon accumulation: basaltic and calcareous parent materials accumulated about twice the carbon stock compared to sedimentary rocks in the forest ecosystems in Cambodia and Thailand. The top soil carbon accumulation, ranging from 32 to 38 MgC ha^{-1} within the 0 – 15 cm layer, was relatively high, probably due to the influence of the limestone parent material, although no clear differences emerged between the teak plantation and the natural forest.

3.5 Soil respiration

The soil respiration rate (gC m^{-2} d^{-1}) showed seasonal fluctuation, peaking in the rainy season and declining in the dry season; ranging from 1.44 to 5.27 for plot T1, 1.71 to 5.46 for plot T2, and 1.85 to 7.21 for plots on the natural forest slope respectively. Applying equations fitting the relationship between soil moisture in the 0 – 30 cm layer monitored by TDR sensors and soil respiration rates, annual carbon efflux from the forest floor was estimated (Takahashi et al., 2009, 2011). Annual carbon efflux in plots T1 and T2 were 11.5 and 10.6 MgC ha^{-1} y^{-1}, respectively. In the natural forest, the soil respiration rate varied with the slope position on the hill (Takahashi et al., 2011) hence the average of the lower and upper slopes was used in this study for annual carbon efflux. In the natural forest, the carbon efflux was 17.7 MgC ha^{-1} y^{-1} on average. To distinguish the CO_2 sources, trenching to separate root respiration and litter removal in the chamber were manipulated (Takahashi et al., 2009, 2011). The proportions of roots, litter, and soil respiration were 15, 17, and 68%, respectively, for plot T2, and 27, 23, and 50 %, respectively, for the natural forest, on average.

Soil respiration is a key channel for returning photosynthesized carbon into the atmosphere, which has been intensively studied in forest ecosystems (e.g. Davidson et al., 2000). In general, annual soil carbon efflux correlates with annual rainfall and the mean annual temperature, as well as with annual litterfall (Raich & Schlesinger, 1992; Raich & Tufekciogul, 2000). For the soil respiration rate, Adachi et al. (2009) reported an average of 6.82 ± 3.55 gC m^{-2} d^{-1} during the rainy season and 2.63 ± 1.35 gC m^{-2} d^{-1} in a forest in Huai Kha Khaeng in northern Thailand. In a dry dipterocarp forest (DDF) in Ratchaburi, western Thailand, the soil respiration rate ranged from 1.26 gC m^{-2} d^{-1} in the dry season to 3.93 gC m^{-2} d^{-1} in the rainy season (Hanpattanakit et al., 2009). Annual carbon efflux from the forest floor was estimated at 13.4 MgC ha^{-1} y^{-1} under a dry evergreen forest (DEF), 12.1 MgC ha^{-1} y^{-1} under an MDF, 10.7 MgC ha^{-1} y^{-1} under a DDF in the Mae Klong watershed basin (Panuthai et al., 2006), and 25.6 MgC ha^{-1} y^{-1} under a hill evergreen forest (HEF) in Chiang Mai, northern Thailand (Hashimoto et al., 2004). As for teak plantations, the soil respiration rate has rarely been measured. In Khon Kaen Province, northeastern Thailand, 15.0 MgC ha^{-1} y^{-1} of CO_2 efflux in a teak plantation on sandy soil was reported (Funakawa et al., 2007). These data, including our results, suggest that soil respiration rates in teak plantations are likely to be similar to those for natural forest vegetation.

3.6 Carbon cycling in teak plantations

The carbon balance in plot T2 of the teak-gmelina plantation was depicted in Fig. 8. To draw this picture, we assumed comparable growth rates for the T1 and T2 plantations, despite the fact T2 were mixed forest with gmelina. We did not measure the litter decomposition of teak and gmelina leaves but, according to the partitioning of soil respiration sources, annual litterfall would be decomposed within a year, which is in accordance with our field observation that leaf litter on the forest floor disappeared during the rainy season. In this watershed, leaves of *Shorea siamensis* and bamboo swiftly decayed; 95 and 85 % of the initial weight having decomposed within a year (Somrithipol, 1997). A rapid decomposition rate was also often reported for teak leaves, usually more than 90 % in a year in several countries (e.g. Sankaran, 1993; Maharudrappa et al., 2000; Pande, 2005). As for forest floor vegetation, this was not measured because in T1, upland rice was initially cultivated between planted teaks for the first two years, whereupon weeding was performed each year. In T2, understory vegetation was sparse, due to bamboo flowering and dying two to three years before our observation commenced. Bamboo recovery was slow compared with the open area outside the forest, hence we ignored forest floor biomass in the teak plantation in this study.

Under these assumptions, the net primary production (NPP), as the gross rate of biomass production (GPP) minus the respiration cost (R): NPP = GPP – R, can be calculated and expressed as an increment of biomass plus necromass, such as litterfall and root litter, while some is consumed by herbivores. In the teak-gmelina plantation, NPP was estimated to be at least 11.5 (=9.3+2.2) MgC ha^{-1} y^{-1}, excluding underground processes. This value would be reasonable and relatively high for plantations in the tropics, referring to the review paper by Pregitzer & Euskirchen (2004). As comparable data, Imvitthaya et al. (2011) estimated the NPP in teak plantations in northern Thailand using BIOME-BGC Model and Spot data and with estimation ranging from 6.06 to 7.76 MgC ha^{-1} y^{-1} with yearly variation.

As for the natural forest, no apparent tree growth was observed from the tree census. If the carbon is balanced, NPP was equivalent to at least over litterfall. Clark et al. (2001) evaluated NPP in tropical primary forests, which ranged from 1.7 to 11.8 MgC ha^{-1} y^{-1} for the lower boundary based on conservative estimates, and featuring close correlation with aboveground biomass increment and fine litterfall. Our data showing the slow carbon sequestration rate by trees seems reasonable. Compared to the carbon cycling in the natural forest, we conclude that teak plantations are certainly valuable for sequestrating carbon, especially the portions above ground, in this area where the soil conditions favor teak.

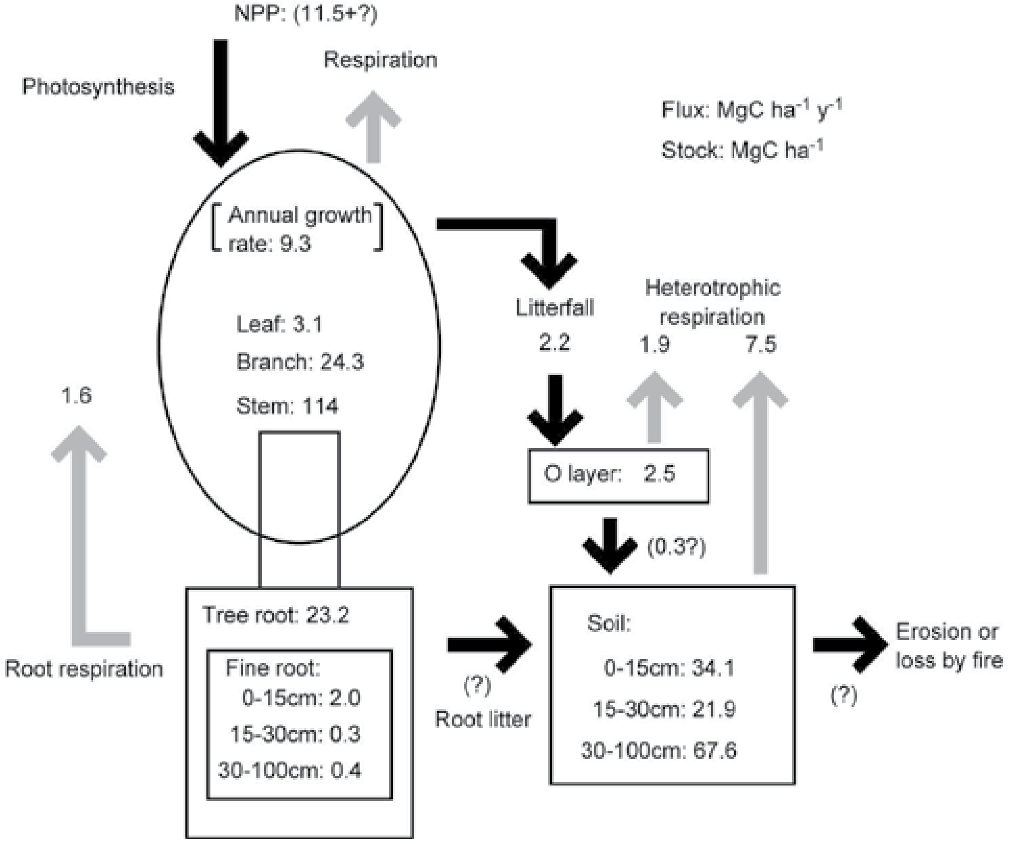

Fig. 8. Carbon cycling of the teak-gmelina plantation (T2). Figures in parentheses indicate uncertain estimates.

3.7 For sustainable teak plantation management

Soil carbon stock usually increased over time after planting trees (Sakai et al., 2010), due to carbon input from litterfall and the turnover of dead roots (Richter et al., 1999), meaning the higher growth of forest plantation would lead to higher soil carbon accumulation. However, despite high production in the plantation studied, there was no apparent difference in the soil carbon between T1 and T2. We speculate that surface soil erosion spoiled the soil carbon sequestrated under the plantation. During our observation, we found that surface soil was eroded due to raindrop splashes in the rainy season, especially in plot T2, which seemed to prevent soil carbon accumulation in the top soil layer. Poor understory vegetation, which induced bamboo flowering and death, dark conditions under the teak canopy, and quick litter decomposition seemed to create soil conditions leading to a bare and exposed surface. A similar observation of erosion under teak plantations was reported by Ogawa et al. (1961), Tangtham (1992), and Boley et al. (2009). This risk of soil erosion in teak plantations, caused by large raindrops falling from broad and large teak leaves, has been pointed by Hall & Calder (1993) and Calder (2002). Another possible risk of preventing carbon accumulation in the soil would be forest fires. Although teak resists fire, litter on the forest floor is lost if fires occur in the dry season, which is considered to be the main cause of low soil carbon accumulation in Myanmar teak plantations (Suzuki et al., 2007).

As well as surface soil, subsurface soil also showed no carbon accumulation in the teak plantation: Soil carbon stocks in the subsurface layer (15 – 30 cm) were smaller than those in the natural forest (Fig. 7). Similarly, in Panama, Kraenzel et al. (2003) also observed that teak plantations on abandoned land promoted no significant increases in soil carbon storage, despite considerable biomass growth. After harvesting, tree stumps remained and decomposed, which may have contributed to the belowground carbon stock to some extent in the short-term. However, for long-term soil carbon storage, undergrowth vegetation with deep rooting systems may help accumulate carbon stock in the subsurface layer.

Apart from soil management, the carbon cycling scheme in Fig. 8 suggests that teak plantations in this watershed are likely to be harvestable with a short rotation cycle, e.g. 20 – 30 years. Such short rotation is also beneficial in terms of carbon sequestration, while the parent material, limestone, of this watershed would promise high future productivity of the soil. However, ideal sites for teak plantation now face competition with agricultural crops and teak is often planted in sites with poor fertility (Enters, 2000), which would thus require longer rotation periods. Appropriate management should be selected in accordance with the site characteristics and management intensity. For sustainable forest management, there is still scope to improve teak plantations from several perspectives, e.g. biodiversity, carbon sequestration, and wood quality (Nair & Souvannavong, 2000).

General criticisms of monoculture plantations in terms of reducing biodiversity were periodically reviewed (e.g. Hartley, 2002; Brocherhoff et al. 2008), with poor undergrowth vegetation in young teak plantations with narrow spacing an example of a serious case. To improve monoculture plantations, mixture with other species, gmelina in our case, would be a live option, although silvicultural prescriptions must be developed. The landscape design of plantations and corridor arrangements may also be helpful (Fischer et al., 2006; Brocherhoff et al., 2008).

Lastly, because teak takes up high levels of nutrients and returns them to the surface soil, the aggrading effect of soil fertility was found on degraded land in Costa Rica (Boley et al., 2009). Similarly, calcium enrichment under teak plantations was observed in Myanmar (Suzuki et al., 2005). If suitable management for top soil conservation is applied, e.g. spacing, weed management, fire control, and mixed planting, teak is likely to represent promising species for land rehabilitation.

4. Conclusion

Teak has been a popular tree species for timber production in commercial and private farmland and remains a promising species for carbon sequestration in the seasonally dry tropics. A carbon cycling scheme obtained in teak (-gmelina) plantations showed a high rate of carbon accumulation in the soil of Alfisols in western Thailand which has high calcium content and high soil pH. In adjacent natural forest, no apparent carbon accumulation was observed, due to slow tree recruitment and disturbance in trees. Based on a comparison of carbon cycling in the natural forest, a teak plantation would represent a reasonable recommendation for tree species when managing plantations with carbon sequestration and high quality timber. However, no soil carbon accumulation is expected, probably due to surface soil erosion caused by raindrop splashes in poor understory vegetation and the ignition of litter by forest fire. Soil erosion control is essential under a teak canopy, which may promote additional carbon sequestration in the soil. Although the results of this study were derived from high productivity sites, teak can be planted as a rehabilitation species on degraded land as well. However, silvicultural prescription must be developed in accordance with economic benefit and ecological services side by side. To achieve this, quantitative measurement of carbon stocks and fluxes are useful for judging forest management appropriately.

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10

Fertility, Microbial Biomass and Edaphic Fauna Under Forestry and Agroforestry Systems in the Eastern Amazon

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1. Introduction

In many countries the rate of deforestation is accelerating. For example, many forest areas of Bangladesh, India, Philippines, Sri Lanka and parts of the rainforest in Brazil could disappear by the end of the century (GLOBAL CHANGE, 2010). The primary forest, especially in the tropics like the Philippines, Malaysia and Thailand such as in Brazil began to be destroyed, because the growth of the agricultural expansion caused a significant decrease in natural resources. Over the past 50 years, the Philippines, there was a loss of 2.4 acres of vegetation every minute, which is attributed to two factors: growth of agriculture and illegal logging

The model of agriculture practiced in Brazil contributes significantly to the expansion of agricultural frontier, increase the production, the productivity and agriculture and the national livestock. However, this performance has led to great reduction of the cover native forest and, consequently, the supply of products of forest origin, besides exposing the lands to loss of fertility, erosion process and water pollution.

In the northeast of Pará state, as in other regions of the Amazon, the intense agricultural activity, with emphasis on removal the primary forest for pasture establishment, agriculture of overthrow and burn, indiscriminate deforestation caused by human activity in terms of economic activities and disorderly logging has been a major factor to accelerate the process of soil alteration.

To mitigate these imbalances, in the Pará state, especially in the northeast region, timber companies, large and small producers located in the cities of Tailândia, Bragança, Igarapé-Açu and Aurora do Pará, began the reforestation on degraded areas in there existent, through use of monocultives and agroforestry systems (ROSA, 2006; RUIVO et al., 2006, SOUZA et al. 2007; RUIVO et al., 2007, CODEIRO et al. 2009; OLIVEIRA, 2009). It was observed that with the reforestation of these areas the quality and quantity of soil organic matter were slow and continuously recovery .

The fertility of the soil, in edaphoclimatic local conditions, is associated with the content of organic matter in the soil (MOREIRA; COSTA, 2004). However the need to seek a sustainable agriculture, the pressure of national and international society requires techniques that protect the agricultural systems After all, the model of traditional agriculture practiced in the Amazon is unsustainable.

For the reduction of land degradation is necessary the use of conservataive techniques to identify the most profitable activities in the region allowing for a harmonious environment coexistence for agricultural economically viable and environmentally sustainable (SOUSA et al., 2007). The challenge is to identify the correct combinations of species to establish synergistic relationships ideals, so that ensure the key ecological services such as nutrient cycling, biological control of pests and diseases and conservation of soil and water (CARDOSO et al., 2005).

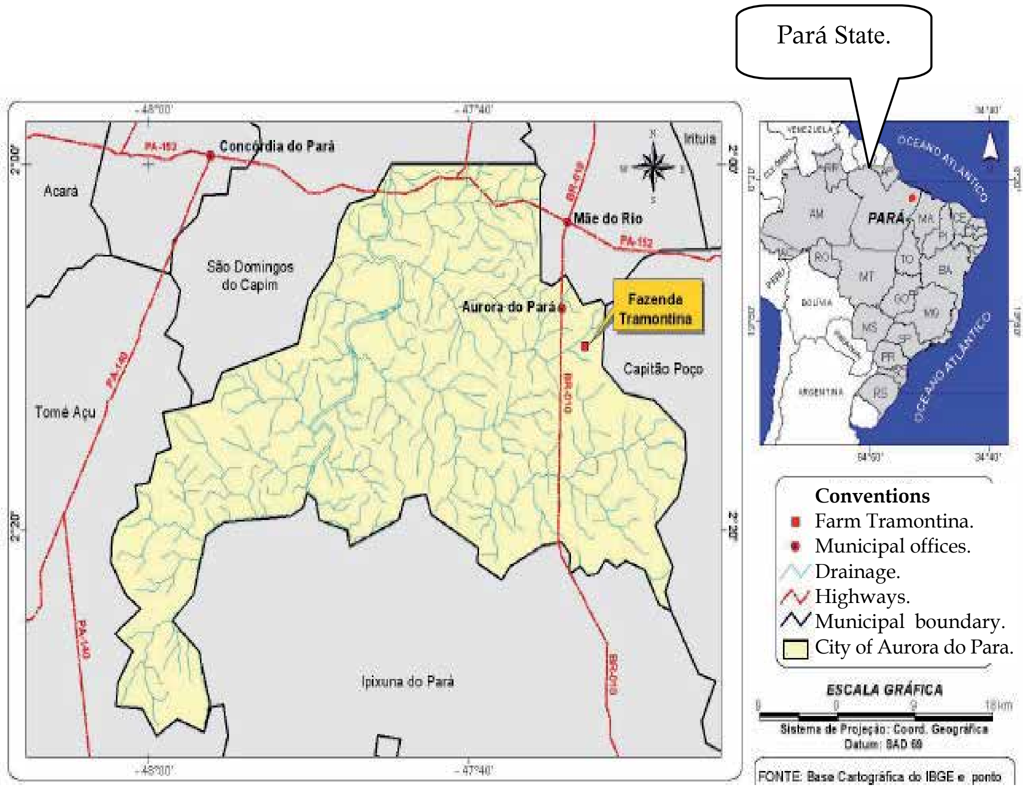
In the state of Para, reforestation with native and exotic species reaches high levels due to the great adaptability of these species in degraded soils. The answers obtained, either in monoculture agroforestry systems, have been effective in the recovery of deforested areas, providing excellent results both for this action as for commercial use, allowing a decrease in aggression to the primary forest and improving the quality of life of populations where this does occur (CORDEIRO, 1999; MONTEIRO, 2004; RUIVO et al., 2007).

Although there are numerous studies on the growth and development of the species native species (CARVALHO, 2004; CORDEIRO, 2007; JESUS, 2004; LORENZI, 2002), comparative studies with the species subjected to different plantation systems and the nutritional behavior of soil in microbiological and biochemists terms are not commonly found in the literature, like as the influence of coverage with different systems involving the vegetables species and their influence on soil quality are still poorly understood. The addition of organic matter to soil, due to stay vegetables residues leads to creation of an enabling environment for better plant development, enhancing microbial activity and consequently the nutritional conditions of the soil. Based on this assumption this research was conducted in the city of Aurora to identifying the soils modifications under physical, chemical and biological properties in areas under reforestation in forestry cropping systems and agro forestry by antropic actions and their impact on edaphic fauna.

2. Materials and methods

2.1 Localization and characterization of the study area

The study was conducted at the Farm Tramontina Belém S/A, located in the city of Aurora do Pará (Figure 1), which belongs to the Mesoregion of Northeast of Pará state and Microregion Bragantina. This area suffered intense anthropogenic changes in the last 50 years due to high extractivist activity, food production and livestock that decimated almost completely their natural vegetation. Over the years a secondary forest (locally known as capoeira) was developed. Despite being a zone considered in environmental impact, this is an area that food supply the capital, mainly grains, greens and vegetables.



Source: Maps IBGE, 2011.

Fig. 1. Map of geographical location of FarmTramontina Belem S/A, Aurora do Pará.

In the locality where this work was developed, a former cattle ranch acquired by an industry of domestic utensils, that was reforested with purposes sustainable economic exploitation and controlled of forest species. The current vegetation is divided in areas of pasture (livestock) abandoned, predominating such as vegetation quicuio-da-amazonia (*Brachiaria humidicola*) among other invasive species, beyond agroforest systems consisting of native species, the main Mogno (*Swietenia macrophylla* King), Paricá (*Schizolobium parayba var. amazonicum* Huber ex Ducke), Freijó (*Cordia goeldiana* Huber) and few exotic, such as eucalyptus (*Eucalyptus* sp) and small areas with secondary forest (capoeira) started around 40 years ago, whose seeds have been used for reforestation native species. The selected capoeiras soil was used as a standard for comparison with the reforestations soil.

The in the region from, According to Thorntwaite (1948) the climate classification in the studied area is type Br A'a, ("humid tropical"). The average annual rainfall is 2,200 mm not equally distributed throughout the year. However, the period from January to June is its greatest concentration (OLIVEIRA, 2009). The average temperature and relative atmospheric humidity are 26 ° C and 74% respectively (CORDEIRO 2007, CORDEIRO et al., 2009). Studies conducted in Brazil (CORDEIRO et al., 2009; 2010) allowed to classify the soil in Aurora do Pará area as Yellow Latossol sandy-clay and the occurrence of concretionary laterite levels in some areas, hydromorphic soils along streams and plain relief to gently rolling inserted on the plateau demoted from Amazon. The nutritional characteristics described in these studies show that they have a low supply of available essential nutrients and low tenor in organic matter (CORDEIRO et al., 2010).

2.2 Cropping systems studied

Since the 1990s were planted around 1,043 ha submitted to different types of planting reforestation with the use of species such as Mogno (*Swietenia macrophylla* King) by the great commercial value abroad, Ipê (*Tabebuia heptaphyta* Vellozo), Cedro (*Cedrella fissilis* Vellozo), Jatobá (*Hymenaea intermedia* Ducke var. *adenotricha* (Ducke) Lee & Lang.). Since 1994, the Paricá (*Schizolobium parayba* var. Amazonicum Huber ex Ducke), is the species with high commercial value used in the reforestation because of its applicability in the production of laminates. In 1996 the Freijó (*Cordia goeldiana* Huber) was introduced by the high referential commercial value in Europe. In 2003, was included in the reforestation process in the Tramontina area the Curauá (*Ananas comosus* var. *erectifolius* LBSmith), a bromeliad that in the Amazon, has a higher concentration in the municipality of Santarém, beyond the regions of Xingu River, Tocantins, Maicuru, Trombetas, Paru, Acará and Guamá. In the Pará state, the Curauá stands out in the Bragança and Santarém districts (OLIVEIRA, 2009).

The experimental design was completely randomized, with four systems under reforestation and three repetitions in each system. (S1) Monocultivation system with curauá, (S2) agroforestry system with paricá and curauá, (S3) monocultivation system with paricá, (S4) agroforestry system with paricá, freijó, mogno and (S5) varied capoeira (Table 1). All cropping systems such as the capoeira were subdivided into four parcels 24 x 19 m (456 m^2), which totals 1,824 m^2 of area analyzed.

At the time of planting was performed organic fertilization with manure of corral (500g/pit) and bed chicken (150g/pit) for agronomic and forest species, respectively. In the first year of the forestal planting were performed three fertilizations, at 45, 180 and 300 days, using 150 g/pl of the formula NPK 10-20-20. In the planting Curauá, we used 10 g/pl of the formula NPK 10-10-10 at the beginning and end of the rainy season, in the first two years of planting.

Systems	Forest species	Age (years)
S1 Monocultivation	Curauá (*Ananas comosus var. erectifolius* L.B.Smith)	06
S2 Agroforestry	Paricá/Curauá (*Ananas comosus var. erectifolius* L.B.Smith)	06
S3 Agroforestry	Paricá, Mogno (*Swietenia macrophylla* King), Freijó (*Cordia goeldiana* Huber)	08
S4 Monocultivation	Paricá	06
S5 Capoeira varied		15

Table 1. System of crops, forest species and ages of reforestation, in the Farm Tramontina Belém S/A, Aurora do Pará.

In cropping systems with curauá (S1), agroforestry system with paricá, mahogany, freijó (S3) and in the cropping system with paricá (S4) occured just the cut of the grass, that was left on the soil of these cropping systems, no irrigation in any of them. In agroforestry cropping system with paricá/curauá was made fertilization with manure of corral (500 g/pit) and bed chicken (150 g/pit) (CORDEIRO et al., (2009).

2.3 Collection and preparation of the soil samples for physical, chemical and biological analysis

In all locations were collected soil samples deformed and undeformed in December 2009. Samples were collected by opening mini-trenches where soil samples were extracted from the depths: 0-10, 10-20, 20-40 cm, from transects in areas previously determined.

In each study area were collected 3 composite samples of soil from 5 single samples and were stored in plastic bags, conditioned in cool boxes containing ice for stagnate or decrease the microbial activity. The chemical, physical and biological analysis were made by technicians in the soil laboratory of the Museu Paraense Emílio Goeldi - MPEG.

2.4 Collection, preparation and identification of the soil fauna

The Pedofauna collections was performed using kind traps "pitfall-traps" (Figure 2).

These traps were consisted of plastic containers (08 cm x 12 cm) buried in the soil to a depth of 12 cm, with the leaked extremity leveled with the surface of soil, where they remained for three days (AQUINO et al, 2006).

In each plot of each treatment, the same depth, were placed four (04) traps, and inside each one of them, was added 60 ml of the preservative substance: 70% alcohol, distilled water (ratio 3:1, regarding the use of alcohol); biodegradable detergent (3 drops) and formaldehyde (10 ml). The fall of undesirable objects was prevented with a cover plate of polystyrene, supported by small wooden rods (AQUINO et al, 2006). The edaphic fauna, after collected, was taken to the laboratory where they were sieved (0.2 mm) to remove the fragments of plant and residues of soil. The identification of edaphic fauna was at the level of Order, with the aid of a stereomicroscope and the specific literature (BORROR, DELONG, 1988, BARRETO et al., 2008).

Fig. 2. Trap for capturing the edaphic fauna implanted in the Farms of Aurora do Pará, Bragança and Tailândia.

2.5 Determination of the physical and chemical caracteristics of soil

The granulometric composition was determined by densimeter method (EMBRAPA, 1997) and textural classification of soil in each system was performed using the textural triangle (LEMOS & SANTOS, 2006). The soil density (Ds) was determined by the volumetric ring method type Kopecky.

In the characterization of soil were performed the following measurements: total N, by distillation in semimicro Kjeldahl (BREMNER, MULVANEY, 1982), pH in potentiometer in the relation soil:water 1:2.5, organic C, by volumetric method of oxidation with $K_2Cr_2O_7$ and titration with ammonium ferrous sulphate, Ca, Mg and Al exchangeable in extractor of KCl 1 mol L^{-1} and measured in atomic absorption, exchangeable K and Na in Mehlich-1 extraction solution and determination by flame photometry, P available in Mehlich-1 extraction solution and determination by calorimetry, H + Al were extracted with calcium acetate 0.5 mol L^{-1}, pH 7.0 and determined volumetrically with NaOH solution.

From the values of potential acidity (H + Al), exchangeable bases and exchangeable aluminum, the capacity of total cation exchange (CTC) and cation exchange capacity effective (CTCe) were calculated. Relations were also calculated C/N of soil and the organic carbon stock (EstC), using the formula EstC = Corg x Ds x e/10, according to Freixo et al. (2002).

2.6 Determination of carbon (CBM) and nitrogen (NBM) of the soil microbial biomass

We used the fumigation-extraction method to estimate microbial biomass carbon (CBM) (Vance et al., 1987, Tate et al., 1988). The determination of microbial biomass carbon (C-BMS) of the fumigated and not fumigated extracts was made by titration (dichromatometry) according to De-Polli, Guerra (1999). For CBM calculation , the C content of fumigated samples were subtracted from the values of non-fumigated samples, the difference being divided by the value kc = 0.26 (FEIGL et al., 1995). The estimate of Nmic was made from Kjeldahl digestion. The correction factor (Kn) used for the calculation was 0.54 (BROOKES et al. 1985; Joergensen; Mueller, 1996). From the original values were calculated relations between C_{mic} and C_{org} of soil (C_{mic}/C_{org}), and N_{mic} and N_{total} of soil (N_{mic}/N_{total}), by the following equations: $(C_{mic}/C_{org})x100$ and $(N_{mic}/N_{total})x100$, respectively. These indices indicate the fractions of C_{org} and N_{total} that are incorporated in BM, expressing the quality of MOS (GAMA-RODRIGUES, 1999).

2.7 Determination of basal respiration of microbial biomass and the soil metabolic quotient

The basal respiration was estimated by the amount of C-CO_2 released within 10 days of incubation (JENKINSON & POWLSON, 1976). This technique allows the determination of the soil microbial activity, being quantified from the evolution of CO2 produced in respiration of the microorganisms in samples free of roots and possible insects. The metabolic quotient (qCO_2) is calculated as the ratio between the rate of basal respiration and the microbial biomass carbon (ANDERSON & DOMSCH, 1993).

2.8 Statistical analysis

The two-way ANOVA was used to verify differences between the cropping systems studied. When found a significant (5%), the averages of each variable were tested by the

Tukey test ($p < 0.05$). Additional analysis was also the determination of principal components (PCA) and cluster analysis to determine the degree of correlation between physical, chemical and biological data to be analyzed by soil grouping. Them, according to the variation of its characteristics a multivariate analysis can be use.

3. Results and discussion

3.1 Physical and chemical properties of soil under forestry and agroforestry systems

The production systems studied showed differences in soil physical properties. The type of soil in cropping systems S1 (monocultivation with curauá), S3 (agroforestry system with paricá, mogno, freijó and curauá) and S4 (monocultivation with paricá) is classified as franc sandy loam and only in the S2 (agroforestry system with paricá and curauá), presented soil type franc sandy clay (Table 2). Study conducted in a Latossoil in the Amazon (SILVA JUNIOR et al, 2009) showed that the study of this aspect of the soil is important because it is related to the dynamics of organic matter. This justifies the textural classification made in our study.

NOTATION	DPT (cm)	Ts	Fs	Cl	S	RSC	TC	Ds
			g/kg					g/cm^3
S1	0 - 10	729	157	68	46	0,67	S L	1,50
	10 - 20	716	147	83	54	0,65		1,43
	20 - 40	610	160	137	93	0,67		1,54
MEAN	---------	**685**	**155**	**96**	**64**	**0.66**		**1.47**
S2	0 - 10	491	189	184	136	0,73	S C	1,37
	10 - 20	408	169	289	134	0,46		1,62
	20 - 40	362	149	343	146	0,42		1,60
MEAN	---------	**420**	**169**	**272**	**139**	**0.54**		**1.53**
S3	0 - 10	687	148	80	85	1,06	S L	1,42
	10 - 20	672	130	80	118	1,47		1,58
	20 - 40	627	156	122	95	0,77		1,51
MEAN	---------	**662**	**145**	**94**	**99**	**1.10**		**1.50**
S4	0 - 10	651	204	96	49	0,51	S L	1,36
	10 - 20	630	222	80	68	0,85		1,48
	20 - 40	588	170	90	152	1,68		1,57
MEAN	---------	**623**	**199**	**90**	**88**	**1.01**		**1.47**

DPT: Depths; **Ts**: thick sandy; **Fs:** fine sand; **Cl:** clay; **S**: silt; **RSC**: relation silt clay; **TC**: textural classification; SL: Sandy loam; SC:Sandy clay; **Ds:** density of soil.

Table 2. Granulometry, textural classification and density of soil of cropping systems studied. Farm Tramontina Belém S/A in Aurora do Pará.

With regard to the clay content in the culture system S2 (agroforestry system with paricá and curauá), in the depth from 0 – 10 cm high levels were detected when compared with other systems in this same depth, as shown in Table 2. Study conducted (LAVELLE et al, 1992) in the humid tropics, showed as a result a lateral variation in the soil granulometry and, according to the researchers, this may influence the training capacity of the stocks of exchangeable cations on the surfaces of colloids, this case, clay mineral. Then, the results found in this study for the S2 cultivation system may be indicative of the improved in the capacity of formation of the exchangeable cations.

The lowest content of clay fraction occur in the cropping systems S1 (monocultivation with curauá), S3 (agroforestry system with paricá, mogno, freijó and curauá) and S4 (monocultivation with paricá). The value for the lowest average was found in the cropping system S4 compared with the other cropping systems studied. Freire (1997) reports that the natural fertility of the soil depends on the adsorptive capacity of clay-minerals and organic colloids, with that, it's possible to affirm that in the cropping system S4, despite the low clay content, there are adsorption capacity and organic colloids in balance that allows the maintenance of natural soil fertility of this cropping system.

The relation silt *versus* clay proved to be higher in the cropping system S3 (Table 2), this demonstrates that the degree of weathering occurred in this area decreases with the depth, ie, the degree of weathering of the soil is high, as occur in the Latosoils.

The analysis of soil density showed that, among the systems studied, soil is more dense in the cultivation system S2 (agroforestry system with paricá and curauá). But, as pointed out Santana et al. (2006) density can be an attribute for analysis on the cohesion of the soil horizons, however there is a limitation for such use, ie, the density of the soil suffers from interference of granulometry that can presents high values, this would correspond to cohesive horizons, and this would affect the penetration of root of vegetables.

In this aspect, it was verified that, in the cropping system S2, the density is more pronounced between 10 to 20 cm when compared with other systems. In addition, this cultivation system, based on the exposed by Santana et al. (2006), we can consider this soil as "cohesive" as a results contained in Table 2.

The results indicate very low acidity (pH > 4.5), and as clay-minerals react with water from the soil, absorbing H +, this may explain the variation of acidity occurred in the cropping system S2, although present statistically significant effect. Was verified that in the cropping systems S1 (curauá monocultivation) and S3 (agroforestry system with paricá, mogno, freijó and curauá) the pH value, on average, has no statistically significant effect (Table 3). This can be explained by the content of total clay and sand which is also equivalent between them, as shown in Table 2.

In the cropping system S4 (paricá monocultivation), the pH was found to be constant in the three depths, and this may be due to small variations in the levels of sand and clay that were lower compared to other cropping systems, and this may explain the decrease of pH value in relation to the cropping system S2 and a slight increase in relation to cropping systems S1 and S3 (Table 2).

The tenors of Corg in cultivation system S2 (agroforestry system with paricá and curauá) were superior to other treatments evaluated (Table 3), even with scarce cover vegetation. Study conducted (Silva Junior et al, 2009) in Amazonian Oxisols after transformation to pasture, showed that carbon concentrations are high in clay soils, independent of vegetation cover. But the most plausible explanation is provided by Cordeiro et al. (2009), because the authors report that the area where this system of crops is located was fertilized with cattle manure (500 g/pit) and bed chicken (150 g/pit). This proves that even on degraded land, the use of organic cover helps soil fertility and improving the quality of it (Monteiro, 2004).

In the systems studied, we observed that the Corg content decreases according to depth and clay content (Table 2) in the depth of 0 - 10 cm, the Corg content of the soil surface within the studied systems are high. The research conducted about the relation of Corg contents and soil depth (Dejardins, et al. 1994; Koutika et al., 1997) showed that the trend of content of Corg is in decreasing accordance with increasing depth. This pattern of behavior on the content of Corg was observed in our study. Study carried out in a toposequence in central Amazonia (Marques et al., 200) report that the Carbon content are high in the surface layers to 25 cm (4.48 ± 0.08). Then, the high content of Corg found in cropping systems study corroborates the assertion of those authors.

The highest average of Carbon stock was found in the cultivation system S2 (Table 2), where was found the highest granulometric average, especially the clay and Ds. In descending order, the cultivation system S1 has the second highest average. In the cultivation systems S3 and S4 the average of carbon stock decreases, although the clay content is approximate to that contained in the cropping system S1. However the content of sand has an average ranging from 800 to 840 g/kg, and the variation in average clay content is between 90 and 96 g/kg (Table 1). This may be one explanation for the carbon stocks present a decrease in average of these treatments compared in the cropping system S2 (Table 2).

NOTATION	DPT	**pH**	**Corg g/kg**	**Cs**
	(cm)			Mg C.ha^{-1}
S1	0 - 10	4.5	13,84	20.76
	10 - 20	4.4	11,70	33.46
	20 - 40	4.1	6,90	42.50
MEAN	**---------**	**4.3**	**10.81**	**32.24**
S2	0 - 10	4.9	24,52	33.61
	10 - 20	4.9	12,96	41.99
	20 - 40	5.0	7,04	45.05
MEAN	**---------**	**4.9**	**14.84**	**40.22**
S3	0 - 10	4.4	8,59	12.02
	10 - 20	4.3	7,89	24.93
	20 - 40	4.3	7,73	46.68
MEAN	**---------**	**4.3**	**8.70**	**27.88**
S4	0 - 10	4.4	9,88	13.34
	10 - 20	4.4	7,38	21,84
	20 - 40	4.4	5,83	36.31
MEAN	**---------**	**4.4**	**7.07**	**23.93**

DPT: Depths; **Corg**: carbon organic; **Cs**: Carbon stock.

Table 3. Values pH (H_2O), tenors of carbon organic (Corg in g/kg) and carbon stocks (Mg C.ha^{-1}).

3.2 Relation between physical and chemical attributes

The result of the correlation (r) between the high content of Corg, clay and sand fraction in the cropping system S2, showed an increasing content of Corg in this cropping system (Table 4).

Attributes analyzed	Total clay (g/Kg)	Sand (g/Kg)	Ds (g/cm^3)	Relation Silt x clay
pH	0.98 ($p < 0.05$)	- 0.98 ($p < 0.05$)	0.77 (ns)	- 0.66 (ns)
Corg (g/kg)	0.81 (ns)	- 0.57 (ns)	0.90 (ns)	- 0.88 (ns)
Carbon stock (Mg C.ha^{-1})	0.82 (ns)	- 0.75 (ns)	0.86 (ns)	- 0.92 (ns)

Corg: carbon organic; Ds: Density of soil.

Table 4. Analysis of canonical correlation between the physical and chemical attributes of soil in the cropping systems studied. Farm Tramontina Belém S/A in Aurora do Pará.

Study ever done on the relation Corg versus clay content (TELLES, 2002) explained that high clay content allows the formation of macroaggregates and microaggregates that promote physical protection to the Corg, and avoid rapid decomposition of the same. Correlating this result with what was obtained in our study; it is possible to explain the high content of Corg found in S2 culture system, using the same argument. As for the stock of carbon (Cs) results showed that this stock decreases in relation to the increased depth in cropping systems studied.

The determination of the hierarchical clustering (HCA) revealed a approximated relation between physical and chemical attributes of soil subjected to analysis, because, according to Barreiro & Moita Neto (1998) this suggests a correlation between the variables of this data set. The results (Figure 3) show that there is formation of two groups where in the group A there was a split in the A1 and A2. In this group there was a correlation between the pH - Ds (Group A1), Ds - Silt/Clay (group A2) and Silt/Clay - Corg (group A3).

Another group, silt and clay (group B), confirm that these two variables are heterogeneous with respect to those that make up Group A. These results show that there is variability in the functioning of studied soils in the cropping systems SI, S2, S3 and S4. S3 and S4 are more similar across pH and relation attributes of silt/clay. The cultivation system S1 showed lower similarity with cropping systems S3 and S4 for the same attributes. Thus, one can verify which variables that differentiate the systems studied each other and can interfere or not in the edaphic fauna.

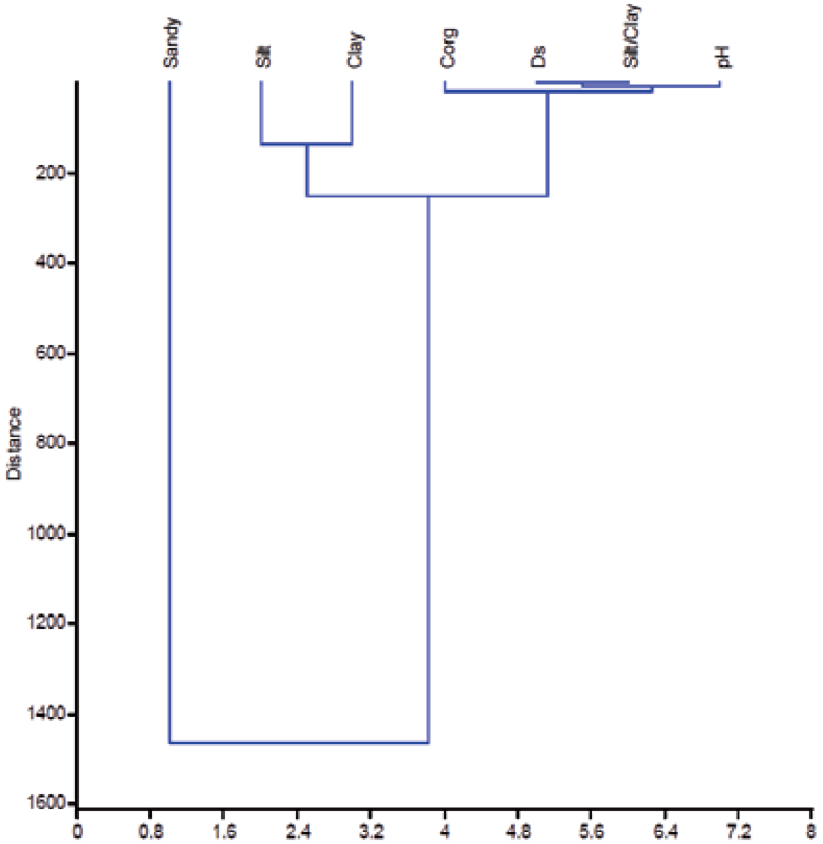


Fig. 3. Grouping of physical and chemical attributes of the cropping systems studied. Farm Tramontina Belém S/A. Aurora do Pará.

3.3 Microbiological attributes

The average content of microbial biomass carbon (CBM) (Figure 4) and the values of the microbial quotient (qMIC) (Figure 5) were higher in the system S4 and S5. In the system S4 the soil was covered with coarse vegetable waste, besides presenting a spontaneous vegetable regeneration between the lines of planting paricá such factors may have favored the maintenance of microorganisms in the soil and therefore increase the microbial carbon content.

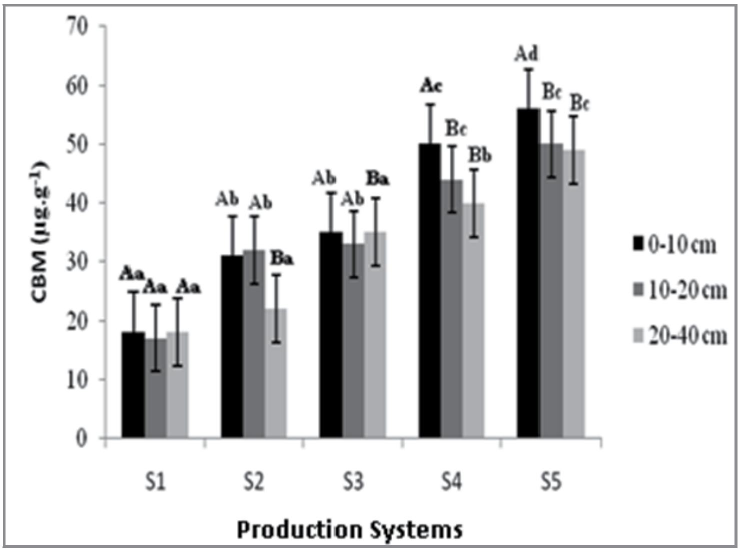


Fig. 4. Values of microbial biomass carbon (CMB) in different production systems.

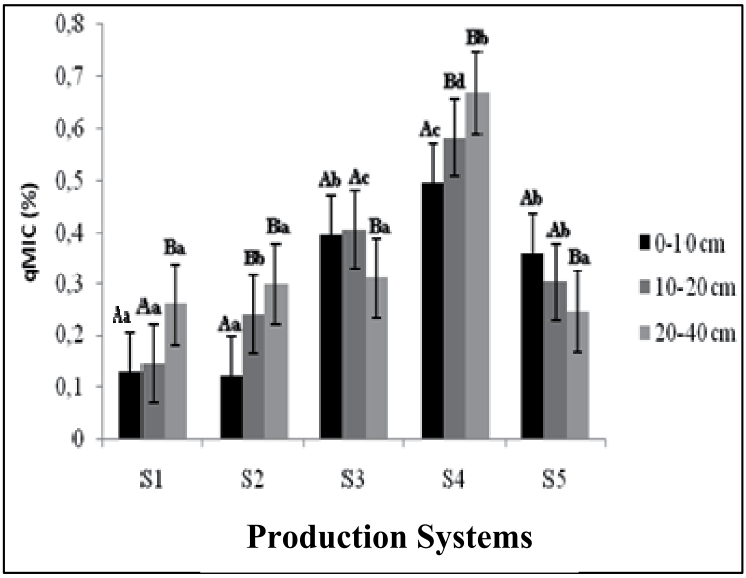


Fig. 5. Values of microbial quotient (qMIC) in different production systems.

For the attribute qMIC very low values were obtained, except in the S4 system, where it was recorded the highest values of qMIC, especially in the layers of the first depth of soil. Jenkinson & Ladd (1981), considered normal that 1-4% of total soil C corresponds to the microbial component, how the collection was done during the dry season, and it is known that water is an important element for microbial activity, it is possible that low values are justified by this fact.

Overall, the results indicate that the incorporation of organic matter is favoring the edaphic conditions and the different systems, especially the S3 and S4 suffering the biggest addition of organic matter, equaling the soils are of capoeira, eventually tending to an equilibrium (OLIVEIRA, 2009; BERNARDES, 2011, PEREIRA Jr, 2011). The Table 5 presents the principal components that shows this relationship. It's possible verify that saturation of bases (V), EC, aluminum saturation (m), Na, and Al were the variables that showed more differences between the systems. In systems S2 and S3, the values of these attributes, in general, are more similar to those found in capoeira.

Attributes	Principal components				
	Comp. 1	Comp. 2	Comp.3	Comp.4	Comp.5
pH	-0,027	0,144	**0,419**	0,195	0,204
Al	**-0,273**	0,003	**-0,314**	0,005	-0,016
H+Al	**-0,303**	0,075	-0,180	-0,018	0,055
Ca	-0,235	**-0,253**	-0,160	0,152	-0,059
Mg	**-0,294**	-0,171	0,119	0,017	-0,008
K	**-0,290**	-0,180	0,095	-0,047	0,032
P	-0,114	**0,371**	-0,206	-0,07	0,071
Na	**-0,254**	0,042	0,091	**0,458**	-0,084
SB	**-0,298**	-0,182	0,074	0,037	-0,024
CTC $_{ef}$	**-0,312**	-0,095	-0,143	0,021	-0,019
CTC $_{pH7}$	**-0,324**	-0,03	-0,086	-0,022	0,022
V%	-0,099	**-0,303**	**0,300**	0,243	-0,063
m%	0,111	-0,176	**0,406**	**-0,326**	-0,064
Cot	-0,164	**0,303**	0,231	0,030	-0,199
EC	-0,126	**0,308**	0,048	**-0,421**	0,002
NT	-0,147	0,153	**0,433**	0,008	-0,161
C/N	-0,132	**0,358**	-0,086	0,036	-0,123
CBM	0,158	**0,304**	-0,018	**0,484**	-0,035
NBM	-0,065	-0,011	0,064	0,02	**0,908**
*q*MIC	**0,279**	-0,078	-0,134	**0,366**	0,031

Table 5. Correlation coefficients between original variables of response and principal components.

The principal component 1 (Comp. 1), that explains 54.00% of the variability of the data, presents the highest correlation for the SB, K, Mg, CEC, Ca and H + Al. The largest negative correlations, which also showed low values occurred with the CBM and qMIC. The principal component 2 (Comp. 2) explains 21.9% of the variability and has the highest correlations for P and COT. The largest negative correlation occurred with the V%.

The principal component 3 (Comp. 3), that explains 12.2% of the variability, presents the higher correlations for P and Ca, and the largest negative correlations were found for pH and COT. In the case of principal component 4 (Comp. 4) explains 5.2% of the variability and was negatively correlated for almost all attributes except for COT. Among the negative correlations stand out CBM qMIC and Ca.

3.4 Edaphic fauna of the forestry system and agroforestry

The faunistic analysis performed on the Farm Tramontina Belém S/A, recorded 2.568 specimens distributed in eighteen (18) taxon of invertebrate and one (01) taxon of vertebrate of the Order Squamata (Gekkonidae) (Table 6) in five culture systems studied, where the prevailing order was Hymenoptera, composed mainly by family Formicidae with 2.151 individuals followed by Coleoptera (78), Collembola (40), Homoptera (67) and Diplopoda (74).

	SYSTEMS						
	S1	S2	S3	S4			
TAXONS	Fi				Total	Fr (%)	(Mean)
INSECTA							
Hymenoptera (Formicidae)	808	667	416	260	2.151	82,82	537,75
Coleoptera	21	15	27	15	78	3.0	19,5
Collembola	6,0	11	21	2,0	40	1.54	9.75
Diptera	13	1,0	11	5,0	30	1.15	7,50
Hemiptera	0,0	1,0	0,0	0,0	01	0.03	0,25
Homoptera	9,0	10	34	14	67	2.57	16,75
Blattariae	0,0	2,0	0,0	2,0	04	0.15	1,00
Odonata	0,0	0,0	1,0	0,0	01	0.03	0,25
Orthoptera	2,0	3,0	5,0	12	22	0.84	5,50
Psocoptera	1,0	0,0	3,0	3,0	07	0.26	1,75
Lepdoptera	0,0	28	0,0	0,0	28	1.07	7,00
Thysanoptera	0,0	0,0	1,0	0,0	01	0.03	0,25
ARACHNIDA							
Acari	8,0	28	14	5,0	55	2.11	13,75
Aranae	3,0	2,0	4,0	6,0	15	0.57	3,75
Opilionida	4,0	3,0	7,0	0,0	14	0.53	3,50
CRUSTACEA							
Isopoda	0,0	1,0	0,0	0,0	01	0.03	0,25
MYRIAPODA							
Chilopoda	1,0	0,0	1,0	0,0	02	0.07	0,50
Diplopoda	17	12	15	30	74	2.84	18,5
SQUAMATA							
Gekkonidae	1,0	3,0	3,0	1,0	08	0.30	1,25
Total	894	785	563	355	2.597	100	

Ordination of taxons second Brusca & Brusca, 2007.

Table 6. Taxons identified, absolute frequency (Fi), relative frequency (Fr) and average of individuals in the cropping systems studied in the Farm Tramontina Belém S/A in Aurora do Pará.

The Diplopoda taxon is present in all treatments, but the highest concentration is in the systems of monocultivation (S1 and S4). In a study of community of invertebrates in litter in agroforestry systems, this order was the second most important (Barros et al., 2006). This importance is due to mobility that they present in the soil, surface and underground, which influences the physical nature of the soil changing porosity, moisture and transport of substances (Correia; Aquino, 2005).

The order Acari is a grouping of vertical habitat in three levels, euedaphics, hemiedaphics and epiedaphics, and the epiedaphics are more tolerant to desiccation (Lavelle & Spain, 2001), although there is low frequency of individuals, it is higher when compared with those obtained in studies in savannas of Pará (Franklin et al., 2007).

Ants have been widely used as biodindicadores in various types of impacts, such as recovery after mining activities, industrial pollution, agricultural practices and other land uses (Smith et al, 2009). In addition, the class Insecta, which belongs to the ant, often grouped according to trophic groups, and the availability of nutrients in the ecosystem (Leivas & Chips, 2008). They are important in below-ground processes, by altering the physical and chemical properties and the environment, its effects on plants, microorganisms and other soil organisms (Folgarait, 1998).

These may be the possible explanations for the faunistic results of this taxons (Hymenopetera) Family Formicidae, with the highest absolute frequency (Fi) in the cropping system S1 (curauá in monocultivation) and lower absolute frequency in the cropping system S4 (paricá in monocultivation) as well as in other culture systems studied (Table 7).

Adult and immature Coleoptera, Collembola, Diplopoda, Diptera and Homoptera adults had higher absolute frequency in the cropping system S3 (paricá + mogno + freijó + curauá) (Table 7). This may show a variety nutritional or of habitat, or still an increase in the prey - predator relation. The same was not found in the monocultivation systems for these taxons.

Macroarthropods of soil has an important role in tropical terrestrial ecosystems, exerting a direct influence on the formation and stability, an indirect influence on the decomposition process through strong participation in the fragmentation of necromass (ARAUJO; BANDEIRA; VANSCONCELOS, 2010). Work already carried out in terra firma forest ecosystems in the state of Pará, also found the presence of Hymenoptera, Coleoptera, Collembola, Homoptera, Acari and Diplopoda, grouped or not (Macambira, 2005; & Garden Macambira, 2007; Ruivo et al. 2007), which corroborates with the edaphic fauna found in Aurora do Pará

The greatest diversity of species occurred at S3 (Table 7), this can be attributed, among other factors, the variety of nutrients, because S3 is an agroforestry system where there is occurrence of paricá, mogno, freijó and curauá. In addition, there may be no natural predators of these species or still the ephemeral life cycle leads to a reproduction in greater numbers, but these factors were not analyzed in this study.

The lowest levels of the Shannon-Wiener diversity, therefore the greater species diversity occurred in the cropping system S1 (curauá in monocultivation) and S2 (agroforestry system paricá + curauá). This may be due to movement of other species of invertebrates through of ecotones that over there exist. It is possible that this displacement has occurred in search of food or place to reproduction, or even to escape from possible predators in areas near to these cultivation systems. It should not be ruled out the hypothesis that the curauá produces some substance that is palatable to invertebrate species diversity and this is a nutritional option for them because this plant is present in both cropping systems that had the lowest diversity indices of Shannon -Wiener.

	Systems			
	S1	S2	S3	S4
Diversity index (H’)	0,22	0,26	0,51	0,48
Population density (individuals/m^2)	0,69	0,58	0,43	0,26

Table 7. Diversity index Shannon-Wiener (H') and population density found in cropping systems studied at Fazenda Tramontina Belém S/A in Aurora do Pará.

The highest indexes of diversity of Shannon-Wiener occurred in cropping systems S3 (parica + magno + freijó + curauá) and S4 (parica in monocultivation). This shows lower diversity of species, although in S3 there is differents plant species, which would cause nutritionals offerings and different habitats, and this would promote greater diversity of species. Study performed about plant diversity and productivity of plants and the effects on the abundance of arthropods (Perna et al, 2005) showed that productivity in the plant structure, local abiotic conditions, physical disorders of the habitats are factors that interact with the diversity of plants and which also influences the abundance of arthropods. This can be an explanation for the low diversity found in the cropping system S3 in our study.

In S4, occurs monocultivation with paricá. This features a lower nutritional diversity and of habitats, which in turn attracts lower diversity of macrofauna, especially ants. Suggest the hypothesis that this plant produces some substance not palatable or that act on the reproductive cycle in the majority of taxons identified. It is also possible that there are a greater number of predators in relation to other systems cultivation studied, or even occurred edaphic variations that did not allow the diversity of species and greater population density because this cropping system, the highest number of absence (seven taxons) among the eighteen taxons identified (Table 6). When the population density, the highest concentration indivíduos/m^2, occurs in S1, where there is a monocultivation of curauá. As this culture system does not present sub-forest for vegetal cover and shading that would mitigate the temperature at the soil surface, it is possible that the solar radiation incident directly on the ground promotes an increase in photosynthetic rate, increasing the supply of nutrients, as well as raises the temperature of the same and is one of the factors that contribute to the reproduction of these ants (Harada & Banner, 1994, Oliveira et al., 2009). But do not dismiss as a possible explanation for the results obtained in two cropping systems, the hypotesis of correlated interferences, for example, environmental variables, ephemeral life cycle, presence or absence of predators, temperature, precipitation, brightness, among other variables in this study were not analyzed.

3.5 Edaphic fauna and attributes of soil

The relation between edaphic fauna and soil attributes (pH, Corg, Ds, relation silt/clay) is shown in Figure 6.

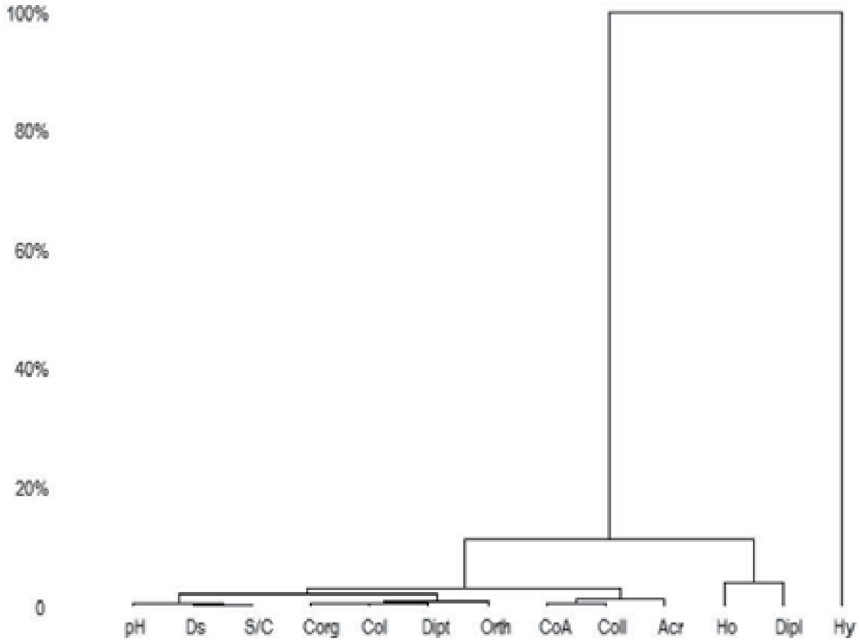


Fig. 6. Grouping between edaphic fauna of greater absolute frequency in the studied treatments, physical and chemical attributes of soil. Campo Experimental of the Tramontina Belém S/A. Corg = carbon organic; S/A = relation silt/clay, Ho = Homoptera; CoA = Coleoptera adult; dipl = Diplopoda; CoI = immature Coleoptera, Coll = Collembola; dipti = Diptera; Orth = Orthoptera; Acr = Acari; Hy = Hymenoptera.

The results showed that (I) the immature Coleoptera taxon has high similarity to the taxon Collembola and constitutes the group 1; (II) the taxon Diptera presents similarity to the taxon Orthoptera and constitute the second group. The group 2 has similarity with group 1, (III) the taxon Acari presents similarities with groups 1 and 2, constituting the third group, (IV) the taxon Coleoptera adult presents similarity to the taxon Diplopoda, constituting the group 4. (V) Groups 1, 2 and 3, have similarity to group 4. (VI) the taxon Homoptera has similarity as group 4, thus constituting the group 5. (VII) Groups 1, 2, 3, 4 and 5 they correlate with the physical attributes (Ds, relation silt/clay), but did not correlate with the chemical attributes (pH, Corg).

The taxon Hymenoptera showed that is not correlated with the physical attributes: Ds and relation silt/clay, and neither with chemical attributes: pH and Corg. Also has no similarity to other taxons analyzed. But it is possible that other edaphic variables correlate with this taxon, but these were not objects of the present study.

Ants have been widely used as biodindicadores in various types of impacts, such as recovery after mining activities, industrial pollution, agricultural practices and other land uses (Smith et al, 2009). In addition, the class Insecta, which belongs to the ant, often grouped according to trophic groups, and the availability of nutrients in the ecosystem (Leivas & Chips, 2008). They are important in below-ground processes, by altering the physical and chemical properties and the environment, its effects on plants, microorganisms and other soil organisms (Folgarait, 1998).

These may be the possible explanations for the faunistic results of this taxons (Hymenopetera) Family Formicidae, with the highest absolute frequency (Fi) in the cropping system S1 (curauá in monocultivation) and lower absolute frequency in the cropping system S4 (paricá in monocultivation).

The order Acari has the major absolute frequency in S2 (Table 3), maybe has better adaptability to the SAF, and the physical attributes shown in Figure 5, which may also is occurring with Homoptera, Collembola and Coleoptera immature. Even in this agroforestry system, the absolute frequency of the taxon Coleoptera, Hymenoptera and the population density decreases, according to data contained in Table 4. This may be related to the increase of soil density and decrease in the silt/clay relation contained in Table 2.

With the modifications imposed by use of soil, particularly by agriculture, the fauna and the microorganisms, in different degrees of intensity, are affected by the impacts caused by agricultural practices, that may alter the composition and diversity of soil organisms.

The addition of new organic matter through the incorporation of waste or the maintenance of forest cover (using the agroforestry system, with or without burning the area) or even a diversified system (as occur in Aurora do Pará), show the importance of maintenance, incorporation and slow decomposition of organic matter on the ground.

So far, the studies show that the types of management adopted did not influence negatively the characteristics of soil and that adding of diversified organic matter in the soil, the retention and incorpration and slow decomposition of these residues led to the creation of an edaph-environment favorable to the maintaining soil quality.

The set of attributes of the soils here studied, especially those related to microbial biomass and chemistry, was adequate to indicate the quality of the substrate. However, the continuation of this kind of work, in the long term, it is necessary, in order to identify differences in biological characteristics of soil between the different management systems, especially taking into account the local climatic variation. Thus, it is necessary to intensify studies of the seasonal variation of soil attributes, the variables listed as indicators of soil quality and intensify the studies in determinated practices of management, such as the tillage and the SAF as potential in the carbon sequestration.

4. Conclusions

The result show that the types of management adopted did not influence negatively the characteristics of soil and adding organic matter to the diverse soil, retention and development and slow decomposition of these residues led to the creation of an edafoambiente of maintaining soil quality. The set of attributes of the soil studied here, especially those related to microbial biomass and chemistry, was adequate to indicate the quality of the substrate. However, the continuation of such work in the long term and different climatic conditions, it is necessary, in order to identify differences in biological characteristics under different soil management systems, especially taking into account the local climatic variation.

The Paricá (*Schizolobium amazonicum* Huber (Ducke)) is a viable native species for recuperation of disturbed areas and with detach in the wood market, nationally and internationally. Its rapid growth and adaptation to areas with low nutrient levels allow it to be optimum in agroforestry, being the second plant species used in reforestation in the Para state , and primarily designed for industry of lams rolled. Thus, it is necessary to intensify studies of the seasonal variation of soil attributes, the variables listed as indicators of soil quality and enhance studies in certain management practices such as tillage and the SAF as a potential in carbon sequestration.

5. Acknowledgements

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11

Plant Productivity is Temporally Enhanced by Soil Fauna Depending on the Life Stage and Abundance of Animals

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1. Introduction

In terrestrial ecosystems, nutrient recycling is driven by the belowground decomposition process because it supplies most of the production to the soil system (Swift *et al*. 1979; Cebrian 1999). Soil links the aboveground plants and the belowground community (Wardle, 2002). Soil nutrient cycling is controlled by interactions among living soil organisms, plant litter quality, soil physical and chemical status, temperature, and water condition. In soil-organism processes, large soil animals rapidly change microbial activity (Hanlon and Anderson 1980) and the litter decomposition rate (Bonkowski *et al*. 1998) and modify soil structure (Barois *et al*. 1993). Consequently, primary decomposition and plant growth are affected not only by microbes but also by soil animals (Wall and Moore 1999; Wardle 2002). The overall faunal contribution to nitrogen (N) mobilization has been estimated as approximately 30% in forest ecosystems (Verhoef and Brussaard 1990). Schröter *et al*. (2003) calculated that the total amount of N mineralized by fauna in European coniferous forests ranged from 11 kg N ha^{-1} a^{-1} in northern Sweden to 73 kg N ha^{-1} a^{-1} in Germany.

The presence of keystone species strongly affects decomposition and nutrient dynamics. In particular, the train millipede *Parafontaria laminata* is widely dominant in soil invertebrate communities of central Japan, with its late-stage (from the 6th to final instar) larvae enhancing N availability by 69% (Toyota *et al.* in press). The enhancement of soil N availability in forest soils by late-stage larvae of this millipede can lead to changes in aboveground plant productivity. Earthworm casts stimulate the growth of most plant species in grassland soil (Zaller and Arnone 1999), but whether soil animals alter plant productivity under natural conditions in forest soils remains poorly understood.

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Previous studies on the effects of soil fauna on plant production have mainly been laboratory microcosm experiments, and they have produced mixed conclusions (Brown *et al.* 1999; Scheu 2003). Some studies found that soil animals increase plant production and nutrient utilization (*e.g.*, Setälä and Huhta 1991; Bardgett and Chan 1999), while others reported redundant or negative impacts of soil animals. One possible reason for this discrepancy is that soil animals have different effects on soil nutrient dynamics depend on their feeding type (Lavelle *et al.* 1997). Another possible reason is that differences in soil chemical composition and organic matter input to soil lead to changes in soil animal effects (Tiunov and Scheu 2004).

The rates of nutrient cycling are usually not constant, even in a mature forest ecosystem, due to the effects of processes such as seed masting (Selås *et al.* 2002) and periodic insect outbreaks. The 17-year periodic appearance of cicadas in North America provides a nutrient pulse to the forest soil resulting from the mass of carcasses, in turn increasing foliage N content and seed mass (Yang 2004). Despite these temporal differences in nutrient dynamics, many studies assume links between plant growth and decomposition processes on a forest floor in the short-term.

Populations of *P. laminata* have a synchronized life cycle and undergo simultaneous molts at particular stages according to seasonal temperature rhythms (Fujiyama 1996). The larvae live in the soil for 7 years (Fig. 1a, b) before they reach the adult stage (Fig. 1c). Their population consists of only a single age cohort, so adult swarming is observed at 8-year intervals (Niijima and Shinohara 1988). The huge abundance and synchronized cohort of *P. laminata* provide a good opportunity to investigate the soil-animal contributions to nutrient dynamics at the forest floor (Hashimoto *et al.* 2004; Toyota *et al.* 2006). Due to their heterogeneous abundance within the same region in forest soil, the effects of *P. laminata* on plants can be distinguished, even under field conditions.

The train millipede *P. laminata* can enhance plant production in two major ways. First, changes in soil N availability through millipede activity affect plant production. Late-stage larvae enhance N mineralization in soil when millipede abundance is high (Toyota *et al.* in press). By contrast, adults contribute to transforming plant litter into soil, but do not increase N availability in the adult phase. Due to differences in soil N dynamics with developmental stage, the larvae and adults may affect plant productivity differently. Second, carcasses of adults contain higher concentrations of available phosphorus (P) for plant (Toyota, unpublished data). Since forest production is usually limited by P availability in soil (*e.g.*, Crews *et al.* 1995; Vitousek and Farrington 1997), the P supplied from their carcasses to the forest floor after the death of adults will result in increased plant production and changes in leaf quality.

Here, we studied how aboveground production can be affected by soil animal abundance and developmental stage. Effects of the train millipede were estimated to compare production between natural low-abundance and high-abundance millipede plots in the field. To test whether they temporally have different effects from late stage larvae to after the death of adults, the periods examined for estimating plant productivity were the 2 years before and after the adult active year, over a total of 5 years. Annual herbaceous plants should detect such temporal effects easily. In this paper, we tested the following two predictions: late stage larvae enhance leaf N content and production in the herb layer, and after adult death, the millipede decomposition increases herbaceous annual plant production and leaf P content. Specifically, we examined the effects of the millipedes on the productivity of annual dwarf bamboo, which dominates the undergrowth of temperate forests in Japan.

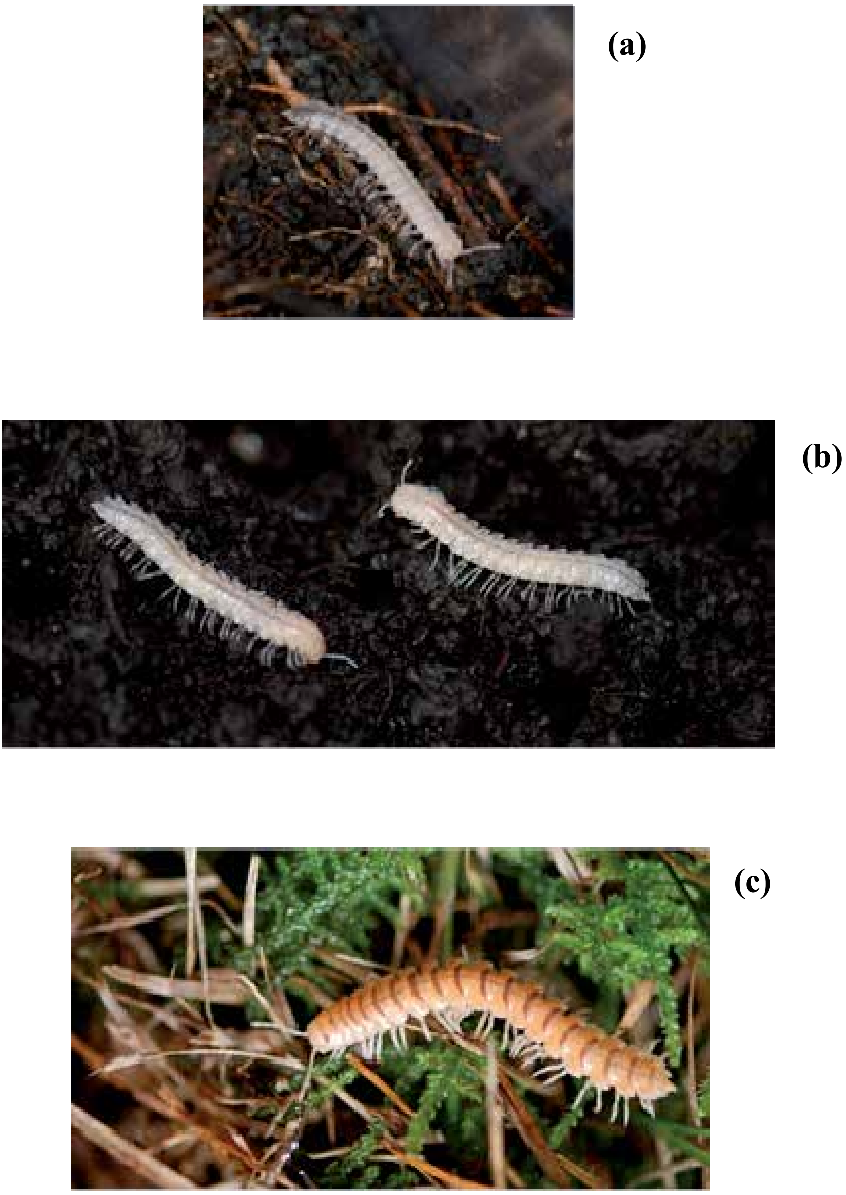

Fig. 1. The train millipede, *P. laminata*, in the soil as (a) a 6th-instar larva, (b) 7th-instar larvae, and (c) on the forest floor as an adult.

2. Materials and methods

2.1 Study site

We established research plots at four different field sites in larch forests of Mt. Yatsugatake in Yamanashi Prefecture, central Japan (1350–1400 m above sea level, 35º54'12–46"N, 138º20'32"–24'03"E). The plots comparing low- (reference) and high-abundance areas of the train millipede were carefully chosen to avoid differences in soils, vegetation, and topography among plots. This region is characterized by a cool–temperate climate with mean annual precipitation of 1100 mm and mean air temperature of 10.6°C (Japan Weather Association 1998). The vegetation is a plantation forest of Japanese larch [*Larix kaempferi* (Lamb.) Sargent]. The sizes and ages of the larch in each plot are shown in Table 1. The shrub layer was sparse and was dominated by *Quercus crispula* Blume, *Prunus incisa* Thumb., *Ligustrum tschonoskii* Decaisne, *Symplocos coreana* Ohwi, and *Rhododendron obtusum* Planch. Dwarf bamboo (*Sasa nipponica* Makino) dominates the herb layer with *Osmunda japonica* at 50–70 cm height.

Plots	Latitude and longitude	Altitude (m a.s.l.)	Aspect and slope	Japanese larch			
				Planted in	Canopy density (ind./ha)	Average height (m)	Average DBH (cm)
L1	35° 54' N, 138° 20' E	1350	S16E, 13°	1952	950	17.5	20.4
L2	35° 54' N, 138° 21' E	1360	S42W, 18°	1951	1100	19.4	21.5
H1	35° 54' N, 138° 23' E	1400	S52E, 20°	1961	800	14.6	19.4
H2	35° 54' N, 138° 24' E	1390	N72E, 24°	1961	750	15.6	21.8

Table 1. Location of the study plots and abundance of the larch trees.

The organic layer on the forest floor is mainly composed of larch foliage mixed with larch twigs and bamboo stalks and leaves. The soil type is a well-developed aggregate structure of Andosols (FAO *et al.* 1998). About 50% of the total soil C at 0–100-cm depth was stored in the surface 10 cm, and about 75% was in the upper 0–30 cm (Morisada *et al.* 2002). Volcanic material was deposited after eruptions of Mt. Yatsugatake from 1,300,000 to 10,000 years before present. After that, forests had expanded. In the region around the study plots, natural larch forests remain, and natural larch regeneration at the arly stage follows wildfires. The vegetation was fired artificially in around 1900 (Suka, 2008). In another disturbance, an extraordinarily strong typhoon passed through this region in 1959.

In October 1998, the population of *P. laminata* at this site consisted of only 6th instar larvae (Fig. 1a), which subsequently molted and became 7th instar larvae (Fig. 1b) in August 1999. Adults emerged in late August 2000, and swarming on the forest floor was observed from September (Fig. 1c); the adults died after egg deposition in July 2001 in the foothills of Mt. Yatsugatake (Toyota personal observations). The density of 6th instars ranged from 160 to 1088 m^{-2} (mean ± SD, 485 ± 302 m^{-2}; n = 3) in October 1998 (Toyota personal observation) and from 106 to 2156 m^{-2} (619 ± 208 m^{-2}; n = 10) in June 1999, in the high-abundance area. The density of 7th instar larvae in the high-abundance area ranged from 144 to 720 m^{-2} (469 ± 240 m^{-2}; n = 6) in April 2000 (Toyota *et al.* 2006). The average dry biomass of 7th instar larvae in the high-abundance areas (plots H1 and H2) was 15.7 g m^{-2} and 12.2 g m^{-2}, respectively, in October 1999, and the average dry biomass of adults reached 28.6 g m^{-2} and 15.1 g m^{-2}, respectively, in October 2000 (Hashimoto *et al.* 2004). By contrast, the average dry biomass of

7th instar larvae in the low-abundance areas (plots L1 and L2) was 3.8 g m^{-2} and 1.0 g m^{-2}, respectively, in October 1999, and average dry biomass of adults was 1.0 g m^{-2} and 1.6 g m^{-2}, respectively, in October 2000 (Hashimoto *et al.*, 2004).

2.2 Measurements

Four quadrats (1 × 1 m) were harvested in each plot to estimate the aboveground dwarf bamboo biomass in the period of maximal development of the dwarf bamboo vegetation (from late August to early September 1999, 2000, 2001, 2002, and 2003). The aboveground herb samples were dried at 40°C for 4 days and weighed. After removing the bamboo stalks, samples were homogenized. The 20-g subsamples of dwarf bamboo leaves were ground in a blender and used for N and P analysis. The N content was analyzed using a gas chromatograph (Sumigraph NC-95A; Shimadzu, Kyoto, Japan). The P content was analyzed using a Futura autoanalyzer (Actack, Alliance Instruments, Frépillon, France) for continuous flow analysis.

2.3 Statistical analysis

To test for differences in aboveground biomass, leaf N and P content through the sampling years, multiple comparisons among sampling years within a treatment were performed using the Tukey–Kramer test. Linear regression was used for correlation analysis between millipede biomass and leaf N and P content. All statistical analyses were performed using R 2.8.0 (R Development Core Team 2008).

3. Results

3.1 Temporal changes in aboveground production and leaf quality

The aboveground biomass in high-density train millipede plots varied significantly among years (H1: $P = 0.037$; H2: $P = 0.001$; Fig. 2). No significant differences among years were observed in low-density millipede plots (L1: $P = 0.187$; L2: $P = 0.09$). The observed pattern of the aboveground biomass in high-density plots tended to be high in 1999 (6th instar larvae). In plot H1, aboveground biomass in 1999 (6th instar larvae) was significantly higher than that in 2003 (2 years after adult death). In plot H2, the aboveground biomass in 1999 (6th instar larvae) and 2002 (1 year after adult death) was significantly higher than in 2000 (7th instar larvae) and 2001 (adult) (Tukey–Kramer, $P < 0.05$).

The N content in leaves varied significantly among years in all plots. Temporal dynamics of the N content differed between high- and low-density plots. Similar to the aboveground biomass in high-density plots, the N content tended to be high in 1999 (6th instar larvae). By contrast, in low-density plots, the N content tended to be low in 1999 (6th instar larvae).

The P content in high-density plots varied significantly among years ($P < 0.001$), but not in the low-density plots (L1, $P = 0.45$; L2, $P = 0.08$). The P contents in 2000 (7th instar larvae), 2001 (adult) and 2002 (1 year after adult death) were significantly lower than that in 1999 (6th instar larvae) and 2003 (2 years after adult death) in both plots H1 and H2 (Tukey–Kramer, $P < 0.05$).

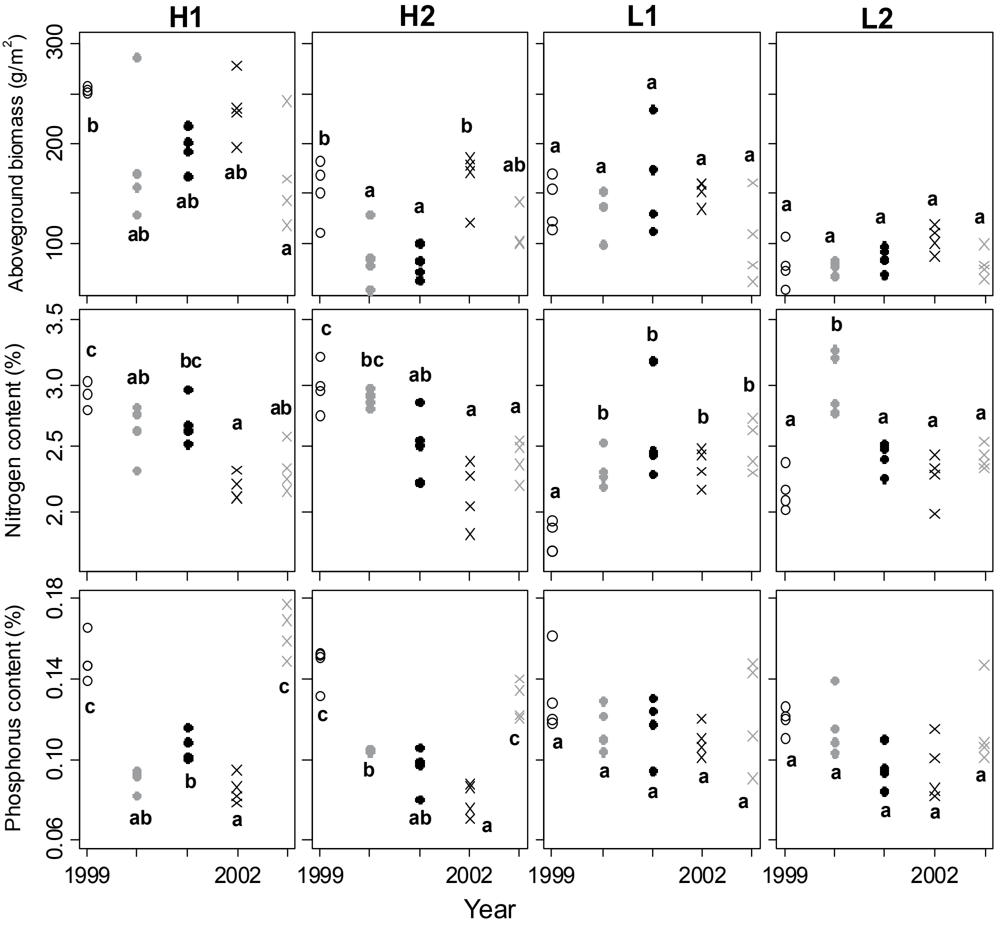

Fig. 2. Temporal variation in the aboveground biomass, nitrogen content, and phosphorus content with developmental stage: open circles, 6th-instar larvae; grey circles, 7th-instar larvae; black circles, adults; and crosses, after the adult period. The same letter indicates no significant difference among years based on the Tukey–Kramer test ($P < 0.05$).

3.2 Effects of the train millipede on leaf quality

The N content of leaves was closely positively correlated with 6th instar larval biomass in 1999 (Fig. 3), but not in other years (Figs. 3, 4). The P content was positively correlated with 6th instar larvae biomass in 1999 (6th instar larvae) and adult biomass in 2003 (2 years after adult death). By contrast, it was negatively correlated with the final instar larvae biomass in 2000 (7th instar larvae) and adult biomass in 2002 (1 year after adult death).

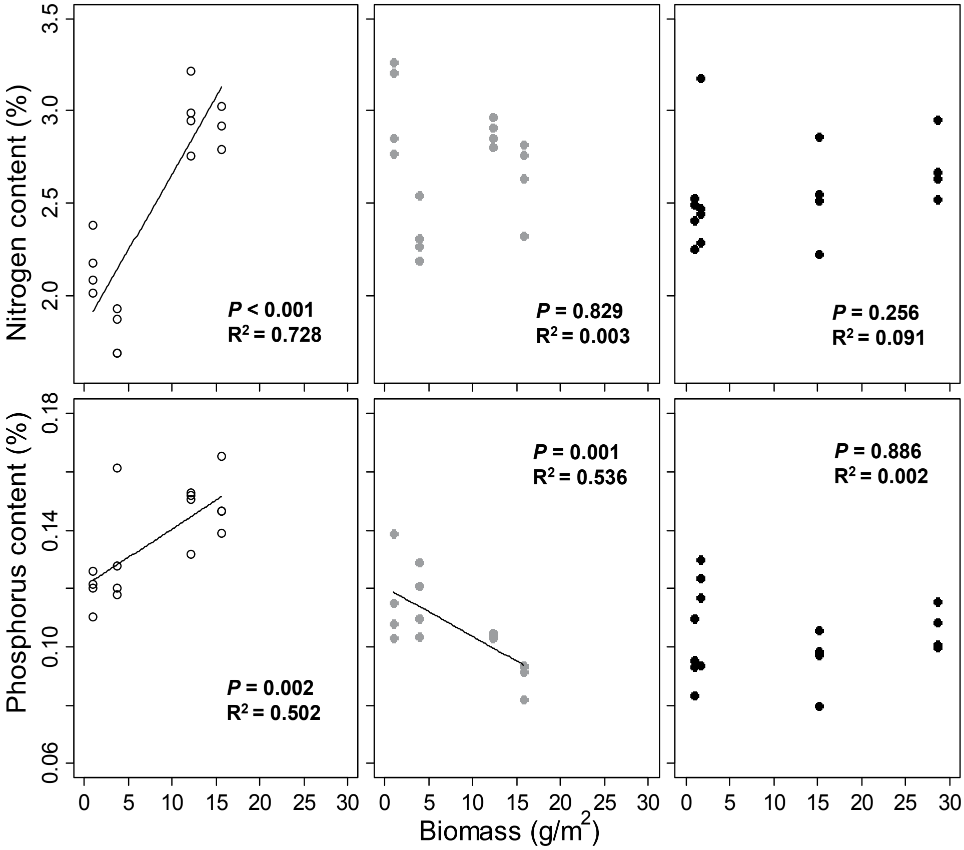

Fig. 3. Developmental stage-dependent effects of the millipede on leaf nitrogen and phosphorus contents: open circles, 6th-instar larvae; grey circles, 7th-instar larvae; and black circles, adults. Solid lines are significant linear regressions.

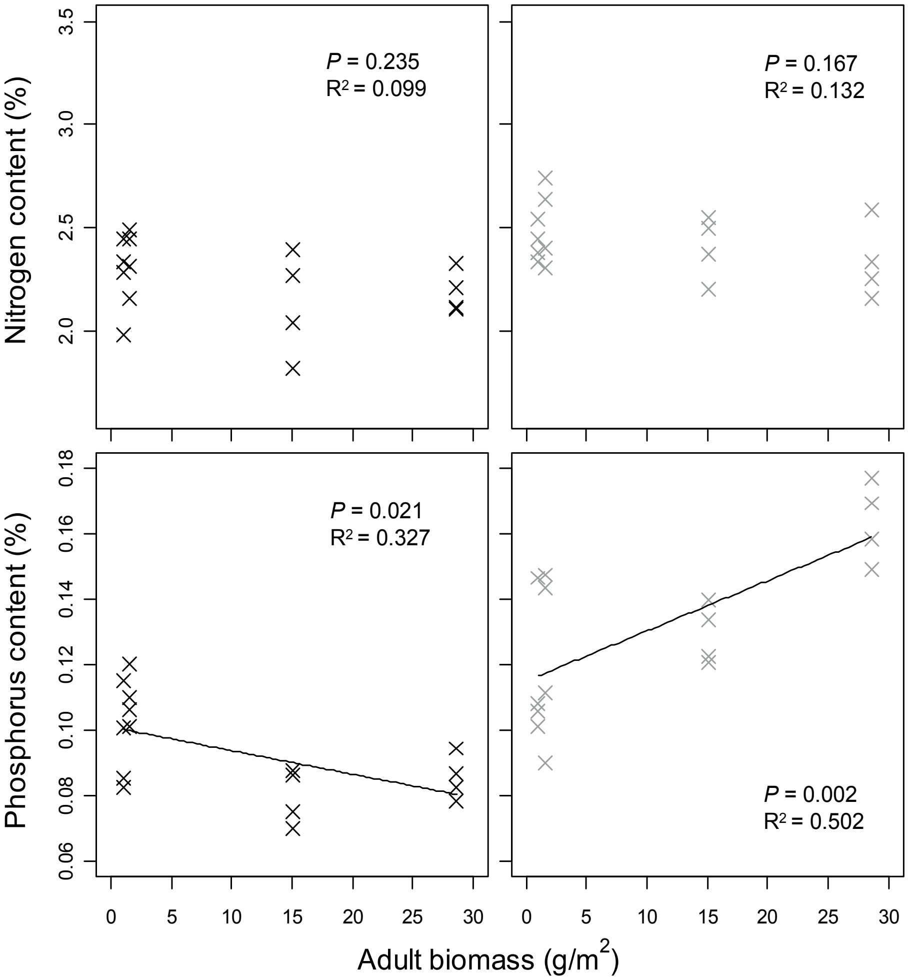

Fig. 4. Effects of adult biomass after adults died on the leaf nitrogen and phosphorus contents. The black crosses indicate 1 year after the adult period. The grey crosses indicate the 2 years after the adult period. Solid lines are significant linear regressions.

4. Discussion

Our results show that temporal changes in dwarf bamboo production and leaf P content occur in plots with high densities of the train millipede, but not in low-density millipede plots. We found that the effects of the millipede on plant leaf N and P content differed with millipede development stage. In agreement with our hypothesis, 6th instar larvae had positive effects on plant production, N and P contents in leaves. In contrast to our hypothesis, the millipede had no effect on dwarf bamboo production and leaf quality during the adult phase, negative effects on the P content for 7th instar larvae and 1 year after the adult phase, and positive effects on the P content in 2 years after the adult phase. The contribution of the millipede to plant growth is therefore twofold. Here, we discuss factors promoting the close relationship between plants and millipedes.

4.1 Temporal differences in production and nitrogen

Observed temporal patterns in production and N content of dwarf bamboo leaves were related to soil N availability in this forest. Increases in soil N availability for plants by 6th instar larval activity (Toyota *et al.* in press) immediately resulted in stimulation of plant biomass and N content in leaves. Under low N availability conditions during the adult phase, plant growth and N content did not increase. These patterns suggest that N limitation may occur in these forests and that millipede larvae can alleviate N limitation in the forest soil system.

4.2 Changes in phosphorus content

Leaf P content increased with the incremental increase in the millipede biomass of 6th instar larvae (Fig. 3). Consequently, the larvae would provide not only available N but also P. However, during the 7th instar, the millipede reduced the leaf P content (Fig. 3). Arbuscular mycorrhizal fungi (AMF), which have a critical role in P uptake by plants, are suppressed by N fertilization (Bradley *et al.* 2006). Similarly, the increase in soil N availability with 6th instar larvae would reduce AMF in the next year, so plants would utilize less P with the incremental increase in millipede biomass. Furthermore, 7th instar larvae may alter soil chemical and physical conditions for the following reasons: (1) excess P consumption by 7th instar larvae might occur to create the adult body, which might result in a reduction of soil P availability, and (2) molting chambers of 7th instar larvae could physically hold P in the soil, lead to a substantial reduction in uptake of P by plants. The train millipedes make molting chambers from their own fecal pellets during summer, for several years the compact structure of the molting chamber of last instar (7th instar) larvae remains in the field at soil depths between 5 and 15 cm (Toyota, unpublished data). Niijima (1984) suggested that the physical structure of soil is greatly altered by 7th instar larvae millipedes due to their large molting chamber (ca. 15 mm in diameter).

After 1 year of the adult phase, the previous adult biomass was negatively correlated with the leaf P content. These decreases in leaf P content can be attributed to the following three reasons. First, P absorption ability in the soil could be high in our forests because of soil engineering by adults (so the P uptake by plants would be low). Second, adult activity might reduce P utilization ability of plants. Adult millipedes were observed in soil to a depth of around 12 cm, near dwarf bamboo roots during the winter (Niijima 1984). This adult activity in soil may damage ectomycorrhizal fungal growth and fine roots of plants due to soil disturbance, which could result in reduced P uptake by plants. Third, there would be fewer adult carcasses on forest floor in high-density millipede plots than adult abundance in the previous year (Hashimoto *et al.* 2004); consequently, phosphate from carcasses would be insufficient to increase the leaf P content.

After 2 years of the adult phase, however, the previous adult biomass was positively correlated with leaf P content. In the previous year, P was probably limited for plants. A lack of P availability leads to the preferential allocation of more resources to root biomass than to aboveground biomass as a plant response (Lynch 1995). Theory predicts a negative correlation between root allocation and aboveground growth rate. Observed low aboveground production in high-density millipede plots after 2 years of the adult phase is consistent with this prediction. Ryan *et al.* (2001) showed that organic acid was supplied from plant roots under low P conditions, and found that roots dissolved iron- or aluminium-bound phosphates by organic acid. Consequently, available P may increase in soil by the activity of plant roots with high-density the millipede. Since plants would allocate carbon to the root system, damaged ectomycorrhizal fungi may recover. Eventually, incremental increases in available P will lead to increases in leaf P content. Further study is required to examine whether P forms and their availability for plants in soil differ according to the developmental stage of train millipedes.

5. Conclusions

By comparing plant production over time between areas with high and low train millipede abundance, we showed that plant growth and leaf quality were differently affected by millipede developmental stage. The plant aboveground biomass and leaf P content varied temporally when millipedes were very abundant but not when their abundance was low. Only 6th instar larvae have a significant role in enhancing both the leaf N and P content with increment in soil mineral N. Last (7th) instar larvae act in the opposite direction; they have a negative effect on the leaf P content. Adults have negative and positive effects after the adult phase probably due to their large impact on rhizosphere and the effects of their carcasses. The roles of the train millipede involve different types of feedback from soil to plant. This different response may lead to changes in competitive ability and in the species composition of the plant community. Although the interactions among plants, microbes, and animals in soil are quite complex, our results indicate that soil animals regulate plant productivity, even in mature forest ecosystems. This insight would be useful for understanding the aboveground–belowground feedback mechanism in the soil community.

6. Acknowledgments

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12

Entomopathogenic Fungi as an Important Natural Regulator of Insect Outbreaks in Forests (Review)

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1. Introduction

With over 1 million species insects are not only the largest group of animals, but also a group that causes the most damage in forest management. Hence it is important to understanding the biology of their natural enemies. Among them are entomopathogenic fungi. Entomopathogenic fungi are a very heterogeneous group. Belong to different systematic groups and even their biology is often very different. However, all of them are pathogenic in relation to insects, and actually all arthropods, and their effectiveness in infecting their hosts is so large that it can become a factor regulating the abundance of insects. Importantly, the harmful insects (from the human point of view) include of course the forest pests.

In this paper we would like to introduce biology, systematics, geographical distribution, and give examples of natural and man-stimulated biocontrol of forest pests by entomopathogenic fungi.

2. Geographical and ecological distribution of entomopathogenic fungi

Entomopathogenic fungi are an important and widespread component of most terrestrial ecosystems. It seems they are not only in places where there are no victims – insects nor other arthropods. Of course spread of individual species of entomopathogenic fungi are different. However some of them can be found practically throughout the world. An example of such species may be *Beauveria bassiana* which is reported from tropical rainforest (Aung et al., 2008), and has been found in Canada as far north as latitude 75° (Widden & Parkinson, 1979). Entomopathogenic fungi have been also recorded north of the Arctic Circle. They have been *Tolypocladium cylindrosporum, B. bassiana* and *Metarhizium anisopliae* in Norway (Klingen et al., 2002), and *B. bassiana, M. anisopliae* and *Isaria farinosa* (=*Paecilomyces farinosus)* in Finland (Vänninen, 1995). What more, entomopathogenic fungi have been reported also from Arctic Greenland (Eilenberg et al., 2007) and Antarctica. In the latter location including endemic Antarctic species *Paecilomyces antarctica* isolated from the Antarctic springtail *Cryptopygus antarcticus* in the peninsular Antarctic (Bridge et al., 2005).

Also cosmopolitan fungi belonging to the genus *Beauveria, Lecanicillium, Conidiobolus* and *Neozygites* have been found on Antarctic sites, but without their arthropod hosts (Bridge et al., 2005).

Studies of Quesada-Moraga showed that altitude has no influence on presence of entomopathogenic fungi in range up to 1608 m, what more altitude was found to be predictive for the occurrence of *B. bassiana* (Quesada-Moraga et al., 2007). However, studies made on wider range of altitudes (up to > 5200 m) made by Sun & Liu showed great importance of this factor on the species diversity of insect-associated fungi (Sun & Liu, 2008).

There are different groups of entomopathogenic fungi in different habitats. Different insect pathogenic mycofloras could be found in the soil and different in the overground environment. Sosnowska found in Poland that in the Białowieża Forest soil litter and soil surface layer dominated *Hypocreales*, but in understory trees and in the canopy – *Entomophthorales*, and in the meadow and rush communities species of spider pathogenic fungi of the genus *Gibellula* (Sosnowska et al., 2004). The *Entomophthorales* are commonly reported as pathogens of forest pests in temperate forest habitats (Burges, 1981), but are rare in tropical forests (Evans, 1982). Humid tropical forests had a rich and varied insect pathogenic fungal species and the great majority of species belong in the genus *Cordyceps* (*Ascomycota: Hypocreales*) (Evans, 1982; Aung et al., 2008). While other species of *Hypocreales* such as *Beauveria*, *Metarhizium* and *Isaria* were the dominant fungi found on soil insects (Samson et al., 1988; Keller & Zimmerman, 1989).

Despite the fact that both *B. bassiana* and *M. anisopliae* are common everywhere there is known that *B. bassiana* seems to be very sensitive to the disturbance effects of cultivation and thus restricted to natural habitats. The ability of *M. anisopliae* to persist in cultivated soils is well established. Therefore the first is more frequent in forest, and second in arable soils (Rath et al., 1992; Vänninen, 1995; Quesada-Moraga et al., 2007; Sánchez-Peña et al., 2011).

Most reports show that frequency of entomopathogenic fungi in intensively cultivated soils is lower than in forest soils (Vänninen et al., 1989; Miętkiewski et al., 1991; Vänninen, 1995; Chandler et al., 1997; Bałazy, 2004). However, there were some exceptions from this rule, e.g. higher frequency of bait insect infections in pasture soils than in soils from either forest or cropland (Baker & Baker, 1998).

Entomopathogenic fungi are commonly found in soil and leaf litter of worldwide forests, however in temperate forests the diversity of entomopathogenic fungi is relatively low in comparison with tropical habitats (Evans, 1982; Grunde-Cimerman et al., 1998; Aung et al., 2008). However, compared to agricultural areas the diversity of entomopathogenic fungi in the temperate forests is quite high (Sosnowska et al., 2004). The differences in their prevalence and diversity of species were also found between the different types of forests (Miętkiewski et al., 1991; Chandler et al., 1997).

3. Systematics and biology of entomopathogenic fungi

3.1 Systematics of entomopathogenic fungi

Entomopathogenic fungi are a very heterogeneous group of insect pathogens. It is known nearly 700 species belonging to approximately 100 orders. Although only a few of them have been studied well. Most of them belong to the order *Entomophthorales* of the phylum

Glomeromycota and to *Hypocreales* of the phylum *Ascomycota* (Hibbett et al., 2007; Sung et al., 2007). Recent phylogenetic studies within entomopathogenic fungi resulted in significant revision of many species of entomopathogenic fungi. For example, such species as *Paecilomyces farinosus* and *P. fumosoroseus* currently belong to the genus *Isaria* (Luangsa-ard et al., 2004), and species *Verticillium lecanii* to the genus *Lecanicillium* (Zare & Gams, 2001). There are many species in the *Ascomycota* in which the sexual phase (teleomorph) is not known and which reproduce entirely asexually (anamorphic fungi). Sexually reproducing hypocrealean fungi occur in the genera *Cordyceps* and *Torrubiella*. These fungi are important natural control agents of many insects in tropical forests. Genus *Cordyceps* has many anamorphs, of which *Beauveria*, *Lecanicillium* and *Isaria* are the best known and described (Blackwell, 2010). Recent phylogenetic studies have demonstrated that the genus *Beauveria* (so far known to be only anamorphic fungus) is monophyletic within the *Cordycipitaceae* (*Hypocreales*), and has been linked developmentally and phylogenetically to *Cordyceps* species (Rehner et al., 2011). Despite recent interest in the genetic diversity of many groups of entomopathogens, the genus *Beauveria,* in contrast to other species, has not received critical taxonomic review (Rehner et al., 2011).

3.2 The life cycles of *Hypocreales* and *Entomophthorales*

The life cycles of *Hypocreales* and *Entomophthorales* are slightly different. Nevertheless, the survival and spread in the environment of both groups is dependent on the infection of the host that invariably leads to its death. The life cycle of entomopathogenic fungus consists of a parasitic phase (from host infection to its death) and a saprophytic phase (after host death) (Fig. 1 and Fig. 2).

In contrast to other entomopathogens (bacteria and viruses), which enters the insects with food, entomopathogenic fungi infect their host through the external cuticle. The process of infection involves: adhesion of the spore on the insect cuticle, penetration of the cuticle by the germ tube, development of the fungus inside the insect body and colonization of the hemocoel by fungal hyphae. The spores of the entomopathogenic fungi are usually covered with a layer of mucus composed of proteins and glucans, which facilitates their attachment to the insect cuticle. Germinating spores of several entomopathogenic fungi produce specialized structures called appressoria. The appressorium is responsible for attachment of germinating spore to the epicuticular surface. The process of penetration of the insect cuticle is a result of mechanical pressure and enzymatic activity of the germ tube. The major role in the penetration plays the secretion of sequential lipases, proteases and chitinases. Inside the insect body most entomopathogenic fungi grow as yeast-like propagules (blastospores), hyphal bodies or protoplasts lacking a cell wall. These structures are spread through the hemocoel. Death of an insect is usually a result of mechanical damage caused by growing mycelia inside the insect (mummification), or toxins produced and released by the pathogen. *Beauveria*, *Metarhizium, and Tolypocladium* are known that secrete a whole range of toxins. Some of them like destruxin, bavericin, and efrapeptins are fully described chemically, and is known their action and contribution in the process of pathogenesis (Roberts, 1981; Hajek & St. Leger, 1994). For *Entomophthorales* there are limited data about the release of toxins (Boguś & Scheller, 2002). In this case, death is the result of the total colonization of host tissues by the fungus.

After host death, the fungus colonizes the cadaver and during 2-3 days forms aerial hyphae and then sporulates (Fig. 1 and Fig. 2). Whereas *Hypocreales* produce only asexual spores, species of *Entomophthorales* produce two types of spores: asexual (primary conidia) and sexual (zygo- or azygospores) called resting spores (Fig. 1 and Fig. 2). Conidia of *Hypocreales* and primary conidia of *Entomophthorales* are produced externally on the surface of an insect after its colonization and death. *Entomophthorales* and *Hypocreales* differ in the way dispersal of spores. The first of these are actively discharged from cadavers by hydrostatic pressure, while the latter are spread by wind. If primary conidium from cadavers does not land on a new host, it germinates and forms secondary conidia (some species can also produce tertiary and quaternary conidia). The majority of *Entomophthorales* produce resting spores (internally within cadavers). Cadavers containing resting spores (azygospores) initially attach to the branches of trees, and then fall to the ground and then azygospores are leached into the soil. Under favourable conditions, azygospores begin to germinate to form germ conidia and infect new hosts. Resting spores allow entomophthoralen species to survive unfavourable periods or the temporary lack of hosts. In this way many species of *Entomophthorales* synchronize their development with the development of insects. Hypocrealen fungi can also survive in the environment (if do not land on a new host), as mummified cadavers or as conidia in soil (Hajek & St. Leger, 1994; Hajek & Shimazu, 1996).

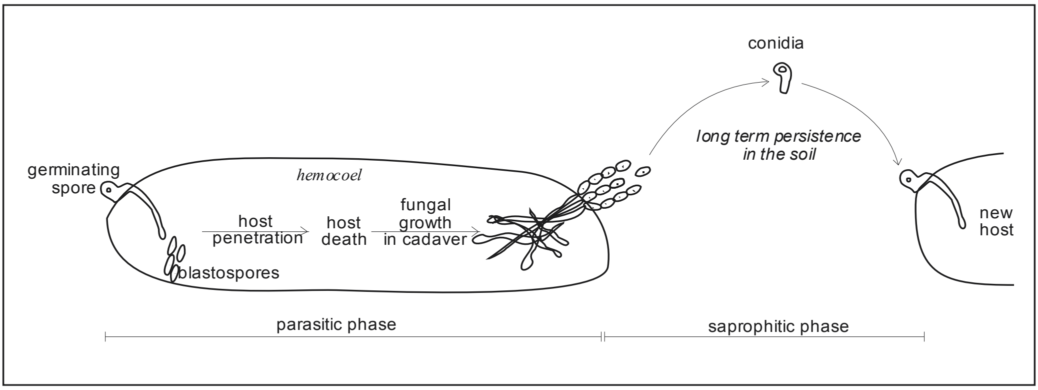

Fig. 1. The life cycle of entomopathogenic fungi from the order *Hypocreales*

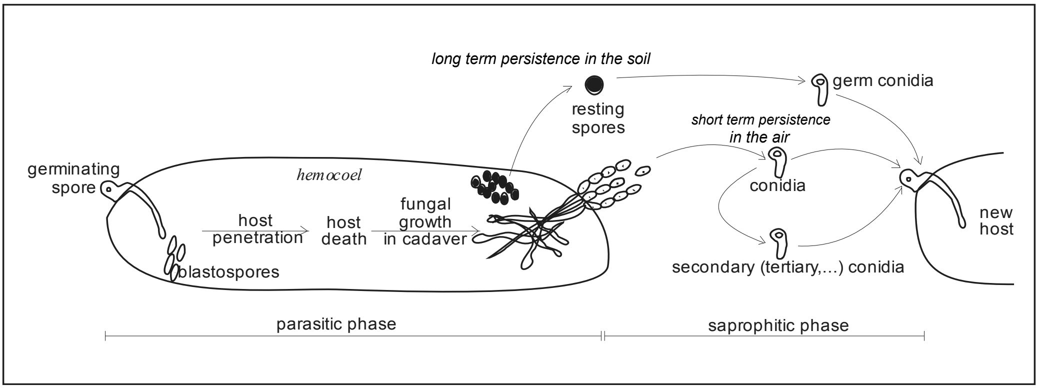

Fig. 2. The life cycle of entomopathogenic fungi from the order *Entomophthorales*

3.3 Intraspecific variation of entomopathogenic fungi

Entomopathogenic fungi can attack insects from different orders: Lepidoptera, Coleoptera, Hemiptera, Diptera, Orthoptera, Hymenoptera, as well as non-insect arthropods. But while some species of fungi (who belongs mainly to the *Hypocreales*) have a very wide spectrum of potential victims, others (mainly *Entomophthorales*) are pathogens only one particular species of insect.

The question arises whether the specialization of the pathogen, and thus its virulence towards particular hosts, is associated with genetic diversity of the pathogen. In the case of entomopathogenic fungi with a wide range of hosts such as *Beauveria bassiana* numerous studies have confirmed that strains of diverse geographical origin but isolated from the same host species showed a greater similarity in the genetic structure than strains from the same area but isolated from different host species (Poprawski et al., 1988; Neuvéglise et al., 1994; Cravanzola et al., 1997; Couteaudier & Viaud, 1997; Maurer et al., 1997; Castrillo & Brooks, 1998). For example, Maurer et al. (1997) by analysing the RFLPs (restriction fragment length polymorphism) and RAPDs (random amplification of polymorphic DNA) of 38 strains of *Beauveria bassiana* isolated from various geographical sites and from diverse species of Lepidoptera (*Ostrinia nubilalis*, *Diatraea saccharalis*, *Maliarpha separatella*) and Coleoptera (*Sitona humeralis*, *S. discoideus*), found a few homogenous groups of strains with similar genetic structure. The first group consisted of all strains isolated from *O. nubilalis*, and the second one included strains from *D. saccharalis*. Strains isolated from various species of *Sitona* formed the third group of strains with similar genetic structure. Furthermore, in laboratory tests, strains from *O. nubilalis* were highly virulent towards this host and less (or not) virulent against the other hosts. Similarly, Neuvéglise et al. (1994) have shown the relationship between the genetic structure of *Beauveria brongniartii* strains and their biological origins (host species). The results of PCR-RFLP revealed a perfectly homogenous group of strains isolated from *Hoplochelus marginalis*. All the strains isolated from *H. marginalis* were more virulent against this host (30-100% mortality) than the strains isolated from different insects (10% mortality). Castrillo & Brooks (1998) also found a high similarity between *B. bassiana* isolates obtained from *Alphitobius diaperinus*.

Literature data on *Metarhizium anisopliae* do not confirm such a clear relationship between genotype and specialization in relation to a particular host (Tigano-Milani et al., 1995; Fungaro et al., 1996; Bridge et al., 1997). A lot of studies indicate the crucial importance of the geographical origin of isolates (St. Leger et al., 1992; Cobb & Clarkson, 1993; Leal et al., 1994; Leal et al., 1997) and habitat type (Bidochka et al., 2001). Studies of Leal et al. (1994; 1997) showed that among 40 isolates of *M. anisopliae*, strains from the same country were more similar in the genetic structure than those from different countries despite the same host. Interesting observations to support a relationship between the genetic structure of *M. anisopliae* isolates and habitat type (agricultural and forested areas) along with abiotic factors (temperature and exposure to UV radiation) provided Bidochka et al. (2001). On the basis of various genetic markers (allozymes, RAPD, RFLP), Bidochka et al. (2001) divided 83 strains of *M. anisopliae* into two distinct groups, each associated with different habitat type. The group from forested areas showed ability for growth at low temperatures (at 8°C), while the group from the agricultural areas showed ability for growth at high temperatures (37°C) and resilience to UV exposure. The association of habitat and thermal preferences was also found for *B. bassiana* (Bidochka et al., 2002). Recently, more sensitive and reliable molecular methods also indicate a certain association between *B. bassiana* isolates and their geographical origins and not between the genetic structure of the fungus and host systematic position (Wang et al., 2005; Fernandes et al., 2009). There is a hypothesis that the saprophytic phase has an evolutionary impact on genetic structure of many species of entomopathogenic fungi including *B. bassiana* (Bidochka et al., 2002; Ghikas et al., 2010; Ormond et al., 2010; Garrido-Jurado et al., 2011). In studies conducted by Ormond et al. (2010) in a conifer forest, molecular analyses (ISSR-PCR) indicate that below-ground and above-ground isolates of *B. bassiana* are genetically diverse.

Relatively little is known about genetic diversity of *Entomophthorales*. The host range within *Entomophthorales* is generally narrow. Therefore, it would seem that the genetic diversity of isolates from the same host may be small. One of the better-studied species in this respect is *Entomophaga maimaiga*. In North America where it produces numerous epizootics in a population of *Lymantria dispar*, *E. maimaiga* characterized by relatively low genetic diversity. *E. maimaiga* was introduced to the USA from Japan, and such low genetic diversity proves that it spread from a small number of individuals (Hajek et al., 1995). Nielsen et al. (2005a) comparing by AFLPs 30 *E. maimaiga* isolates originating from the USA, Japan, China and Russia found that native populations from Asia were more diverse than the USA populations. The authors hypothesize that the population now present in the USA came from Japan of a result of accidental introduction rather than the deliberate release. In contrast to the Asian isolates, no correlation between geographical location and clade was found among the US isolates. The authors explain this by the fact that *E. maimaiga* was introduced into the USA relatively recently; therefore genetically distinct subpopulations may not have evolved yet.

Another specialized entomophthoralen species *Erynia neoaphidis* – major aphid pathogen - shows greater genetic diversity. Rohel et al. (1997) using PCR-ITS and RAPD methods, identified four separate groups with high genetic variability among 30 isolates originating from diverse countries and hosts. Only in some cases RAPD groupings could be related with geographical origin and there was no apparent relationship between host and ITS or RAPD pattern. Similar results have received Tymon & Pell (2005) using ISSR, ERIC and RAPD techniques.

Very little intraspecific variation has been demonstrated for *Entomophthora muscae*, a common pathogen of flies (Jensen et al., 2001; Jensen & Eilenberg, 2001). These studies show low genetic variation within isolates from the same host taxon. In a study conducted by Jensen et al. (2001) several different genotypes within *E. muscae s. str.* have been documented, and each of the genotypes was restricted to a single host taxon, suggesting high host specificity.

Molecular studies of entomopathogenic fungi are very important in the context of choosing the appropriate species or strains for biological control, as well as distinguish wild strains from those introduced artificially in order to monitor and to track isolates after field application.

4. Epizootiology of insect disease

4.1 Fungal epizootic as a limiting factor of insect outbreaks

Insects are essential part of forest ecosystems and at low density have negligible impact on tree growth. Although occasionally, some insect species quickly increase their numbers giving catastrophic impacts on trees and, in some cases this can lead to the complete destruction of large areas of natural or planted forests. Insect outbreaks are often the result of disturbance in biocenotic balance caused for example by sudden events such as fire or hurricane, or as a result of human activities, such as changes in the planting structure (monocultures), but also by more global processes like climate change (Hunter, 2002). In many specific cases, the initiation of insect outbreaks is the result of many factors, and mechanisms of their occurrence are not fully understood and explained. Similarly, there are many factors causing the collapse of outbreaks: depletion of food resources, natural enemies, and unfavourable weather.

Among the natural enemies of insect, infections (epizootics) caused by entomopathogenic fungi are one of the frequently observed causes of collapse of outbreaks. In insect pathology epizootic is defined as an unusually large number of cases of disease in a host population. Epizootic diseases are sporadic, limited in time, and in a given area, and characterized by a sudden change in prevalence (Fuxa & Tanada, 1987). Entomopathogenic fungi are constantly present in populations of insect hosts but when density of the host population is normal infections occur sporadically (enzootic phase of insect diseases). However, during insects outbreaks fungi that infect insects can increase their numbers enough to spread in the environment and contribute to the reduction of insect's population (epizootic phase) (Fuxa & Tanada, 1987). It is very difficult to predict the occurrence of epizootic and not always in different pathogen-host systems the same factors initiate its development in pest population. Furthermore, epizootics caused by entomopathogenic fungi in forested habitats are less numerous than those in other habitats, particularly in agricultural areas because the forest ecosystem is more complex and more stable compared with "agroecosystem". Forest ecosystems also have many different mechanisms for regulating the number of pests.

Spatial and temporal spread of the epizootic depends on the effective transmission of the pathogen in the population of the target insect and insect susceptibility to infection. These two main factors are closely related to climatic factors (mainly temperature and humidity) and biotic environments (other pathogens, parasitoids and predators). All these factors act simultaneously on both sides of pathogen-host system by modifying the growth and development of both pathogen and insect population. Transmission is the transfer of infective propagules between individuals through direct contact. Entomopathogenic fungi in the insect population can be transmitted in three ways: horizontally (from infected insects on healthy individuals within a single generation), vertically (between generations), and be moved by vectors. This third method plays an important role in the transmission of fungi to new habitats (Fuxa & Tanada, 1987). It is supposed that natural epizootic in a population of insects do not have to be initiated by a highly virulent strain of the fungus. In the laboratory, the virulence of the strain can be increased with passaging (repeated in-vitro transmission of the tested strains of fungi from infected to healthy individuals of target insect) (Hyden et al., 1992; Hughes & Boomsma, 2006). Most likely, under natural conditions there is a natural passage during which the pathogen increases its virulence.

Fungal epizootics occur naturally in many insect populations during outbreaks and are frequently the primary cause of the collapse of many insect populations (Table 1). Hicks & Watt (2000) reported that in 1998 outbreak of the pine beauty moth (*Panolis flammea*) in lodgepole plantations in Scotland collapsed by a fungal epizootic. *Entomophaga aulicae*, *Nomuraea rileyi* and *Beauveria bassiana* were recorded from infected larvae. Together they caused 88% mortality in the population of *P. flammea*.

Epizootics *Lymantria dispar* are found in areas of natural occurrence of the pest (from Europe to Asia), but also in new areas where *L. dispar* is an invasive species (North America). Shimazu & Takatsuka (2010) in Japan, during outbreak of *L. dispar* found many dead and living larvae on the surface of boles of the host trees. Laboratory investigation of the gypsy moth cadavers revealed that most of them were infected with the nuclear polyhedrosis virus (NPV), the fungal pathogen *Entomophaga maimaiga*, or a mixed infection of those two pathogens. They also found larvae infected by *Isaria javanica*. Earlier Aoki (1974) reported *Paecilomyces canadensis* and *Entomophthora aulicae* (=*Entomophaga maimaiga*) from *L. dispar* larvae in the same Prefecture as the study of Shimazu & Takatsuka (2010). Aoki (1974) found that 80% of collected larvae were killed by *Entomophthora aulicae* and 19% by a mixed infection with *P. canadensis*.

In North America *Lymantria dispar* is an invasive species. It was imported into the USA from France that was accidentally introduced in Massachusetts in 1869, while *E. maimaiga* – natural enemy causing widespread epizootics in the areas of natural occurrence – was first recorded in North America in 1989. *E. maimaiga* probably comes from the introductions that took place in 1910 and 1911 when diseased gypsy moth cadavers collected in the Tokyo area were released near Boston, Massachusetts. However, no fungal infections were recovered and establishment was presumed to have failed. And until 1989, despite several attempts of introduction, neither *E. maimaiga* nor any other entomophthoralean fungus has ever been observed in the North American gypsy moth populations (Andreadis & Weseloh, 1990; Hajek et al., 1995). Since 1989 almost every year epizootics caused by *E. maimaiga* in the USA gypsy moth populations have been observed and *E. maimaiga* is considered the main factor suppressed outbreaks of *L. dispar* (Hajek et al., 1995; Hajek, 1997). During outbreaks of *L. dispar*, epizootics of nuclear polyhedrosis virus (NPV) are as common as fungal infections caused by *E. maimaiga* (Table 1). However, NPV requires high-density populations for development of epizootics, whereas *E. maimaiga* can cause high level of infection in low-density as well as high-density populations (Hajek et al., 1995). Furthermore, it was found that climatic conditions especially moisture is critical in the development of epizootics of *E. maimaiga*. Hajek (1997) found that in the year of low rainfall prevailed viral infections, whereas in year with more rainfall dominated fungal infections. In other surveys it was found that the greatest production of conidia of *E. maimaiga* by cadavers took place on the day of rainfall, whereas maximum germination of resting spores occurred 1-2 days after significant precipitation (Weseloh & Andreadis, 1992).

Mixed infections of entomopathogenic fungi and viruses are also common in other pathogen-host systems (Table 1). Ziemnicka (2008a) has confirmed that in the population of *Leucoma salicis* nuclear polyhedrosis virus acts as a density-dependent mortality factor and most epizootics were recorded at temperature above 15°C and low humidity. Some laboratory studies and field observations also indicated that fungi and viruses that occur within one insect's population might act in a synergistic manner (Malakar et al., 1999; van Frankenhuyzen et al., 2002; Ziemnicka, 2008b). For example, artificially induced viral epizootic in the population of *L. salicis* not interfere with the occurrence of the epizootic caused by *Beauveria bassiana*, which extended the population decline phase of 6 to 8 years (Ziemnicka, 2008b).

In Japan, outbreaks of *Syntypistis punctatela* in beech stands are known to occur synchronously among different areas at intervals of 8–11 years. Kamata (2000) has found that this periodicity is the result of several factors (predators, parasitoids, pathogens, delayed induced defensive response), which act as time-delayed and density-dependent factors. Among them fungal disease caused by predominantly *Cordyceps militaris*, was considered to be the most plausible factor for generating cycles of the beech caterpillar population. Kamata (1998, 2000) observed the most severe infections caused by *C. militaris* at the population peak and in the period of its decreasing phase. His field observations also showed that infections caused by *C. militaris* affected the beech caterpillar population both in outbreak and non-outbreak areas. During outbreaks mortality of *S. punctatela* caused by *C. militaris, B. bassiana* and *P. farinosus* (= *I. farinosa*) ranged from 96 to 100% suggesting important roles of these parasites in natural control of this pest (Kamata, 1998).

Quite unique epizootic loci in the summer-autumn complex of the multispecies communities of forest lepidopterans and sawflies in Siberia had been discovered by Kryukov et al. (Kryukov et al., 2011). In this survey at least 30 species from 7 families were found to be *C. militaris* hosts. Field observations were carried out from 2007 to 2009 in three localities where the number of insects infected by *C. militaris* in the period of mass appearance of stromata ranged, depending on the location, an average from 0.5 to 1.5 specimens/m^2 (in some places even up to 20 specimens/m^2). They also observed that with reduction in the number of caterpillars in the tree crowns also decreased the level of defoliation of trees (5-25%). Moreover, they did not find any living pupa in leaf litter on the trial sites.

Similarly, widespread epizootic caused by entomopathogenic fungi have been found in the population of the pine sawfly *Diprion pini* in Poland (Sierpińska, 1998). During outbreak of 1794 collected larvae 1826 isolates of fungi were isolated. The most frequently isolated species were *I. farinosa* (603 isolates), *C. militaris* (542), *B. bassiana* (311), and *L. lecanii* (179). These species have caused 30-80% mortality of overwintering larvae.

There are also examples (though very rare) epizootic caused by fungi of not fully proven insecticidal properties. Marcelino et al. (2009) discovered in the population of *Fiorinia externa* epizootic caused by *Colleotrichum* sp. - a fungus widely known as phytopathogen. Poprawski & Yule (1991) also determined in natural populations of *Phylophaga* spp. such phytopathogenic fungi as *Aspergillus*, *Penicillium* and *Fusarium*, but only occasionally, not as in the case of *Colleotrichum* on a large scale. Some authors consider that phytopathogenic fungi, under some circumstances, may infect and kill insects (Teetor-Barsch & Roberts, 1983; Poprawski & Yule, 1991).

Relatively few studies have investigated the influence of insects' behaviour on fungal infection and development of epizootics. For example, Hajek (2001) studied the unusual behaviour of late stage larvae of *L. dispar* to the risk of infection by *E. maimaiga*. Late instars larvae of *L. dispar* move down from the tree canopy and wander during daylight hours under leaf litter or in cryptic locations on tree boles. Hajek (2001) has found in field experiment that larvae caged over the soil were at much greater risk of *E. maimaiga* infection compared with larvae caged in the understory vegetation or on tree trunks. She also found that infections occurred with even brief exposures to the soil. The author assumes that infection of all larvae caged on the ground where initiated by germ conidia from germinating resting spores. The density of resting spores at the base of the tree is usually the highest. During epizootics, cadavers of late instars fall from tree trunks and *E. maimaiga* resting spores are leached into the soil. Therefore, such behaviour of larvae, rather uncommon in other Lepidoptera, to remain near tree base exposes them to the areas with highest titers of *E. maimaiga* resting spores.

Outbreak pest	Tree host or type of forest	Country	Epizootics/limiting factors	References
Cinara pinea	Pine forests	China	*Erynia canadensis*	Li et al., 1989
Dendrolimus pini	*Pinus silvestris*	Poland	*Isaria farinosa* *Cordyceps militaris* *Beauveria bassiana* *Lecanicillium lecanii*	Sierpińska, 1998
Dendrolimus punctatus	*Masson pine*	China	*Beauveria bassiana*	Ge et al., 2009,
Fiorinia externa	*Tsuga canadensis*	USA	*Colletotrichum* sp. *Lecanicillium lecanii*, *Beauveria bassiana*	Marcelino et al., 2009
Hyblaea puera	*Tectona grandis*	India	parasites, Buculovirus HpNPV and *Beauveria bassiana*	Gowda & Naik, 2008
Leucoma salicis	*Populus nigra*	Poland	nuclear polyhedrosis virus *Beauveria bassiana*	Ziemnicka, 2008a, 2008b Ziemnicka & Sosnowska, 1996
Lymantria dispar	*Larix leptolepis*	Japan	*Entomophthora aulicae* mixed infection with *Paecilomyces canadensis*	Aoki, 1974
" – "	Mixed hardwood forest	USA	*Entomophaga maimaiga* and nuclear polyhedrosis virus	Andreadis & Weseloh, 1990 Elkinton et al., 1991 Hajek, 1997
" – "	*Larix leptolepis* and *Alnus japonica*	Japan	nuclear polyhedrosis virus and mixed infection with *Entomophaga maimaiga*, and *Isaria javanica*	Shimazu & Takatsuka, 2010
Malacosoma disstria		New York and Maryland, USA	*Furia gastropachae* (=*Furia crustosa*)	Filotas et al., 2003
Multispecies communities of lepidopterans and sawflies	Different coniferous and deciduous forests	Siberia, Russia	*Cordyceps militaris* *Cordyceps sp.*	Kryukov et al., 2011
Orgyia leucostigma	*Abies balsamea*	Nova Scotia, Canada	*Entomophaga aulicae*, nucleopolyhedrovirus	van Frankenhuyzen et al., 2002
Panolis flammea	*Pinus contorta*	Scotland	*Isaria farinosa*, nuclear polyhedrosis virus *Entomophaga aulicae*, *Nomuraea rileyi*, *Beauveria bassiana*	Hicks et al., 2001 Hicks & Watt, 2000 Watt & Leather, 1988
Syntypistis (=*Quadricalcarifera*) *punctatella*	*Fagus crenata*	Japan	*Cordyceps militaris* *Isaria farinosa* *Beauveria bassiana*,	Kamata, 1998, 2000

Table 1. Examples of outbreaks of forest pests and epizootics caused by entomopathogenic fungi

Many insects spend at least part of his life in the soil. Soil is also a natural environment for entomopathogenic fungi. Therefore, such natural behaviours of insects related to their biology, such as accumulation in the soil or leaf litter to wintering or pupation, conducive to fungal infections and natural reduction of many insect pests. Tkaczuk and Miętkiewski (1998) determined the natural reduction of *Dendrolimus pini* population caused by entomopathogenic fungi during hibernation period. Microbiological analysis of the pine sawfly cocoons showed that entomopathogenic fungi were responsible for the mortality of overwintering larvae, depending on location from 12 to 52%. Epizootics described by Kryukov et al. (2011) and Sierpińska (1998) also occurred during the overwintering of insects in the form of pupae and larvae in leaf litter.

On the other hand, many forest pests occupy cryptic habitats, where they are protected from direct contact with fungi, and where thermal and moisture conditions are not conducive to the development of fungal infection. For example, such group of insects are bark beetles (Curculionidae: *Scolitynae*). In the available literature we did not find studies that describe extensive epizootics in this group of insects, although there are numerous reports of entomopathogenic fungi isolated from the bark beetles (Bałazy, 1968; Glare et al., 2008; Brownbridge et. al., 2010; Draganova et al., 2010; Tanyeli et al., 2010) and tested in the context of biological control this group of insects (Kreutz et al., 2004a; Draganova et al., 2007; Sevim et al., 2010; Tanyeli et al., 2010, Zhang et al., 2011)

4.2 Insect resistance to fungal infections

In the population of a particular host, individuals are not equally susceptible to infection. Different species of hosts are also not equally susceptible to infection from a particular species or strain of the pathogen. On the one hand, different species or even strains of the fungus may display different levels of virulence and parasitic specialization against a specific host. But on the other hand, susceptibility of the host may change with its development (larvae are usually more sensitive than adults) or may depend on its behaviour and individual resistance to infection. Insects have relatively primitive immunological system, although they can react to the entrance of the fungal pathogen inside their body. Cellular and humoral defence mechanisms, such as antimicrobial proteins, phagocitosis and multihaemocytic encapsulation of fungal structures, have been observed. Encapsulation is always associated with production of melanin. After infection, the fungal propagules are encapsulated within melanin (melanization process). Melanins act antagonistic to fungi, inhibiting their growth (Butt, 1987; Hajek & St. Leger, 1994; Boguś et al., 2007).

They are also known examples of non-specific: morphological (Smith & Grula, 1982; Saito & Aoki, 1983) behavioural (Viliani et al., 1994; Myles, 2002) and physiological (Serebrov et al., 2006; Rohlfs & Churchill, 2011) defence mechanisms to avoid fungal pathogens. Viliani et al., (1994) found in laboratory experiments that the application of mycelial particles in soil affected the behaviour of both larval and adult Japanese beetles, *Popilia japonica*. Grubs avoided soil that contained high concentrations of *Metarhizium anisopliae* mycelium for up to 20 days after application. Some insects have the ability to detect and alert the presence of an infected individual in the population. Very interesting behaviour in this regard have social insects such as termites. The presence of conidia-dusted termites in colony caused the alarm manifested by rapid bursts of longitudinal oscillatory movement by workers. The intensity of alarm peaked about 15 minutes after introduction of the conidia-dusted termites, at which time 80% of the termites were aggregated near the treated individual. Alarm and aggregation significantly subsided after 24 minutes and were then followed by grooming, biting, defecation, and burial of the infected termite (Myles, 2002). In defence against infection, insect may produce on the surface of its body fungistatic compounds that inhibit spore germination and growth. It was found that certain fatty acids on the surface of *Heliothis zea* larvae inhibit the germination of spores of

Beauveria bassiana and *Isaria fumosorosea* (formerly *Paecilomyces fumosoroseus*). Non-pathogenic (saprophytic) fungi and bacteria occurring naturally on the insect cuticle could inhibit germination of spores of entomopathogenic fungi (Smith & Grula, 1982; Saito & Aoki, 1983).

5. Entomopathogenic fungi in biological control of insects

5.1 Strategies of biological control

Chemical insecticides are commonly used in plant protection. The consequence of this is to increase the resistance of insects to various chemical substances contained in plant protection products. Over 500 arthropod species now show resistance to one or more types of chemicals (Mota-Sanchez et al., 2002). Other serious problem is invasive species that are accidentally introduced to a new country or continent and which escape their coevolved natural pathogens or predators. This forces to seek new, alternative and more environmentally safe, methods of reducing outbreaks of pests. In recent years more attention paid to the possibility of using natural enemies, including entomopathogenic fungi, in control of insect pests. Aside from playing a crucial role in natural ecosystems, entomopathogenic fungi are being developed as environmentally friendly alternatives in agriculture and forestry. They can be increasingly exploited for forest pest management as biological control agents and in the attempts to improve the sustainability of forest ecosystem.

Biological control is defined as the use of living organisms to suppress the population density, or impact of a specific pest organism, making it less abundant or less damaging than it would otherwise be (Eilenberg et al., 2001). Thus, the aim of biological control is not a complete elimination of target species, but reducing its population below the economic threshold of harmfulness.

There are four strategies for biological control: classical, inoculation, inundation and conservation biological control. However, in forestry, only classical and inundation biological control strategies are widely used. Classical biological control is the intentional introduction of an exotic, usually co-evolved, biological control agent for permanent establishment and long-term pest control (Eilenberg et al., 2001). In the case of microorganisms, widely distributed in nature, the term exotic means the use of a particular strain or biotype, which is not native to the area where the pest is controlled. Introduced species to induce long-term effect has to acclimate to the area under certain climatic conditions, multiply and spread. So it is important to understand of the biology of species "exotic" and target, as well as the ability to monitoring its presence in the area. Inoculation biological control is also the intentional release of a living organism as a biological control agent with the expectation that it will multiply and control the pest for an extended period, but not permanently (Eilenberg et al., 2001). Inoculation involves releasing small numbers of natural enemies at prescribed intervals throughout the pest period, starting when the density of pest is low. The natural enemies are expected to reproduce themselves to provide more long-term control. Inundation biological control is the use of living organisms to control pests when control is achieved exclusively by the released organisms themselves (Eilenberg et al., 2001). In practice this means the release of large numbers of mass-produced biological control agents (so-called biopesticides) to reduce a pest population without necessarily achieving continuing impact or establishment. Pest population is treated such a quantity of biopesticide to get immediate results (on the pattern of use of chemical insecticides). Conservation biological control is such modification of the environment or existing practices to protect and enhance specific natural enemies or other organisms to reduce the effect of pests (Eilenberg et al., 2001). Conservation techniques involve the identification and manipulation of factors that limit or enhance the abundance and effectiveness of natural enemies.

5.2 Field application of entomopathogenic fungi

Attempts for practical application of entomopathogenic fungi, in classical or inundation biological control strategy, are always preceded by laboratory tests. Laboratory tests are mainly aimed to select for highly virulent strains, determine the optimal dose of inoculum, to examine the impact of biotic and abiotic factors on the fungus used and testing different methods of application (Lingg & Donaldson, 1981; Markova, 2000; Wegensteiner, 2000; Kreutz et al., 2004a; Dubois et al., 2008; Shanley et al., 2009; Augustyniuk-Kram, 2010; Zhang et al., 2011). Laboratory tests do not always coincide later with their practical use, but provide valuable information on the activity of entomopathogenic fungi and their potential role in biological control of many dangerous pests. In laboratory conditions, Markova (2000) studying the susceptibility of *Lymantria dispar* larvae, *Ips typographus*, *Hylobius abietis* beetles and diapausing *Cephaleia abietis* larvae on various strains of *Beauveria bassiana*, *Isaria farinosa* (=*Paecilomyces farinosus)*, *Metarhizium anisopliae* and *Lecanicillium lecanii* (=*Verticillium lecanii*) obtained very different results. Larvae of *L. dispar* were susceptible to only one strain of *B. bassiana*, but this strain acted too slowly. Beetles of *Ips typographus* were susceptible to all tested strains, while the beetles of *H. abietis* were only susceptible to one strain of *M. anisopliae* and one strain of *B. bassiana*. Similarly *Cephaelia abietis* larvae were susceptible to infections by one strain of *B. bassiana* and one strain of *I. farinosa* (Markova, 2000). From other studies it is known that good results in the control of *L. dispar* were obtained using the entomophthoralen fungus *Entomophaga maimaiga* that is a major natural enemy in endemic Asian gypsy moth population. Nielsen et al. (2005b) assessed virulence and fitness of the six strains of *E. maimaiga* originating from Japan, Russia, China and North America in different gypsy moth population (originating from Japan, Russia, Greece and USA). They found that all *E. maimaiga* isolates tested were pathogenic to all populations of *L. dispar*, regardless of the geographical origin of the fungal isolates, with at least 86% mortality. However, fungal isolates differed significantly in virulence (measured as time to death) and fitness (measured as fungal reproduction) (Nielsen et al., 2005b).

The use of a microorganism in practice is not easy. The biggest problem is that it is very difficult to predict the effects of biological control agents before their release. The success of field trials depends on many factors that must be taken into consideration. Quite often observed is the phenomenon of lower efficiency of biological control agents applied in the field compared with laboratory tests. Among many factors such features of entomopathogenic fungi as high virulence against target insect, harmless for beneficial organisms (non-target species), warm-blooded animals and humans, high resistance to biotic and abiotic environmental conditions are critical in achieving satisfactory results in field trials (van Lenteren et al., 2003; Jackson et al., 2010). Impact on non-target organisms

Pest	Pathogen	Country	Methods	Effect	References
Agrilus planipennis	*Beauveria bassiana*	USA	Pre-emergent trunk spray (10 or 100 x 10^{13} conidia/ha) and polyester fiber bands impregnated with a sporulating culture of *B. bassiana* (6.4 x 10^{8} conidia/cm^{2})	Infection rates ranged from 58.5 and 83% at two application rates, longevity of females and males was significantly reduced, females laid fewer eggs, prolonged larval development. Fiber bands method – 32% mortality adult on treated trees vs. 1% on control trees.	Liu & Bauer, 2008
Anoplophora glabripennis	*Beauveria bassiana,* *B. brongniartii*	China	Two methods were compared: fiber bands fastened around tree trunks was compared with trunk sprays	Longevity was decreased by both strains compared with controls, with females killed earlier by *B. brongniartii* than by *B. bassiana*. This decrease in longevity was independent of the application method used. Daily oviposition rate per female were also reduced by both strains.	Dubois et al., 2004
Ips typographus	*Beauveria bassiana*	Germany	Introduction of *B. bassiana*-inoculated beetles into untreated population or natural population of beetles were lured into a pheromone traps and treated there with conidia of *B. bassiana*	Significant reduction in the length of maternal galleries and the number of larvae and pupae were observed. In experiment with pheromone traps significant reduction in the number of bore holes were observed. Additionally, no larvae, pupae and juveniles were found under the bark of trunks of treated trees.	Kreutz et al., 2004b

Pest	Pathogen	Country	Methods	Effect	References
Lymantria dispar	*Entomophaga maimaiga*	USA	Resting spores were released around the bases of oaks in 41 plots (2-years trials).	In the second year of study *E. maimaiga* infections were detected in 40 of the 41 release plots. Infection levels in release plots averaged 72.4 % and were associated with declining egg mass densities. The next year after the first application *E. maimaiga* was abundant 1,000 m from release plots.	Hajek et al., 1996
" – "	" – "	Bulgaria	Cadavers of *L. dispar* containing *E. maimaiga* resting spores	Only 6.3% larvae collected in experimental plots contained spores and resting spores of *E. maimaiga*	Pilarska et al., 2000
Melolontha melolontha	*Beauveria brongniartii*	Denmark	Barley kernels colonized by fungus were placed in holes of 10 cm depth around trees or barley kernels were mixed with the soil and placed around the new trees during re-plantation	30% more trees without damages	Eilenberg et al., 2006
" – "	" – "	Denmark	10 or 30 g barley kernels per tree were thrown directly into the planting hole before the tree was inserted into the hole	Significant effect was achieved 1 and 1/2 year after the application. Almost 13% of the untreated trees had been killed, 25% showed substantial discoloration and needle trees. None of the treated trees died and only single trees showed discolouration.	Eilenberg et al., 2006

Pest	Pathogen	Country	Methods	Effect	References
" – "	" – "	Switzerland	Blastospores were applied by helicopter at the swarming places. The mean dose 2.0-3.7 x 10^{14} spores ha^{-1}	The infection rates of the treated adults ranged between 30 to 99 %. The treatment reduced the average reproduction rate. The population density 6 and 9 years decrease 50-80%	Keller et al., 1997
Strophosoma capitatum and *S. melanogrammum* larvae	*Metarhizium anisopliae*	Denmark	Conidial suspension – 1.0 x 10^{14} per ha; procedure was repeated twice, year after year	In the same year after the first application were not achieved satisfactory results. One year and two years after the first application the accumulated density of *S. melanogrammum* weevils was reduced by 60 and 40%. For *S. capitatum* only in the first year after the first application achieved a reduction of up to 38% of beetles.	Nielsen et al., 2007

Table 2. Examples of biocontrol of forest pests by using entomopathogenic fungi

must always be considered as a side effect during field applications of entomopathogenic fungi. The results of numerous works suggest little impact of entomopathogenic fungi on non-target organisms (James et al., 1995; Parker et al., 1997; Traugot et al., 2005; Nielsen et al., 2007). And finally, the use of entomopathogenic fungi on a large scale depends above all on the possibility of cheaper mass rearing on artificial media. Unfortunately, most fungal biopesticides are produced on the basis of hypocrealen fungi, among which the majority belongs to polyphagous species that is a broad spectrum of potential hosts. Entomophthoralen fungi amongst many species are more specialized (monophagous), therefore not of interest among potential producers of mycoinsecticides because of difficulties in their cultivation on artificial substrates and the multiplication of infective material on a mass scale (Pell et al., 2001).

Examples of practical application of entomopathogenic fungi can be found in Table 2. Each example briefly describes the method of application and the final effect measured in the reduction of the target insect populations, or health status of trees. In the described examples, depending on the target insect and fungus, different methods of application were used. In the case of soil-dwelling pests the most appropriate and most common method is introduction into the soil barley kernels colonized by fungus. In European countries, this method is widely used against larvae of *Melolontha melolontha* in various crops (Keller et al., 1997; Fröschle & Glas, 2000; Bajan et al., 2001; Vestergaard et al., 2002). Recently, a commercial product based on barley kernels colonised by *Beauveria brongniartii* (Melocont®-Pilzgerste) was tested under EU-funded project BIPESCO which aim was to study and develop entomopathogenic fungi for the control of subterranean insect pests like scarabs and weevils. Another fairly common method is the use of fiber bands (=fungal bands) impregnated with entomopathogenic fungi and placed around tree trunks or branches. This method was first developed as a biological control method to control adults of Japanese pine sawyer, *Monochamus alternatus*, the main vector of pine wilt disease caused by the pinewood nematode, *Bursaphelenchus xylophylus* (Shimazu, 2004). Currently, this method gives satisfactory results in biological control of invasive species *Anoplophora glabripennis* and *Agrilus planipennis* (Table 2). Despite rare reports of natural epizootics among bark beetles, attempt to biological control, particularly laboratory tests, are very promising. In laboratory studies efficacy of entomopathogenic fungi against bark beetles is very high, reaching up to 80-100% for some strains (Draganova et al., 2007; Sevim et al., 2010; Tanyeli et al., 2010). In field trials Kreutz et al. (2004b) also achieved significant reduction in number of larvae, pupae and juveniles. According to Hunt, as high mortality of bark beetles may be associated with the lack in their cuticle certain lipids that inhibit germination of fungal spores (Hunt, 1986).

5.3 Conservation biological control and Integrated Pest Management (IPM strategy)

Recently more attention is focused on the study of entomopathogenic fungi in natural environments, and hence in conservation biological control strategy. Conservation biological control is a strategy in which forest management and environmental manipulations are adopted to enhance conditions for the development of different groups of natural enemies of pests. In forestry conservation biological control requires actions on a large scale, not only in wooded areas, but also beyond, in adjacent areas. In Europe, an example of pest that control is not limited to one environment is the previously mentioned *Melolontha melolontha*. Adults are pests of deciduous trees. Eggs are laid in the soil usually in the areas adjacent to large forest complexes such as arable fields, nurseries, orchards, where the larvae feed on roots.

The use of entomopathogenic fungi, particularly in this strategy, requires a thorough knowledge of the biology and ecology of both pests and their natural enemies. It also requires recognition of factors that may interfere with their effectiveness. Conservation biological control also needs long-term and large-scale researches on multitrophic relationships between natural enemy and their hosts and their impact on natural regulation of serious insect pests (Tscharntke et al., 2008).

Natural enemies and their potential hosts always exist within a particular biocenosis, where are affected by abiotic and biotic factors. One of them are pesticides that kill natural enemies as well as their potential hosts (Miętkiewski et al., 1997; Chandler et al., 1998; Meyling & Eilenberg, 2007). For this reason, many countries prohibited the use of chemical insecticides to control forest pests (e.g. Denmark). Therefore the only alternative is biological or integrated pest control. Integrated Pest Management in forestry is defined as "a combination of prevention, observation and suppression measures that can be ecologically and economically efficient and socially acceptable, in order to maintain pest populations at a suitable level" (FAO, 2011). Biological control of pests through the use of natural enemies and other methods like mechanical control, planting proper trees in proper sites during reforestation is preferred over synthetic pesticides. Such actions favour sustainable control and efficiency of natural enemies (FAO, 2011). The previously mentioned project BIPESCO was intended to help replace or reduce the input of chemical pesticides in European agriculture, forestry and horticulture.

Numerous studies indicate that forest communities display greater diversity of entomogenous species than arable fields. Bałazy (2004) compared species richness of entomopathogenic fungi in forest areas (mainly in protected areas like national parks) with areas used for agriculture found that out of all 210 species over 60% was collected in the forest protected areas. Only 20 species were found in annual crops. Significantly more infected host cadavers were found in other habitats such as extensively utilized meadows, mid-field, shelterbelts, woodlots and swamps. Evans (1974) also found that even in forests with very high biodiversity as tropical rain forests, the diversity of entomopathogenic fungi in damaged forests is less than undisturbed, and that the incidence of natural epizootic decreased. Such natural and semi-natural habitats are often refuges for insects and entomopathogenic fungi. Thus, the protection of this group of pathogens and their natural habitats is also important question in the context of conservation of biodiversity. Improving our understanding of the ecology of entomopathogenic fungi is also essential to further develop these organisms in biological control of many serious insect pests.

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13

Quantitative Chemical Defense Traits, Litter Decomposition and Forest Ecosystem Functioning

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1. Introduction

In forest ecosystems, litter decomposition, which plays a critical role in nutrient cycling, is influenced by a number of biotic and abiotic factors, including quantitative chemical defense (Ross *et al.*, 2002), environmental conditions such as soil properties and climate (Badre *et al.*, 1998, Vanderbilt *et al.*, 2008), and decomposer community and its complex nature. However, Lavelle *et al.*, (1993) proposed a hierarchical model for the factors controlling litter decomposition. The levels of the hierarchal model are: climate (temperature and moisture)> physical properties of soil (clay and nutrients)>litter quality> macro and microorganisms (Lavelle *et al.*, 1993). Leaf litter quality, which is inherited from living leaves, has repeatedly been emphasized as one of the most important factors controlling the decomposition process (Swift *et al.*, 1979, Melillo *et al.*, 1982, Osono & Takeda 2005). Decomposition rate may be decreased with latitude and lignin content of litter but increased with temperature, precipitation and nutrient concentrations at the large spatial scale (Zhang *et al.*, 2008).

Bernhard-Reversa & Loumeto (2002) mentioned that litter fall serves three main functions in the ecosystem such as energy input for soil microflora and fauna, nutrient input for plant nutrition, and material input for soil organic matter building up. The first two functions are completed through decomposition and mineralization, and the third one through decomposition and humification.

Litter decomposition is a primary source of soil nutrients such as nitrogen and phosphorus, which are often limiting to plant growth in terrestrial ecosystems. The litter is broken down by insects, worms, fungi and microorganisms, organically-bound nutrients are released as free ions to the soil solution which are then available for uptake by plants. The variation in soil carbon and nutrient cycling has been clearly linked to variation in particular aspects of litter chemistry. For example, net N mineralization rates in monocultures of different grass species were correlated with root lignin content, suggesting that substrate chemistry is an important control over mineralization and/or immobilization processes (Hobby & Gough 2004).

De Santo *et al.,* (2009) revealed that litter decomposition rates at the boreal forest were significantly lower than at the temperate one and did not differ between needle litter and leaf litter. In the boreal forest mass-loss was positively correlated with the nutrient release. In this site, Mn concentration at the start of the late stage was positively correlated with lignin decay and Ca concentration was negatively correlated to litter mass loss and lignin decay. In the temperate forest neither lignin, N, Mn, and Ca concentration at the start of the late stage, nor their dynamics were related to litter decomposition rate and lignin decay (Santo *et al.,* 2009). On the other hand, litter quality had stronger effects on decomposition than the temperature in temperate forest (Rouifed *et al.,* 2010). In arid and semi-arid sites, photodegradation could be an influential factor for litter decomposition (Austin & Vivanco 2006). Powers *et al.,* (2009) used a short-term litter bag experiment to quantify the effects of litter quality, placement and mesofaunal exclusion on decomposition in 23 tropical forests in 14 countries. They concluded that decomposition in tropical forest is controlled by soil fauna and litter chemistry, which would vary with the precipitation regime.

Zhang *et al.,* (2008) stressed that the combination of total nutrient elements and C:N accounted for 70.2% of the variation in the litter decomposition rates. On the other hand, the combination of latitude, mean annual temperature, C: N and total nutrient accounted for 87.54% of the variation in the litter decomposition rates. They also indicated that litter quality is the most important direct regulator of litter decomposition at the global scale.

The management of scheme options can influence vegetation and wildlife value for delivering ecosystem services by modifying the composition of floral and faunal communities (Smith *et al.,* 2009). Most European temperate forests have been managed according to “classical” sustainable yield principles for a very long time. In France, vast areas of deciduous forests have been cultivated on short rotations for the production of fuelwood under so-called “low forest” regimes. Many of these forests are now being converted back to high forest management (FAO, 2011). Clear felling is common in harvesting operations in mature softwood stands in Northern America. Thinning is a very common and recommended management practice to manage the plantation and forest stands in general (Blanco *et al.,* 2011). Intensive forest management, which may include operations such as: site preparation; tree planting; tending; thinning; and fertilizer application is often influence the litter decomposition process. Litter decomposition in unmanaged systems is affected mainly by climatic variables (Aerts 1997, Blanco *et al.,* 2011).

However, for better understanding of litter decomposition process and forest ecosystem functioning, we need to know more detail about quantitative chemical defense and their effects on the litter decomposition process which influence the ecosystem functioning. This paper will discuss the quantitative defense traits of forest litter, their effects on litter decomposition and ecosystem functioning.

2. Quantitative chemical defense traits of litter

Quantitative chemicals are those that are present in high concentration in plants (5 – 40% dry weight). The most quantitative metabolites are digestibility reducers that make plant cell walls indigestible to animals. The effects of quantitative metabolites are dosage dependent and the higher these chemicals’ proportion in the herbivore’s diet, the less nutrition the herbivore can gain from ingesting plant tissues. Because they are typically large molecules, these defenses are energetically expensive to produce and maintain, and often take longer to synthesize and transport (Nina & Lerdau 2003). These secondary compounds may be secreted within the cells, for example, in vacuoles, or excreted extracellularly. They include poisonous compounds whose concentration in the cell tends to be relatively low, e.g. alkaloids, cyanogenic glycosides and cardenolides. Some of these secondary metabolites accumulate to levels high enough to reduce the plant's digestibility and palatability for herbivores (McKey 1979; Lindroth & Batzli 1984; Lambers 1993).

However, quantitative chemical defensive traits of litter may divide into three main categories: 1. Lignin 2. Total phenolics 3. Tannins (Hydrolyzable tannins and Proanthocyanidins or Condensed tannins).

2.1 Lignin

Lignin is a polymer of aromatic subunits usually derived from phenylalanine. It is an important constituent of plant secondary cell walls and comprises the largest fraction of plant litter. Lignified leaves are rigid in structure, and highly recalcitrant to decay. Its chemical assay is difficult and different methods may lead to different results. Because it constitutes a barrier preventing decomposition of cellulose, lignin content of litter has been reported to control litter decomposition rate (Sterjiades & Erikson 1993).

2.1.1 Chemistry and occurrence of lignin

Lignins are complex polymers formed by the dehydrogenative polymerization of three main monolignols, *p*-coumaryl, coniferyl, and sinapyl alcohols (Fig. 1).

Gymnosperm lignins are mainly formed from coniferyl alcohol, together with small proportions of *p*-coumaryl alcohol. Angiosperm lignins are mainly formed from coniferyl and sinapyl alcohols with small amounts of *p*-coumaryl alcohol (Lewis 1999). Table 1 shows the % lignin content of different leaf litter.

2.1.2 Effects of lignin on litter decomposition

Lignin is an essential component of plant litter, and is among the most recalcitrant compounds, and consequently is of major importance in soil humus building. Lignin concentration in leaves (or lignin to mineral ratios) has been widely used as an index of organic-matter quality. For instance, lignin concentrations alone, or lignin to N ratios in leaves could explain the rate of decomposition; negative correlations have been reported between lignin concentrations (or lignin to mineral ratios) and decomposition rates (Meentemeyer 1978; Melillo *et al.,* 1982; Vitousek *et al.,* 1994; Hobbie 1996; Kitayama *et al.,* 2004). The ratio of lignin and N as a factor that is more related to decomposition than lignin content (Fig. 2).

On the other hand, hemicellulose and lignin concentrations were reported to be negatively correlated with decomposition (Vivanco & Austin 2008). The initial lignin content of leaf litter influenced the rate of decomposition. The species exhibiting higher initial lignin contents showed lower rates of decomposition of leaf litter. For example, the decomposition of *Quercus dealbata* litter is slower than that of *Quercus fenestrata* (Laishram

& Yadava, 1988). However, the concentrations of the lignin fraction increased as decomposition proceeded, reaching relatively steady levels in the range of 45–51% (Berg 2000; Devi & Yadava, 2007). These increases showed partially linear relationships with accumulated mass loss (Berg *et al.,* 1984).

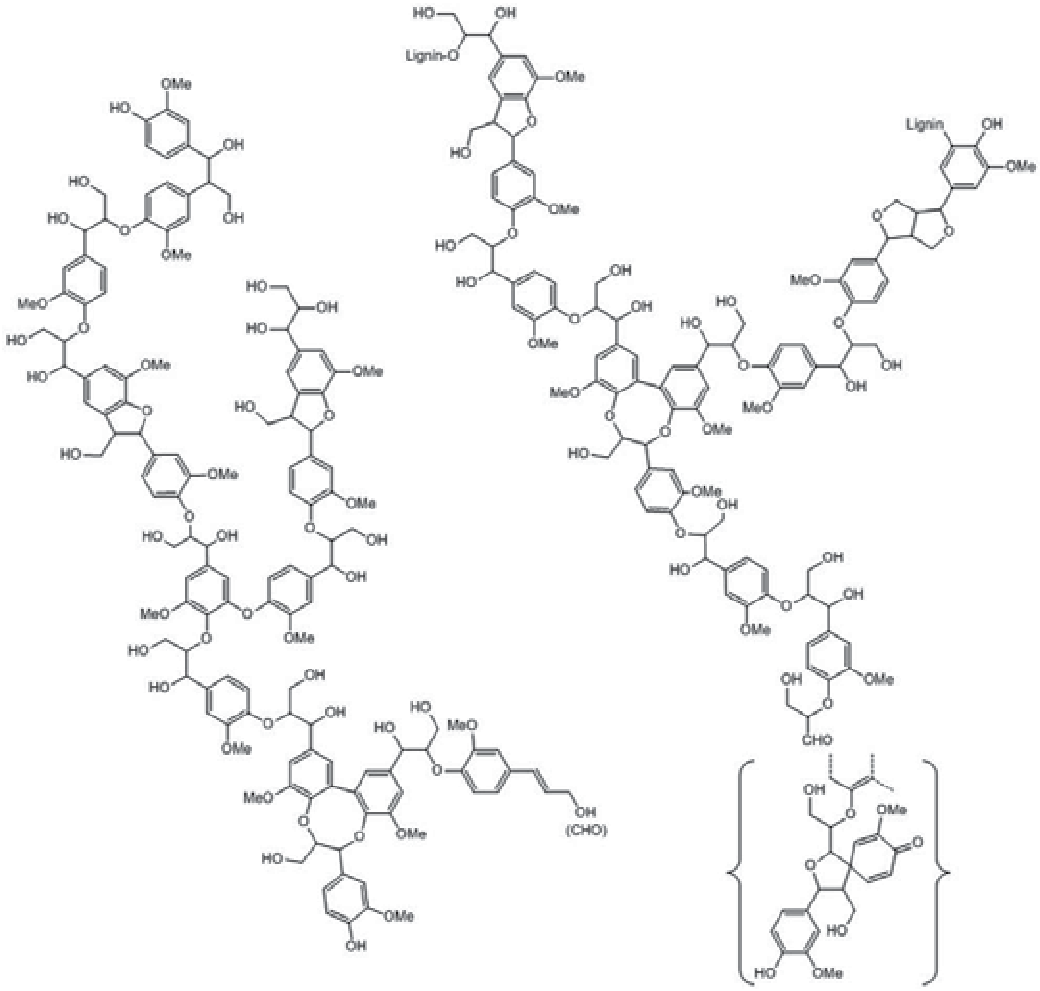


Fig. 1. Common structure of lignin.

Name of the species	Category of Plant	Lignin content of litter (%)
Acacia auriculiformis	Broadleaf tree	54.4
Acacia mangium	Broadleaf tree	43.1
Acer saccharum	Broadleaf tree	10.8
Alphitonia petriei	Broadleaf tree	40.4
Betula pubescens Ehrh	Broadleaf tree	14.0
Castanea sativa	Broadleaf tree	21.1
Dipterocarpus tuberculatus	Broadleaf tree	7.45
Eucalyptus grandis	Broadleaf tree	21.1
Gaultheria griffithiana	Shrub	5.0
Nothofagus dombeyi	Broadleaf tree	19.3
Nothofagus nervosa	Broadleaf tree	29.2
Nothofagus obliqua	Broadleaf tree	27.6
Picea orientalis	Coniferous tree	21.5
Pinus contorta Dougl	Coniferous tree	37
Pinus sylvestris L.	Coniferous tree	29.3
Populus nigra	Broadleaf tree	21.5
Quercus rubra	Broadleaf tree	23.1
Quercus dealbata	Broadleaf tree	6.0
Quercus fenestrata	Broadleaf tree	4.0
Quercus griffithii	Broadleaf tree	3.8
Rhododendron arboreum	Shrub	8.0
Tilia americana	Broadleaf tree	20.0
Broadleaves		21.57±14.23
Coniferous tree		29.26±7.75
Shrub		6.50±2.12

Table 1. The lignin content of different plant species litter (percentage of dry weight) (adapted from Rahman *et al.,* 2011).

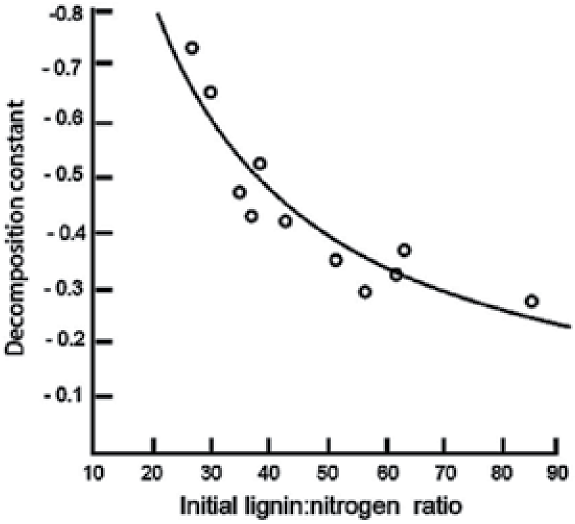


Fig. 2. Relationship between the decomposition constant (*k* = lose of dry mass, to initial lignin concentration of litter) and the lignin: nitrogen ratio of litter (adapted from Melillo *et al.,*1982).

As decomposition proceeds the litter becomes enriched with lignin and N along with other components (Devi & Yadava, 2007). Earlier works have shown that as the lignin concentration increases during litter decomposition, the decomposition rates get suppressed (Fogel & Cromack, 1977; Devi & Yadava, 2007). The suppressing effect of lignin on litter mass-loss rates can be described as a linear relationship in the later stages of decomposition, which, for pine litter, may start at ca. 20–30% mass loss (Fig. 3a). For these later stages, the slope and intercept of this negative relationship varies among sites under different climates (Berg *et al.,* 1993). The lowest effect of lignin concentration on mass-loss rates was found near the Arctic Circle (where long-term average actual evapotranspiration was about 385–390 mm).

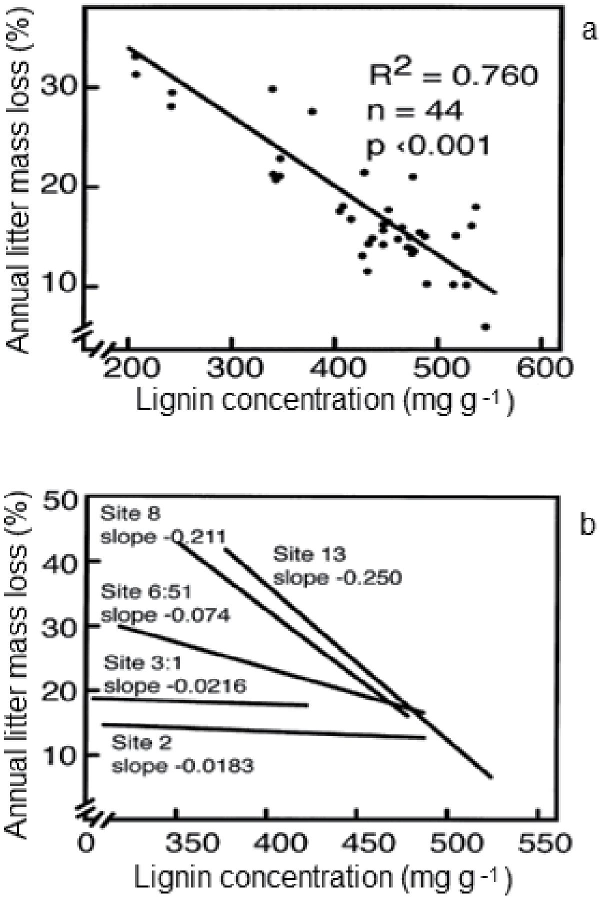


Fig. 3. Annual litter mass loss (%) as a function of initial lignin concentration at the start of each one year period. (a) The linear relationship indicated here, namely a decreasing rate with increasing lignin concentrations for one type of liter. (b) The same relationships under different climatic conditions (five climatically different sites with the AET values 385, 387, 472, 509 and 560 mm for sites 2, 3, 6:51, 8 and 13, respectively) indicate that the rate retarding effect of lignin is stronger in warmer wetter climates (adapted from Berg 2000).

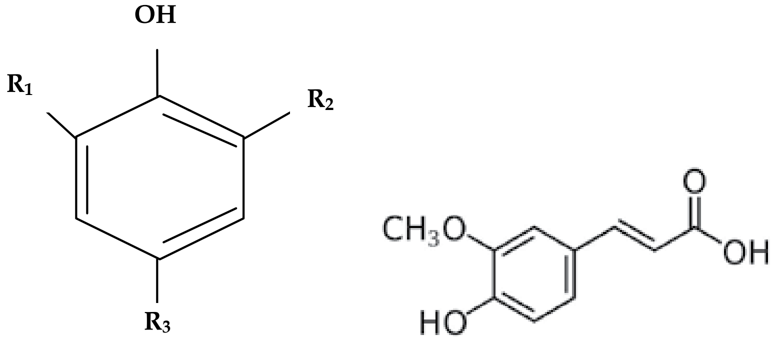
In contrast, in Northern Germany and on the European continent the rate-regulating effect of lignin was found to be higher (Fig. 3 b). In a research on decomposition study from India, it is reported that lignin and fibre contents have showed a negative relation with weight loss of litter (Devi & Yadava, 2007). Many studies have reported a decline in the rate of weight loss of litter due to high initial lignin content (Singh & Gupta, 1977; Devi & Yadava, 2007). More recently, the scientists have found a highly significant, positive correlation between lignin contents and litter decay rates (Raich *et al.,* 2007).

2.2 Total phenolics

Phenolic compounds are one of the most abundant and widely distributed groups of substances in the plant kingdom with more than 8000 phenolic structures currently known (Harbone, 1980). They are products of the secondary metabolism of plants and arise biogenetically from two main primary synthetic pathways: the shikimate pathway and the acetate pathway (Paixao *et al.,* 2007).

2.2.1 Chemistry and occurrence of total phenolics

Phenolics are a heterogeneous group of natural substances characterized by an aromatic ring with one or more hydroxyl groups (Fig. 4). These substances are chemically diverse carbon-based secondary plant compounds occurring in plant tissues (Harborne 1997).



a b

Fig. 4. Simple phenols (C_6), a. phenolic acids b. ferulic acid.

Phenols can be roughly divided into two groups: (1) low molecular weight compounds; and (2) oligomers and polymers of relatively high molecular weight (Hättenschwiler & Vitousek, 2000). Low molecular weight phenolics occur universally in higher plants, some of them are common in a variety of plant species and others are species specific. Because of the large variety of analytical methods and problems with choosing the appropriate standards, polyphenol concentrations reported in the literature vary immensely and might not be comparable with each other. Nevertheless, the two most frequently used polyphenol measurements (i.e. 'total phenolics' and Proanthocyanidins) are accepted reasonably well, and they commonly yield results in the range of about 1% to 25% of total green leaf dry mass (Hättenschwiler & Vitousek, 2000). The amount of phenolics in plant tissues varies with leaf species, age and degree of decomposition (Table 2) (Barlocher & Graca, 2005).

Name of the Species	Plant type	Phenolics (% leaf dry mass)
Acer saccharum (s)	Deciduous tree	15
		2.7
Alnus glutinosa (s)	Tree	6.6
		6.8-7.6
Carya glabra (s)	Deciduous tree	9.1
Eucalyptus globulus (s)	Evergreen tree	6.4 9.8
Fagus sylvatica (s)	Deciduous tree	8.0
Quercus alba (s)	Tree	16.2
Sapium sebiferum (l, s)	Deciduous tree	3.0
Spartina alterniflora (y)	Perennial deciduous grass	0.4-1.5

Table 2. The phenolics concentrations (%) in selected plant tissues, including senescent leaves (s), live (l) and yellow-green to brown-dead grass leaves (y) (after Barlocher and Graca, 2005).

2.2.2 Effects of total phenolics on litter decomposition

Total phenolics are considered to be biologically active, e.g. by protecting plants against biotic (e.g. microbial pests, herbivores) or abiotic stresses (e.g. air pollution, heavy metal ions, UV-B radiation) (Hutzler *et al.,* 1998), by contributing to allelopathic reactions (Waterman & Mole 1994) and by retarding decomposition rates of organic matter (Hattenschwieler & Vitousek 2000). In particular, phenolics play a major role in the defense against herbivores and pathogens (Lill & Marquis 2001).

In addition, some phenolics may prevent leaf damage resulting from exposure to excessive light (Lee & Gould 2002). The bulk of phenolics remain present during leaf senescence and after death, these compounds may also affect microbial decomposers (Harrison 1971) and therefore delay microbial decomposition of plant litter (Salusso 2000). Canhoto & Graca (1996) observed a strong negative correlation between the phenol content of different native litter types and litter decomposition rates in a stream, whereas Canhoto & Graca (1999) showed that phenolics from *Eucalyptus* leaves decrease feeding by detritivores. Thus, effects of phenolics on detritivores may be one reason for the low decomposability of *Eucalyptus* litter. The initial concentration of total phenolics in litter is positively correlated with dry organic carbon loss (Madritch & Hunter 2004). High amount of phenolics compounds in plants tissue decrease N concentration, which impedes the litter decomposition (Xuefeng *et al.,* 2007). Barta *et al.,* (2010) confirmed that a low amount of phenolics and low phenolics/N ratio in plant litter is closely related to higher differences in microbial respiration rates and mineral N release during the four months of litter decomposition in spruce forest.

Lin *et al.,* (2006) observed a negative correlation between total phenolics and N contents for *Kandelia candel* and *Bruguiera gymnorrhiza* leaf litter at various stages of decomposition (Fig. 5). The perception of phenols as inhibitors, however, is far too simple, and the variety of phenolic compounds can have many different functions within the litter layer and the underlying soil (Hattenschwiler & Vitousek 2000). Even intraspecific variation in litter polyphenol concentrations can strongly influence soil processes and ecosystem functioning (Schweitzer *et al.,* 2004). Phenols may influence rates of decomposition as they bind to N in the leaves forming compounds resistant to decomposition (Palm & Sanchez 1990). Gorbacheva & Kikuch (2006) found that dynamics of easily oxidized phenolics may influence the litter decomposition rate in the monitored subarctic field. Some scientist mentioned that phenolics stimulate microbial activity and subsequently reduce plant available N (Madritch & Hunter 2004; Lin *et al.,*, 2006). These results contribute important information to the growing body of evidence, indicating that the quality of C moving from plants to soils is a critical component of plant-mediated effects on soil biogeochemistry and, possibly, competitive interactions among species. Gorbacheva & Kikuch (2006) found that the essential part of phenolics that participates in the formation of mobile forms of organic matter, leaches from the organic horizon and migrates through the soil profile.

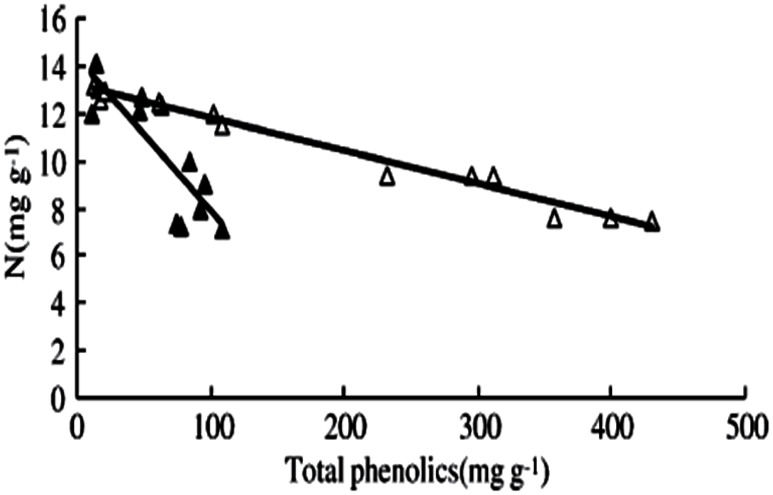


Fig. 5. Relationship between total phenolics and N contents during leaf decomposition of *Bruguiera gymnorrhiza* (Bg) and *Kandelia candel* (Kc). Symbols are: black triangle for Bg leaf; white triangle for Kc leaf (Adapted from Lin *et al.,* 2006).

2.3 Tannins

Tannin is the fourth most abundant biochemical substance in vascular plant tissue after cellulose, hemicellulose and lignin (Kraus *et al.,* 2003). Leaves and bark may contain up to 40% tannin by dry weight (Matthews *et al.,* 1997; Kraus *et al.,* 2003) and in leaves and needles tannin concentrations can exceed lignin levels (Benner *et al.,* 1990). Tannin reduce herbivore load either directly through toxicity or growth alteration or indirectly through reduction of palatability (Feeny 1970).

2.3.1 Chemistry and occurrence of Tannins

Tannins are heterogenous group of phenolics compounds derived from flavonoids and gallic acid. Bate-Smith & Swain (1962) defined tannin as water-soluble polyphenolic compounds ranging in molecular weight from 500 to 3000 Daltons that have the ability to precipitate alkaloids, gelatins and other proteins. Haslam (1998) has substituted the term "polyphenol" for "tannin", in an attempt to emphasize the multiplicity of phenolic group's characteristic of these compounds. Haslam also notes that molecular weights as high as 20,000 Daltons have been reported, and that tannins complex not only with proteins and alkaloids but also with certain polysaccharides. However, tannins found in higher plants are divided into two major classes termed Proanthocyanidins or Condensed tannins and hydrolyzable tannins (Fig. 6).

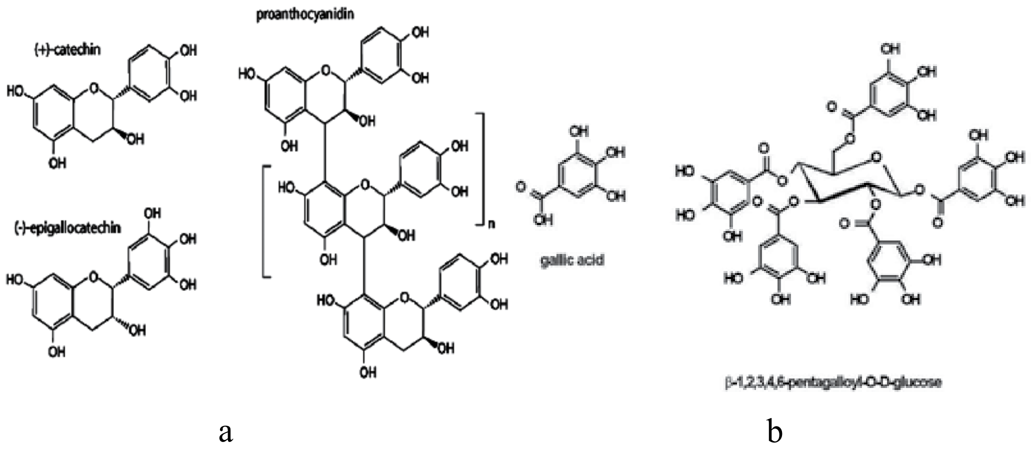


Fig. 6. Structures of tannins; a. Flavan-3-ols (+)-catechin and (-)-epigallocatechin, examples of monomeric precursors that polymerize to form macromolecular products such as linear proanthocyanidins composed of monomeric flavanoid units connected by C4-C8 linkages. b. hydrolyzable tannins β-1,2,3,4,6-pentagalloyl-O-D-glucose.

Tannins are distributed in species throughout the plant kingdom. They are commonly found in both gymnosperms as well as angiosperms. Tannins are mainly physically located in the vacuoles or surface wax of plants. Because tannins are complex and energetically costly molecules to synthesize, their widespread occurrence and abundance suggests that tannins play an important role in plant function and evolution (Zucker 1983). Tannins occur in plant leaves, roots, wood, bark, fruits and buds (Peters & Constabel, 2002; Ossipov *et al.,* 2003). Tannin distribution in plant tissues appears to vary from species to species. In leaf tissues, tannins have been reported to occur preferentially in the epiderm, hypoderm, periderm, mesophyll, companion cells and vascular tissues, as well as throughout the leaf tissue (Grundhöfer *et al.,* 2001). In roots, anatomical studies have identified a 'condensed tannin zone' in pine and eucalyptus located between the growing tip and the more developed cork zone (Peterson *et al.,* 1999; Enstone *et al.,* 2001). Hydrolyzable tannins have a more restricted occurrence than condensed tannin, being found in only 15 of the 40 orders of dicotyledons (Hättenschwiler & Vitousek 2000).

2.3.2 Effects of tannin on litter decomposition

N and lignin concentration or C: N and lignin: N ratios are often used to predict rates of litter decomposition. However, a number of studies have shown that tannin and/or polyphenol content is a better predictor of decomposition, net N mineralization and N immobilization (Palm & Sanchez, 1991; Gallardo & Merino, 1992; Driebe & Whitham, 2000; Kraus *et al.,* 2003). Coq *et al.,* (2010) mentioned that litter decomposition in tropical rainforest correlated well with condensed tannin concentration. They concluded that leaf litter tannins play a key role in decomposition and nutrient cycling in the tropical rainforest.

In the past decades, many studies have shown that tannins are involved in defense mechanisms of plants against attack by bacteria, fungi, and herbivores (Zucker 1983; Scalbert 1991). There is not much knowledge about the mechanisms of action of the tannin (Zucker 1983; Scalbert 1991) even though modern analytical methods have improved the analysis of these complex structures (Mole & Watermann 1987; Schofield *et al.,* 2001). Proposals on the mechanism of action include tannins forming stable complexes with plant proteins to make the tissue unattractive and difficult to digest (Schofield *et al.,* 2001) and tannins acting like a toxin through highly specific reactions with digestive enzymes or directly at the cell membranes (Zucker 1983) or through depletion of essential iron by complexation (Mila *et al.,* 1996). Leaves with high initial contents of condensed tannins, seem to decompose slowly in both terrestrial (Valachovic *et al.,* 2004) and aquatic ecosystems (Wantzen *et al.,* 2002). Condensed tannin may play an important role in aquatic leaf litter decomposition, as they may deter invertebrate shredders (Wantzen *et al.,* 2002). Condensed tannin deters herbivore feeding by acting as toxins and not as digestion inhibitors by protein precipitation. Other researchers have obtained data that suggest the toxic nature of tannins (Robbins *et al.,* 1987; Provenza *et al.,* 1990; Clausen *et al.,* 1990). Alongi (1987) noticed that if decomposers are inhibited by high contents of tannins in their food, strong effects on litter breakdown would be expected. Handayanto *et al.,* (1997) found a strong negative correlation between N mineralization rates and the protein precipitation capacity of litter material, a measure of tannin reactivity. Litter material high in tannin content is commonly associated with reduced decomposition rates (Gallardo & Merino, 1992; Kalburtji *et al.,* 1999). The convergent evolution of tannin-rich plant communities has occurred on nutrient-poor acidic soils throughout the world. Tannins were once believed to function as anti-herbivore defenses, but more and more ecologists now recognize them as important controllers of decomposition and nitrogen cycling processes. Tannins inhibit soil nitrogen accumulation and the rate of terrestrial and aquatic decomposition (Hissett & Gray 1976). Tannins make plant tissues unpalatable and indigestible for animals. Tannins impede digestion of plant tissues by blocking the action of digestive enzymes, binding to proteins being digested or interfering with protein activity in the gut wall (Howe & Westley 1988; Lambers 1993). Tannins may also reduce insect predation because they increase the leaf toughness (Haslam 1988). Kraus *et al.,* (2003) summarized that tannins may limit litter decomposition in a number of different ways: (1) by themselves being resistant to decomposition (2) by sequestering proteins in protein-tannin complexes that are resistant to decomposition (3) by coating other compounds, such as cellulose, and protecting them from microbial attack (4) by direct toxicity to microbes, and (5) by complexing or deactivating microbial exoenzymes.

The studies by Schimel *et al.,* (1998) in the Alaskan taiga provide some of the most comprehensive examinations of the diversity of phenolics and condensed tannin effects on soil processes.

Secondary succession in these forests starts with *Salix/Alnus* communities and continues to an *Alnus/Populus*, a *Populus*, and finally a *Picea alba*–dominated community. *Populus balsamifera* was found to play a key role during succession by the production of polyphenols that interfere with soil processes. Plants from strongly N-limited ecosystems are generally defended by tannins, whereas N-based and structural defenses become more abundant with increases in N supply (Gartlan *et al.,* 1980).

For example, in the savannas of southern Africa, infertile miombo woodlands and savannas on soils derived from highly weathered granites have trees whose leaves are defended by tannins, while on nearby savannas on higher-nutrient soils such as shales and young volcanic soils, plants are defended by spines. The prevalence of chemical defenses depends on ecosystem nutrient supply (Craine *et al.,* 2003). Fig. 7 represents the schematic overview of the effects of quantitative chemicals from leaf litter on various soil processes and its consequences for the nitrogen cycle and successional dynamics in terrestrial ecosystems.

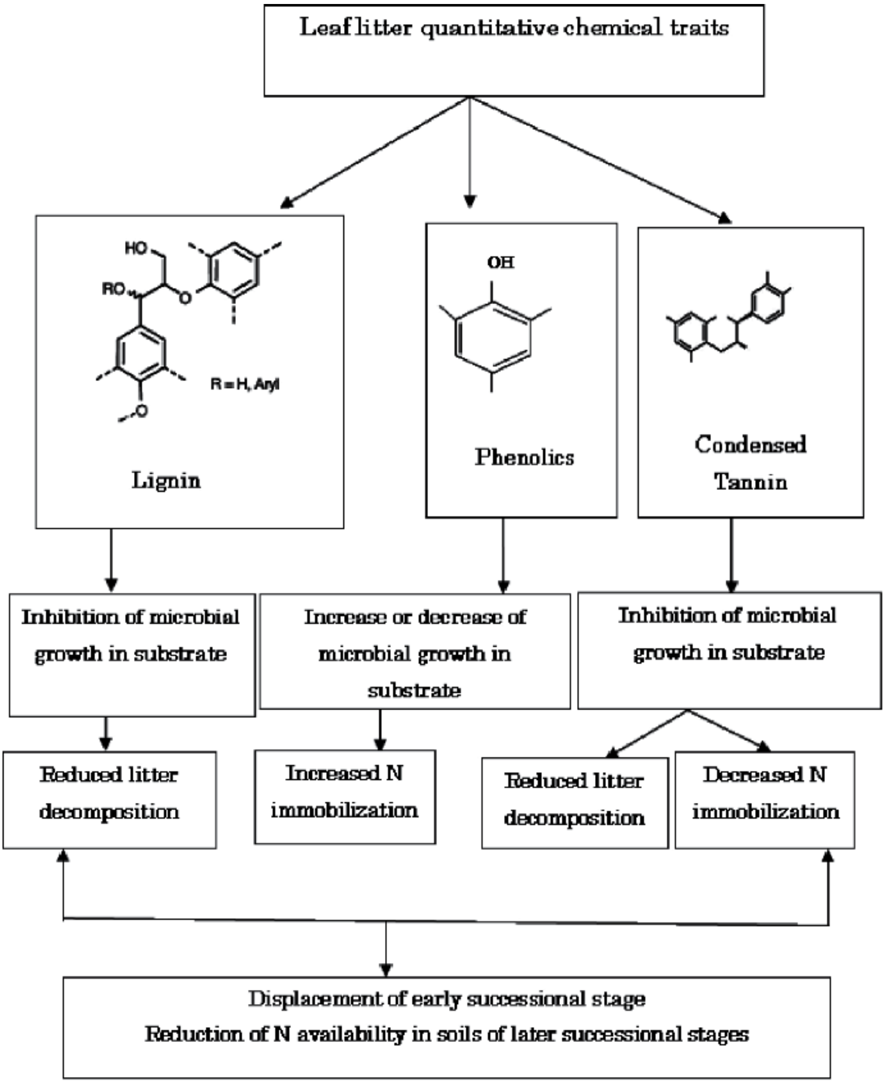


Fig. 7. Schematic reorientation of the effects of quantitative chemicals from leaf litter on various soil processes and its consequences for the nitrogen cycle and successional dynamics in terrestrial ecosystems (modified after Schimel *et al.,* 1998).

3. Litter decomposition and ecosystem functioning

Ecosystem is composed of three subsystems i.e., producer- consumer- and decomposer-subsystem. Ecosystem functioning is affected not only by the function of each subsystem but also by interactions between them. Quantitative defense is the driving force of ecosystem functioning (fig. 8).

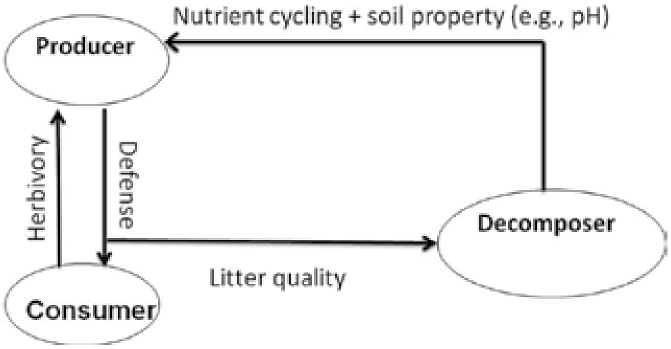


Fig. 8. Ecosystem functioning.

Wardle *et al.,* (1997) demonstrated the importance of tree species composition in determining turnover rate of organic matter and N mineralization by comparing the forests dominated by early successional, fast-growing species and those dominated by slow-growing climax species. This is a verification of the hypothesis in the boreal zone the climax of which is characterized by slow rate of decomposition of hardly decomposable spruce needle litter.

Plant litter decomposition is important to many ecosystem functions such as the formation of soil organic matter, the mineralization of organic nutrients, and the carbon balance (Austin & Ballaré 2010). It is estimated that the nutrients released during litter decomposition can account for 69-87% of the total annual requirement of essential elements for forest plants (Waring & Schlesinger 1985).

Decomposition and nutrient cycling are fundamental to ecosystem biomass production. Most natural ecosystems are nitrogen (N) limited and biomass production is closely correlated with N turnover (Vitousek & Howarth, 1991; Reich *et al.,* 1997). Typically external input of nutrients is very low and efficient recycling of nutrients maintains productivity (Likens *et al.,* 1970). Decomposition of plant litter accounts for the majority of nutrients recycled through ecosystems. Rates of plant litter decomposition are highly dependent on litter quality; high concentration of phenolic compounds, especially lignin, in plant litter has a retarding effect on litter decomposition (Hattenschwiler & Vitousek 2000). At the ecosystem level, chemical defense can influence litter decomposition and nutrient cycling rates (Hattenschwiler & Vitousek 2000; Kraus *et al.,* 2003). Ecosystems dominated by plants with low-lignin concentration often have rapid rates of decomposition and nutrient cycling (Chapin *et al.,* 2003). Simple carbon (C) containing compounds are preferentially metabolized by decomposer microorganisms which results in rapid initial rates of decomposition. More complex C compounds are decomposed more slowly and may take many years to completely breakdown. Phenols and tannins, affect nutrient cycling in soil by inhibiting organic matter degradation, mineralization rates and N availability (Kraus *et al.,* 2003).

3.1 Effects of management on litter decomposition

Litter decomposition rate may be regulated by species composition, leaf litter chemistry, management activities, or any of the combinations of them. The forest management activities had significant effects on leaf litter decomposition. They also had significant effects on leaf litter chemistry during decomposition process. Clear cut or selective thinning method for timber harvesting may change litter decomposition by altering microclimatic conditions of the forest floor, leaf litter chemistry and composition of the microbial community (Li *et al.,* 2009; Blanco *et al.,* 2011). In a cold climate, selective thinning can increase the temperatures of the forest floor, and thus increase decomposition rate whereas selective thinning in a warm climate may slow decomposition by reducing the moisture content of surface organic matter (Li *et al.,* 2009; Blanco *et al.,* 2011). Blanco *et al.,* (2011) observed that thinning effects clearly influenced litter chemistry in Continental forest and Mediterranean forest, generally appeared sequentially, first nutrients and cellulose and then total C and lignin.

4. Concluding remarks and future direction

Leaf litter decomposition is the fundamental process of ecosystem functioning. Quantitative chemical is hypothesized to play a key role in regulating litter decomposition and to be important for the production of dissolved organic matter and CO_2. Lignin decomposition may be relatively slower in boreal forest than tropical forests. Results after three years of decomposition experiments of Canadian boreal forest, Moore *et al.,* (1999) concluded that lignin/N ratio, and some other climatic variables were valuable parameters for predicting mass loss.

Plants growing in tropical regions have higher polyphenolics concentrations in their tissues compared to temperate zone species (Coly 1983). Tannins are abundant in tropical tree foliage and have the potential effects on litter decomposition. Wieder *et al.,* (2009) used natural variations in species litter chemistry combined with a through fall removal experiment to understand how climate–chemistry interactions regulate tropical forest litter decomposition. Their results suggested that widely used predictors of litter decomposition based on chemical quality are still useful in tropical forests and that these wet systems also require an understanding of litter solubility to best prediction rates of decomposition.

The above discussion justifies that quantitative chemical traits can be used as a predictive tool for litter decomposability and ecosystem functioning. The decomposition of plant litter is an essential process in terrestrial ecosystems, resulting in carbon and nutrients being recycled for primary production. While a great deal of research has addressed quantitative chemical defense and their effect on decomposition and ecosystem functioning, there are many areas of quantitative chemical's biogeochemistry that are not known. There is still little information found regarding how different types of quantitative chemicals influence soil organisms, and how these chemicals' biodegradation affects the soil quality. An understanding of the role of quantitative chemicals in plant litter decomposition will allow for more accurate predictions of carbon dynamics in terrestrial ecosystems. When we can make a relationship between quantitative chemicals and decomposition then we can easily predict ecosystem functioning, which is important for conservation and restoration management of endangered ecosystems. Hence, it is imperative that future research focuses more attention on quantitative chemicals' biogeochemistry and their effects on litter decomposition, CO_2 emission and soil quality. There is a specific need to understand the role of lignin and of lignified cellulose, and their interactions during the late stages of decomposition. How do different types of lignin building blocks influence litter decomposition processes? What is the fate of quantitative chemicals after litter decomposition? Identifying and quantifying links between quantitative chemical defense traits and litter decomposability would enhance our understanding of ecosystem functioning and will provide us with a predictive tool for modeling decomposition rates under different vegetation types.

5. Acknowledgements

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14

Genetic Sustainability of Fragmented Conifer Populations from Stressed Areas in Northern Ontario (Canada): Application of Molecular Markers

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1. Introduction

The Earth's genes, species, and ecosystems are the product of over 3 billion years of evolution and the basis for the survival of our own species. Biological diversity, the measure of the variation in genes, species and ecosystems is valuable because future practical uses and values are unpredictable and our understanding of ecosystems is insufficient to be certain of the impact of removing any component. Genetic diversity is an indicator of ecosystem condition and sustainability. It is a fundamental component of biodiversity and it encompasses all of the genetically determined differences that occur between individuals of a species. The loss of biodiversity is due above all to economic factors, especially the low values given to biodiversity and ecological functions such as watershed protection, nutrient cycling, pollution control, soil formation and photosynthesis. Biodiversity is very much a cross-sectoral issue, and virtually all sectors have an interest in its conservation and the sustainable use of its components. Biological resources are renewable and with proper management can support human needs indefinitely. These resources, and the diversity of the systems which support them, are therefore the essential foundation of sustainable development.

The past two decades have been a time of great change in the management of natural resources in Ontario and around the world. Ontario's forest policy has shifted to a more balanced ecological approach as the forest is now viewed as part of a larger ecosystem OMNR, 2001). All forest policies and associated management practices in Ontario conform to the Policy Framework for Sustainable Forests (OMNR, 2001). Many Ontario communities especially in the North depend on forests. There are some 60.9 million hectares of forested land in the province, representing approximately 57% of the 106.8

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million hectare provincial land base (including water). Crown forest accounts for approximately 91% of this forested land located mostly in the Northern Ontario region. It represents the boreal and the Great Lake St. Lawrence Forests that are composed mainly of conifer species (Natural resources of Canada, 2003; OMNR, 2001). The Forest Resource Inventory is the primary survey for sustainable forest management. Information generated by forest inventories has contributed greatly to our knowledge of one of Ontario's renewable resources and continues to serve as the basis for major forest resource planning and policy decisions in the OMNR. But this information is not sufficient to ensure the sustainable management of the forest resource. To achieve this goal, information on genetic diversity of tree populations is essential.

In addition, forest management practices must change to keep pace with climatically induced changes in forest ecosystems. The sustainability, biodiversity, health, and economic benefits of forests will be affected to varying degrees by climate change. A detailed analysis of the level of genetic variability in species and populations is essential in developing climate change models (Colombo et al., 1998).

Evolutionary adaptation to new climate conditions can only occur where sufficient genetic variation exists to allow selective forces to discriminate between adaptive and maladaptive traits. Adaptation may occur more rapidly in species with shorter life cycles, as long as conditions are favourable for reproduction, than in long-lived species such as trees which will undergo a time lag response to changing conditions (Colombo et al., 1998). Forest tree species generally have high levels of genetic variability and gene dispersal rates.

On the other hand, genetic structure of Northern Ontario forests has been seriously affected by past forest management, mining, and forest fire activities. In an effort to maintain the long term viability of the forest landbase in Northern Ontario, forest companies and local government organizations have concentrated on artificial regeneration of conifer seedlings as a primary means of reforestation. To date, over nine millions of forest trees mostly conifers have been planted within the Greater Sudbury Region and surrounding areas.

The Sudbury region in Ontario, Canada has a history over the past 100 years of logging, mining, and sulphide ore smelting, releasing more than 100 million tonnes of SO_2 and tens of thousands of tonnes of cobalt, copper, nickel, and iron ores into the atmosphere from the open roast beds (1888-1929) and smelters (1888-present) (Freedman and Hutchison, 1980). These factors have caused acidification, severe metal contamination of the soils and water at sites within approximately 30 km of the smelters in the Sudbury region. Sudbury area is one of the most ecologically disturbed regions in Canada. There have been numerous studies documenting the effects of SO_2 in the Sudbury region (Cox and Hutchinson, 1980; Amiro and Courtin, 1981; Gratton *et al.*, 2000). In general, information on landscape degradation, soil toxicity, acidification, plant metal accumulation and forest composition in Northern Ontario is readily available but knowledge of genetic variation within and among forest tree populations is lacking. This genetic diversity information is crucial to ensure sustainability of the forest resource. The impoverished plant communities that are currently found in the Greater Sudbury Region (GSR) are not only structurally and floristically different from plant communities found in uncontaminated areas in the basin, but they appear to have a different genetic make-up.

Many studies have used morphological markers to assess genetic variability within and among species and populations. Those markers are not usually reliable since phenotypic variation is often related to environmental factors. Molecular markers are an important and very powerful tool for genetic analyses of plant species. Molecular markers such as Random Amplification of Polymorphic DNA (RAPD), Inter-Simple Sequence Repeats (ISSR), Simple Sequence Repeats (SSR), and Amplified Fragment Length Polymorphism (AFLP) have been successfully used to assess the genetic diversity in many plant species (Semagn et al., 2006; Sharma *et al.*, 2008). Each one of these marker systems offers a unique combination of advantages and disadvantages (Sharma *et al.*, 2008). They differ in the type of sequence polymorphism detected (insertion/deletions vs. point mutation), information content, the dominance relationships between alleles (dominant vs. codominant markers), amount of DNA required, the need for DNA sequence information in the species under analysis, development costs, the ease of use, and the extent to which they can be automated.

The overall objective of this chapter is to provide current stage of knowledge from several studies on genetic variability in planted and natural fragmented conifer populations from Northern Ontario using ISSR and microsatellite (SSR) markers.

2. Materials and methods

2.1 Genetic material

Needles from White pine (*Pinus strobus*), jack pine (*Pinus banksiana*), red pine (*Pinus resinosa*), white spruce (*Picea glauca*), and black spruce (*Picea mariana*) individual trees were sampled from natural (Na) and planted (P) populations. The locations of some sampling sites are illustrated in Figure 1. Additional samples were from the nursery used for the Sudbury land reclamation program and were considered as introductions. For each site, needles and seed samples from first and second generations trees were collected separately. In general 10% to 20 % of each population was analyzed. For each tree, 15 grams of needles were weighed in duplicates, frozen in liquid nitrogen and stored at -80 ^{o}C until DNA extraction.

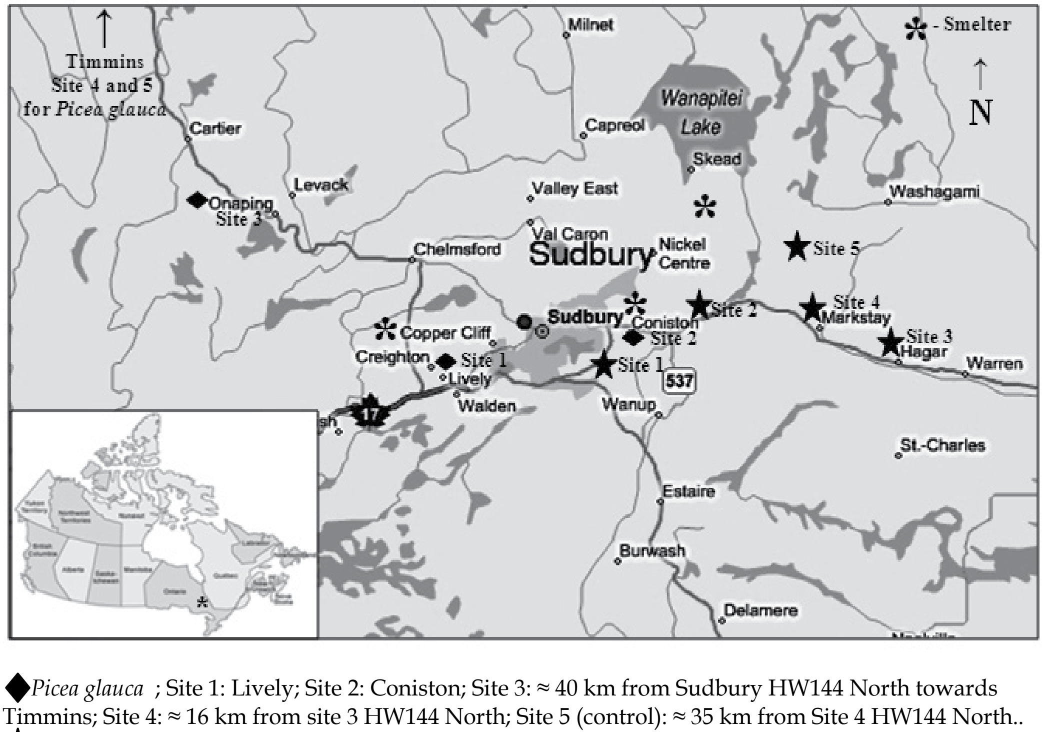
2.2 Soil characterization

Soil samples were analyzed in collaboration with TESTMARK Laboratories Ltd. Sudbury, Ontario, Canada. The laboratory is ISO/IEC 17025 certified, a member of the Canadian Council of Independent Laboratory (CCIL) and the Canadian Association of Environmental Analytical Laboratories (CAEAL), and is accredited by the Standards Council of Canada (SSC). The laboratory employs standard QA/QC procedures, involving blank and replicate analyses and with recovery rate of 98 ± 5% in analyses of spiked samples depending on element selected, in their inductively coupled plasma mass spectrometry (ICPMS) analyses reported here. The minimum detection limits (MDL) following microwave digestion of plant tissue Aqua Regia for elements reported here, were: Aluminum 0.05 µg/g (0.5 µg/g), Arsenic 0.05 µg/g (0.5 µg/g), Cadmium 0.05 µg/g (0.5 µg/g), Cobalt 0.05 µg/g (0.5 µg/g), Copper 0.05 µg/g (0.5 µg/g), Iron 1.0 µg/g (10 µg/g), Lead 0.05 µg/g (0.5 µg/g), Magnesium 0.2 µg/g (2.0 µg/g), Manganese 0.05 µg/g (0.5 µg/g), Nickel 0.05 µg/g (0.5 µg/g) and Zinc 0.05 µg/g (0.5 µg/g). These MDLs reflect actual sample weights and dilutions; instrument detection limits were lower.

The data for the metal levels in soil samples were analyzed using SPSS 7.5 for Windows. All the data were transformed using a $\log_{10}$ transformation to achieve a normal distribution. Kruskal-Wallis test the non-parametric analog of a one-way ANOVA was used to compare independent samples, and tests the hypothesis that several populations have the same continuous distribution. ANOVA followed by Tukey's HSD multiple comparison analysis were performed to determine significant differences ($p < 0.05$) among the sites.

2.3 DNA extraction

The total cellular DNA from individual samples was extracted from seedling tissue using the method described by Nkongolo (1999), with some modifications. The modification involved addition of PVP (polyvinylpyrrolidone) and β-mercaptoethanol to the CTAB extraction buffer. The DNA concentration was determined using the fluorochrome Hoechst 33258 (bisbensimide) fluorescent DNA quantitation kit from Bio-Rad (cat. # 170-2480) and the purity was determined using a spectrophotometer (Varian Cary 100 UV-VIS spectrophotometer).



◆*Picea glauca* ; Site 1: Lively; Site 2: Coniston; Site 3: ≈ 40 km from Sudbury HW144 North towards Timmins; Site 4: ≈ 16 km from site 3 HW144 North; Site 5 (control): ≈ 35 km from Site 4 HW144 North..
★*Pinus strobus:* Site 1: Daisy Lake (HW17 Bypass); Site 2: Coniston (HW17); Site 3: Hagar ≈ 60km from Sudbury; Site 4: Markstay ≈ 38km from Sudbury; Site 5: Kukagami Road (≈ 9 km from HW17).

Fig. 1. Sudbury (Ontario) map showing locations of some sampling sites.

2.4 ISSR analysis

The ISSR amplification was carried out in accordance with the method described by Nagaoka and Ogihara (1997), with some modifications described by Mehes et al. (2007). All DNA samples were primed with each of the ten primers used (Table 1). All PCR products were loaded into 2% agarose gel in 1X Tris-Borate-EDTA (TBE) buffer. Gels were pre-stained with 4 µl of ethidium bromide and run at 3.14V/cm for approximately 120 minutes. These agarose gels were visualized under UV light source, documented with the Bio-Rad ChemiDoc XRS system and analyzed for band presence or absence with the Discovery Series Quantity One 1D Analysis Software.

The resulting data matrix of the ISSR phenotype was analyzed using POPGENE software (version 1.32) to estimate genetic diversity parameters (Yeh and Boyle, 1997a, 1997b). POPGENE is computer software used for the analysis of genetic variation among and within populations using co-dominant and dominant markers and quantitative traits. The program was used to determine the intra and inter-population genetic diversity parameters such as percentage of polymorphic loci (P%), Nei's gene diversity (h), Shannon's information index (I), observed number of alleles (Na) and effective number of alleles (Ne). The genetic structure was investigated using Nei's gene diversity statistics, including the within population diversity (H_s) and total genetic diversity (H_t) (Nei, 1973) calculated within the species using the same software. The mean and the total gene diversities, the variation among populations and gene flow were also calculated. The genetic distances were calculated using Jaccard's similarity coefficient estimated with the RAPDistance program version 1.04 (Armstrong *et al.*, 1994).

Primer identification	Nucleotide sequence (5′→3′)	G + C content (%)
ISSR Primers		
Echt 5	AGAC AGAC GC	60.00
HB 13	GAG GAG GAG GC	72.70
HB 15	GTG GTG GTG GC	72.70
ISSR 1	AG AG AG AG AG AG AG AG RG	50.00
ISSR 5	ACG ACG ACG ACG AC	64.28
ISSR 9	GATC GATC GATC GC	57.14
UBC 825	AC AC AC AC AC AC AC AC T	88.88
UBC 841	GA AG GA GA GA GA GA GA YC	45.00
17899A	CA CA CA CA CA CA AG	50.00
17898B	CA CA CA CA CA CA GT	50.00

Table 1.The nucleotide sequences of ISSR primers used to screen DNA samples of *Picea glauca* and *Pinus strobus.*

2.5 Microsatellite analysis

The microsatellite analysis involved three species (*Pinus banksiana, Pinus resinosa,* and *Picea mariana*). Ten microsatellite primers, synthesized by Invitrogen, were chosen for amplification of DNA from *Pinus banksiana* and *P. resinosa* populations. These primers described in Vandeligt et al. (2011) include PtTX 3013, PtTX 3030, PtTX 3098, PtTX 309, PtTX 2123, PtTX 3088, RPS 2, RPS 20, RPS 25b, and RPS 84. For *Picea mariana*, the primers used are described in Dobrzeniecka et al. 2009. DNA amplification was performed following the procedure described by Mehes et al. 2009. The Popgene software, version 1.32 (Yeh and Boyle, 1997) was used to assess the intra- and interpopulation genetic diversity parameters such as the mean number of alleles (N_A) across loci, the total number of alleles (N_T) per locus and Shannon's information index (i)(Yeh and Boyle, 1997). The observed and expected heterozygosities (H_O and H_E respectively) were calculated using the Genepop software, version 3.4 (Raymond and Rousset, 1995). The probability test was computed using the Markov chain method (1000 iterations) in order to determine populations in Hardy-Weinberg Equilibrium (Genepop). Hardy-Weinberg equilibrium deviations were tested using alternative hypotheses, deficiency and excess of heterozygotes, for each locus and across loci and populations using Fisher's method. A test for null allele was also done using the EM algorithm of Dempster et al. (1977). The average effective number of migrants exchanged between populations in each generation, or gene flow (N_M) is estimated from F_{ST} (subdivision among populations).

3. Results

3.1 Soil analysis

Recovery and precision for all elements in reference soil samples were within acceptable range. The estimated levels of metal content in different sites from the Greater Sudbury Region in Canada are illustrated in Table 2. The levels of the metals measured were low in the control sites. Overall, the results indicated that nickel and copper continue to be the main contaminants of top soil (Table 2) in sites near the smelters (site 1 and 2). The values ranged from 30.9 to 1600.0 mg kg^{-1} and from 52.3 to 1330.3 mg kg^{-1} for nickel and copper respectively (Table 1). Arsenic concentration exceeded the OMEE (Ontario Ministry of Environment and Energy) guidelines in site 1 and manganese level exceeded the guideline in site 2. Their concentration ranged from 2.2 to 46.0 mg kg^{-1} and 163.6 to 6610.3 mg kg^{-1} for arsenic and manganese, respectively (Table 2).

Aluminum, iron and magnesium concentrations were significantly higher in sites 1 to 4 (top layer, Table 2) compared to the control site 5. The values ranged from 1673.3 to 9193.3 mg kg^{-1}, 2193.3 to 31433.3 mg kg^{-1} and 349.6 to 6866.6 mg kg^{-1} for aluminum, iron and magnesium, respectively (Table 2). Cadmium, cobalt, lead and zinc levels were within the OMEE guideline. The values for these metals ranged from 0.3 to 2.1 mg kg^{-1}, 1.6 to 37.9 mg kg^{-1}, 18.2 to 176.0 mg kg^{-1} and 52.0 to 86.8 mg kg^{-1} (Table 2). The control site 5 was always among the least contaminated for the metals analysis. All the metal concentrations obtained from the bottom layer (5 – 20 cm) were within the OMEE guideline (data not shown). Surprisingly, the data from tailings were similar or significantly lower than other contaminated sites. The pH for all the sites including the controls were low (acidic).

Sampling sites	**Elements**											**pH**
	Aluminum	Arsenic	Cadmium	Cobalt	Copper	Iron	Lead	Magnesium	Manganese	Nickel	Zinc	
Site 1	7360b	46b	2b	29b	1330bc	31433bc	176bc	2970b	163a	1600b	86bc	4.6
Site 2	9193b	10a	1b	37b	373ac	12933ac	46ac	6866b	6610c	318bc	52ab	4.5
Site 3	7670b	10a	0.9b	22a	170a	6476a	39ac	2706b	539b	120bd	60ac	-
Site 4	7090b	2a	0.3a	6a	52a	10233ac	18a	2996b	165a	54acd	32a	4.0
Site 5 (control)	1673a	2a	0.7b	2a	93a	2913a	88ab	349a	206a	30acd	55a	3.8
Tailings	-	-	0.3a	34b	300ac	-	46ac	-	-	292bc	59ac	-

**Means in columns with a common subscript are not significantly different based on Tukey multiple comparison test ($P \geq 0.05$). Site 1: Lively; Site 2: Coniston (close to HW17); Site 3: ≈ 40 km from Sudbury HW144 towards Timmins; Site 4: ≈ 16km from site 3 HW144 towards Timmins; Site 5 (control): ≈ 35km from Site 4 HW144 towards Timmins. Tailings data represent means of two tailings located near smelters.*

Table 2. Metal concentrations in top layer (0 – 5 cm) of soil from the Sudbury region sites, concentrations are in mg kg^{-1}, dry weight*.

3.2 Analysis of populations using ISSR markers

Ten ISSR oligonucleotides (Table 1) were used for the amplification of spruce and pine populations. For each population in each species, the levels of polymorphism for the two generations analyzed were similar. Thus, the data were compiled and analyzed per population.

3.2.1 *Pinus strobus* (white pine)

The percentage of polymorphic loci within each population varied between 22% observed in the site 5 (control) to 36% in site 4 (Table 2). The level of genetic variation was similar between natural and planted populations in site 1. For site 2, the polymorphic loci were significantly higher in planted populations compared to the natural population. Data for the Nei' gene diversity (h) ranged from 0.05 (S5) to 0.14 (S4) with a mean of 0.19. A similar pattern was observed for the Shannon's information index (I), with the high value of 0.20 observed in S4 and a low value of 0.08 observed in S5. The observed number of alleles (Na) and the effective number of alleles (Ne) ranged from 1.22 to 1.36 and 1.08 to 1.25 respectively. The genotype diversity among population (H_t) was 0.15 and the within population diversity (H_s) was 0.09. Mean coefficient of gene differentiation (G_{st}) was 0.366 indicating that 63.4% of the genetic diversity resided within the population. The observed structure of genetic variability shows that there is a low level of differentiation among the *Pinus strobus* populations. The overall rate of gene flow (N_m) among population was 0.87.

Population*	P (%)	Na	Ne	h	I
S1P	30	1.30	1.14	0.08	0.13
S1Na	30	1.30	1.18	0.10	0.15
S2P	34	1.34	1.21	0.12	0.18
S2Na	22	1.22	1.12	0.07	0.11
S3M	32	1.32	1.19	0.11	0.17
S4M	36	1.36	1.25	0.14	0.20
S5M	22	1.22	1.08	0.05	0.08
Mean	29	1.29	1.17	0.10	0.15

*Population: P represents Plantation and Na represents Natural populations. M represents mixed populations including natural and planted trees.

Table 2. Genetic diversity parameters of *Pinus strobus* based on ISSR data.

3.2.2 *Pinus banksiana* (jack pine)

For Jack pine, a low to moderate levels of genetic variation was revealed within each population. The percentage of polymorphic loci (P %) ranged from 14.6 % to 45.8 % with a mean of 31.6 %. The mean level of polymorphism for the eight populations from the greater Sudbury area was 27.6% while this value was higher for populations from the nurseries with an average of 42.4% detected polymorphic loci. The levels of genetic variation detected in populations from metal-contaminated areas were similar to those found in control sites. The Nei's gene diversity (h) for all jack pine populations analyzed varied from 0.046 to 0.169 with an average of 0.100, and Shannon's index (I) ranged from 0.070 to 0.250 with an average of 0.153. The mean observed number of alleles (Na) ranged from 1.146 to 1.458, while the mean effective number of alleles (Ne) varied from 1.107 to 1.31 (Table 3).

Populations	P (%)	h	I	Ne	Na
Nursery 1 (Introduction 1)	39.58	0.0961	0.1535	1.1579	1.3958
Nursery 2 (Introduction 2)	41.67	0.1380	0.2106	1.2248	1.4167
Nursery 3 (Introduction 3)	45.83	0.1687	0.2501	1.2946	1.4583
Inco 1	31.25	0.1120	0.1653	1.2035	1.3125
Inco 2	31.25	0.1171	0.1727	1.2061	1.3125
Falconbridge 1	14.58	0.0456	0.0701	1.0756	1.1458
Falconbridge 2	27.08	0.0995	0.1467	1.1758	1.2708
Falconbridge 3	20.83	0.0630	0.0982	1.1004	1.2083
Inco Tailing	35.42	0.0977	0.1552	1.1514	1.3542
Temagami (control)	29.17	0.0818	0.1284	1.1310	1.2917
Low Water Lake (control)	31.25	0.0812	0.1297	1.1256	1.3125
Mean	31.63	0.1001	0.1528	1.1679	1.3163

P represents percentage of polymorphic loci; h, Nei's gene diversity; I, Shannon's information index; Ne, effective number of alleles; Na, observed number of alleles.

Table 3. Genetic variability parameters of *Pinus banksiana* populations growing in the Sudbury area based on ISSR data.

3.2.3 *Pinus resinosa* (red pine)

The level of genetic variation was much lower in the red pine populations. For this species, the level of polymorphic loci varied from 4.55 % to 27.27 % (Table 4). The mean level of polymorphic loci for populations from the greater Sudbury region excluding the population from the nursery was only 8.3%. Like in jack pine populations, the polymorphism detected in contaminated populations was similar to that found in non contaminated site used as a control. Overall, the mean for Nei's gene diversity and Shannon's information index, were 0.034 and 0.053, respectively for all the red pine populations analyzed. The mean observed number of alleles (Na) ranged from 1.045 to 1.27 while the mean effective alleles (Ne) varied from 1.00 to 1.17 (Table 4). The highest genetic diversity values were observed in the populations used for the Sudbury reforestation program. High levels of metal content did not affect the level variation for both species.

Population	P (%)	h	I	Ne	Na
Near Falconbridge	4.55	0.0044	0.0092	1.0049	1.0455
Very near Falconbridge	13.64	0.0411	0.0638	1.0672	1.1364
Falconbridge	4.55	0.0226	0.0314	1.0450	1.0455
Coniston	9.09	0.0180	0.0309	1.0244	1.0909
Daisy Lake	9.09	0.0272	0.0433	1.0389	1.0909
Verner (control)	9.09	0.0267	0.0423	1.0398	1.0909
Introduction 1 (control)	27.27	0.0988	0.1465	1.1710	1.2727
Mean	11.04	0.0341	0.0525	1.0559	1.1104

P represents percentage of polymorphic loci; h, Nei's gene diversity; I, Shannon's information index; Ne, effective number of alleles; and Na, observed number of alleles.

Table 4. Genetic variability parameters of *Pinus resinosa* populations growing in the Sudbury area based on ISSR data.

3.2.4 *Picea glauca* (white spruce)

All the selected primers amplified 11 to 21 fragments across the six populations studied. The amplified fragment size ranged from 170 bp to 2,240 bp. The percentage of polymorphic loci within each population varied between 50% observed in the natural site 5 Na (control) to 61% in site 1, P (Table 5). Nei' gene diversity (h) ranged from 0.17 (site 1, P) to 0.21 (site 5, Na; control) with a mean of 0.19. A similar pattern was observed for the Shannon's information index (I), with the highest value of 0.32 observed in the planted population of site 1P and the lowest value of 0.26 observed in site 5Na (control). The observed number of alleles (Na) and the effective number of alleles (Ne) ranged from 1.50 to 1.61 and 1.29 to 1.37 respectively. The genotype diversity among population (H_t) was 0.19 and the within population diversity (H_s) was 0.23. The mean coefficient of gene differentiation (G_{st}) was 0.168 indicating that 83.2% of the genetic diversity resided within the population. The observed structure of genetic variability shows that there is a low level of differentiation among the *Picea glauca* populations in the target regions even when the populations located as far as 100 km from the Sudbury were included. The overall rate of gene flow (N_m) among population was 2.47.

3.2.5 *Picea mariana* (black spruce)

The genetic diversity within each population was high. For each population, the percentage of polymorphic loci was the same for the parental and the offspring generations analyzed. Thus, the data from the two generations were combined. The percentage of polymorphic loci (P%) ranged from 65% to 90 % with a mean of 75% . Nei's gene diversity (h) varied from 0.264 to 0.359 with an average of 0.310, and Shannon's index (I) ranged from 0.381 to 0.524 with an average of 0.449 (Table 6). The mean observed number of alleles (Na) ranged from 1.650 to 1.900, while the mean effective number of alleles (Ne) varied from 1.168 to 1.632 (Table 6). Among the nine populations investigated, the highest genetic diversity was observed in population 9 from lowland in Timmins while the lowest level of diversity was detected in population 4 from upland in Chelmsford. Overall, the average level of polymorphic loci was much higher in lowlands (85%) than in uplands (68%). There was no difference between metal contaminated and uncontaminated sites for genetic variation.

Population*	P (%)	Na	Ne	h	I
Site 1 (P)	61	1.61	1.37	0.22	0.32
Site 2 (P)	53	1.53	1.33	0.19	0.29
Site 3 (Na)	55	1.55	1.32	0.19	0.29
Site 4 (Na)	53	1.53	1.33	0.19	0.28
Site 5 (control) (Na)	50	1.50	1.30	0.18	0.26
Nursery	57	1.57	1.35	0.20	0.30
Mean	55	1.55	1.33	0.19	0.29

*Population: P represents Plantation and Na represents Natural populations

Table 5. Genetic diversity parameters of *Picea glauca* based on ISSR data.

Populations	P (%)	h	I	Ne	Na
Site 1	80	0.328	0.473	1.603	1.800
Site 2	85	0.350	0.508	1.630	1.850
Site 3	70	0.269	0.396	1.473	1.700
Site 4	65	0.264	0.381	1.490	1.650
Site 5	75	0.317	0.456	1.582	1.750
Site 6	70	0.274	0.402	1.482	1.700
Site 7	70	0.308	0.441	1.567	1.700
Site 8	70	0.325	0.459	1.168	1.700
Site 9	90	0.359	0.524	1.632	1.900
Mean	75	0.310	0.449	1.514	1.750

P represents percentage of polymorphic loci; h, Nei's gene diversity; I, Shannon's information index; Na, observed number of alleles; and Ne, effective number of alleles.

Table 6. Genetic variability parameters of black spruce (*Picea mariana)* populations growing in the Sudbury area based on ISSR data.

3.2.6 Genetic differentiation among populations

For *Pinus banksiana*, the mean gene diversity within populations (Hs) and the total gene diversity (Ht) were 0.100 and 0.1438, respectively. The variation among populations (Gst) was 0.304 indicating that 30.4 % of total genetic diversity were attributed to the differences among populations. The observed structure of genetic variability shows that there is a sensitive level of differentiation among the jack pine populations in the target regions. The overall rate of gene flow (Nm) among populations was 1.144. For *Pinus resinosa* the Hs and HT values were 0.0341 and 0.0437, respectively. About 22% of the total genetic diversity in *Pinus resinosa* was attributed to differences among populations. For *Pinus strobus*, the genotype diversity among population (H_t) was 0.15 and the within population diversity (H_s) was 0.09. Mean coefficient of gene differentiation (G_{st}) was 0.366 indicating that 63.4% of the genetic diversity resided within the population. The observed structure of genetic variability shows that there is a low level of differentiation among the *Pinus strobus* populations. The overall rate of gene flow (N_m) among population was 0.87.

For *Picea glauca* Ht and Hs were 0.19 and 0.23, respectively. The mean coefficient of gene differentiation (Gst) was 0.168 indicating that 83.2% of the genetic diversity resided within the population. The observed structure of genetic variability shows that there is a low level of differentiation among the *Picea glauca* populations in the target regions even when the populations located as far as 100 km from the Sudbury were included. The overall rate of gene flow (N_m) among population was 2.47.

For *P. mariana,* the mean gene diversity within populations (Hs) and the total gene diversity (Ht) were 0.310 and 0.385, respectively. The variation among populations (Gst) was 0.19. This indicates that 19.3% of total genetic diversity was attributed to the differences among populations. Like in *P. glauca*, the observed structure of genetic variability shows that there is a low level of differentiation among the *P. mariana* populations. The overall rate of gene flow (Nm) among populations was 2.088.

3.3 Genetic relationships among conifer populations based on ISSR analysis

3.3.1 ***Pinus banksiana***, ***Pinus strobus***, and ***Pinus resinosa***

Because of limited genetic variation in *Pinus resinosa* samples analyzed, the genetic relatedness was analyzed only for *Pinus banksiana* and *Pinus strobus* populations The Jaccard similarity coefficients and genetic distance were calculated using ISSR data. The genetic distance scale runs from 0 (identical) to 1 (different for all criteria). In general, the genetic distance values were low as they ranged from 0.06 to 0.21 for *Pinus strobus* and from 0.037 to 0.365 (Table 7) for *Pinus banksiana*. Overall the genetic distance values revealed that all the eleven *P. banksiana* and *P. strobus* populations were genetically closely related (Table 7). For *P. banksiana*, the two populations from control site (uncontaminated), Low Water Lake and Temagami were the most closely related. The largest genetic distance was observed between population 5 from INCO 2 and the new population used in 2006 for reclamation (called introduction 2 in the present study). The dendrogram constructed, based on ISSR data revealed a particular clustering (Fig. 2). All the populations from the greater Sudbury that we analyzed clustered together while the three newly introduced populations from nurseries were grouped in a separate cluster (Fig. 2). For *Pinus strobus* the genetic distance values ranged from 0.06 (S1P and S2P) to 0.21 (S2P and S2Na) (Table 8). Dendrogram was not constructed considering the low levels of genetic distances. For *Pinus resinosa*, the level of genetic variation was too low to calculate genetic distance among populations or to construct a dendrogram.

	1	2	3	4	5	6	7	8	9	10	11
1	0	0.132	0.229	0.243	0.321	0.321	0.333	0.250	0.259	0.247	0.280
2		0	0.186	0.273	0.365	0.345	0.356	0.277	0.286	0.274	0.306
3			0	0.219	0.341	0.321	0.333	0.250	0.280	0.268	0.280
4				0	0.225	0.250	0.198	0.175	0.185	0.195	0.207
5					0	0.134	0.146	0.190	0.221	0.188	0.179
6						0	0.085	0.085	0.096	0.084	0.073
7							0	0.120	0.108	0.096	0.108
8								0	0.038	0.049	0.038
9									0	0.037	0.049
10										0	0.037
11											0

1 represents introduction 1; 2, Introduction 2; 3, Introduction 3; 4, Inco 1 site; 5, Inco 2 site ; 6, Falconbridge 1 site; 7, Falconbridge 2 site; 8, Falconbridge 3 site; 9, Inco Tailing; 10, Temagami site; and 11, Low Water Lake site.

Table 7. Distance matrix generated using bulk sample analysis from various populations of *Pinus banksiana* ISSR data (RAPDistance version 1.04).

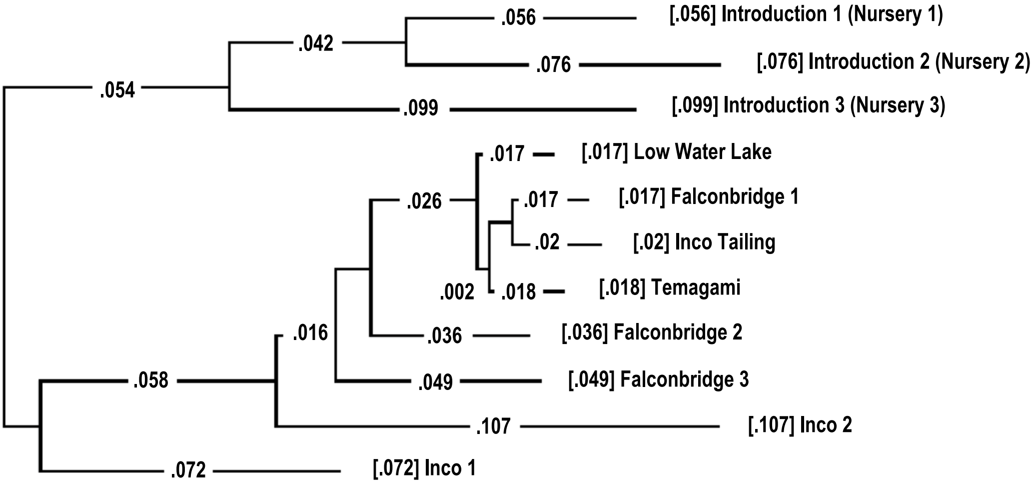


Fig. 2. Dendrogram of the genetic relationships among *Pinus banksiana* populations based on Jaccard similarity matrix using ISSR data. The values above the branches indicate the patristic distances based on the neighbor-joining (NJ) analysis.

	S1P	S1Na	S2P	S2Na	S3M	S4M	S5M
ISSR							
S1P	0.0000	0.1489	0.0667	0.1956	0.1304	0.1739	0.2128
S1Na		0.0000	0.1702	0.1778	0.1111	0.1556	0.1956
S2P			0.0000	0.2174	0.1522	0.1556	001956
S2Na				0.0000	0.0714	0.1191	0.2045
S3M					0.0000	0.0930	0.1778
S4M						0.0000	0.1818
S5M							0.0000

Population: P represents Plantation and Na represents Natural populations. M represents mixed populations including natural and planted trees. Site 1: Daisy Lake (HW17 Bypass); Site 2: Coniston (HW17 Hydro Dam ≈ 10 km from Bypass); Site 3: Hagar ≈ 60 km from Sudbury; Site 4: Markstay ≈ 38km from Sudbury; Site 5: Kukagami Road (≈ 9 km from HW17).

Table 8. Distance matrix generated from ISSR data using the Jaccard similarity coefficient analysis for *Pinus strobus* populations (Free Tree Program).

3.3.2 *Picea glauca* and *Picea mariana*

The genetic distance values were close to 0 as they varied between 0.02 (site 3, Na and site 4, Na) and 0.07 (site 2, P and site 5, Na) (Table 9) for *Picea glauca*. For *Picea mariana*, the genetic values ranged from 0.171 to 0.351 (Table 10). Overall the genetic distance values revealed that all the populations were genetically closely related (Table 10) for each of the Picea species. For *P. mariana*, the dendrogram constructed, based on ISSR data revealed a particular clustering between upland (dry) and lowlands (wet lands) (Figure 3). With the exception of site 7, no upland (dry land) population clusters with a population from a lowland (wet land). For example, the low – land (wetland) population 1 from Falconbridge clusters with the lowland (wetland) population 9 from Timmins; the upland (dry land) population 4 from Chelmsford clusters with the upland (dry land) population 8 from Timmins; the lowland (wetland) population 2 from Falconbridge clusters with the lowlands (wetland) population 5 from Cartier; and the up-land (dry land) population 3 from Capreol clusters with the upland (dry land) population 6 from Cartier.

	Site 1	Site 2	Site 3	Site 4	Site 5 (control)	Nursery
ISSR						
Site 1 (P)	0.0000	0.0520	0.0417	0.0417	0.0626	0.0209
Site 2 (P)		0.0000	0.0729	0.0729	0.0737	0.0316
Site 3 (Na)			0.0000	0.0213	0.0632	0.0417
Site 4 (Na)				0.0000	0.0632	0.0417
Site 5 (Na)					0.0000	0.0625
Nursery						0.0000

Population: P represents Plantation and Na represents Natural populations

Table 9. Distance matrix generated from ISSR data using the Jaccard similarity coefficient analysis for *Picea glauca* populations.

	Site1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7	Site 8	Site 9
Site 1	0	0.236	0.235	0.171	0.282	0.270	0.307	0.222	0.212
Site 2		0	0.324	0.263	0.230	0.307	0.256	0.350	0.351
Site 3			0	0.235	0.297	0.181	0.324	0.235	0.225
Site 4				0	0.325	0.270	0.263	0.171	0.314
Site 5					0	0.236	0.230	0.325	0.324
Site 6						0	0.263	0.222	0.264
Site 7							0	0.307	0.351
Site 8								0	0.314
Site 9									0

Table 10. Distance matrix generated using the neighbour-joining analysis from *Picea mariana* ISSR data (RAPDistance version 1.04).

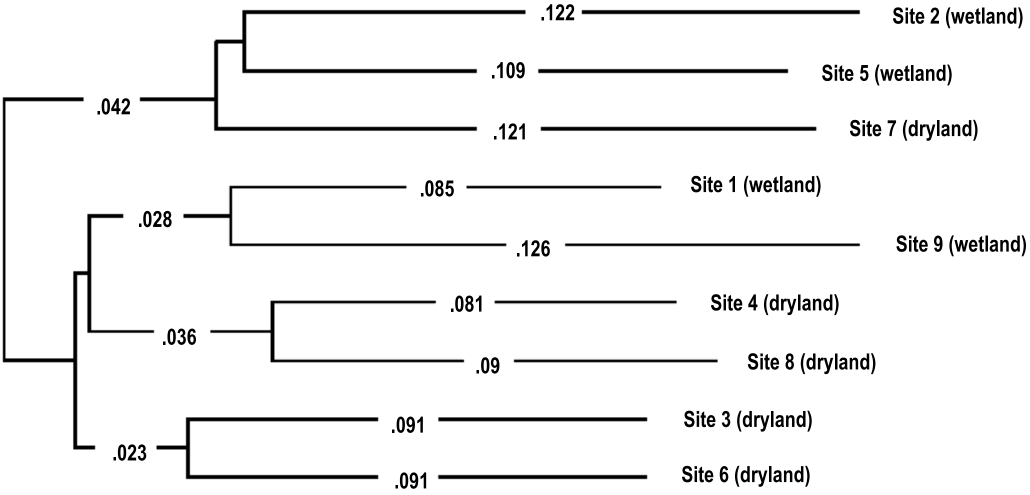


Fig. 3. Dendrogram of the genetic relationships among *Pinus banksiana* populations based on Jaccard similarity matrix using ISSR data. The values above the branches indicate the patristic distances based on the neighbor-joining (NJ) analysis.

3.4 Analysis of populations using microsatellites

3.4.1 Genetic diversity

The microsatellite loci analyzed in *Pinus banksiana* and *P. resinosa* populations are summarized in Table 11. For *P. banksiana,* the mean number of alleles per locus was 9 and the mean effective number of alleles was 3.5 (Table 11). The mean number of alleles across loci per population ranged from 3.00 to 4.67 with the samples from the INCO 3 (site 4) and the introduction 3 (population or site 11) having the highest allelic diversity. The lowest allelic diversity was observed in samples from the INCO tailing (site 7) populations (Table 11).

For *Pinus resinosa* the mean number of alleles per locus was six and the mean effective number of alleles was 2.50. The mean number of alleles across loci per population ranged from 2.33 to 3.00 for the *P. resinosa* populations (Table 11). The highest allelic diversity was observed the samples from site 2 near Falconbridge and site 7 located in Verner. The lowest allelic diversity was found in the samples from site 4 in Coniston/Wahnipitae and the newly introduced population (introduction or site 2) from nursery 2 identified as population or site 8 (Table 11).

Species/Population	N_A	N_{Ap}	HO	HE	i
Pinus banksiana					
Val Caron (site 1)	4.3333	3.3604	0.6667	0.6983	1.2967
Introduction 1 (site 2)	4.0000	2.7951	0.4667	0.6096	1.1051
Introduction 2 (site 3)	4.0000	2.6056	0.4000	0.5850	1.0650
Inco 3 (site 4)	4.6667	2.9764	0.7333	0.6133	1.1734
Inco 1 (site 5)	4.0000	2.9054	0.5000	0.6500	1.1727
Inco 2 (site 6)	3.6667	2.7763	0.6333	0.5367	0.9716
Inco tailing (site 7)	3.0000	2.1221	0.3333	0.5129	0.8551
Falconbridge (site 8)	3.6667	2.1973	0.5852	0.5421	0.9443
Temagami (site 9)	4.0000	2.6277	0.6333	0.6050	1.1054
Low Water Lake(site 10)	3.6667	2.7987	0.2593	0.6235	1.1098
Introduction 3 (site 11)	4.6667	3.7420	0.4000	0.7283	1.3936
Introduction 4 (site 12)	3.6667	2.0854	0.2583	0.4554	0.8578
Mean	4.0000	2.7422	0.4912	0.7194	1.5155
Standard error	±0.4678	±0.1723	±0.3679	±0.0133	±0.0939
Pinus resinosa					
Introduction 1 (site 1)	2.6667	2.0994	0.1000	0.4150	0.7118
Falconbridge (site 2)	3.0000	2.1847	0.5506	0.4258	0.7809
Falconbridge (site 3)	2.6667	1.8039	0.1667	0.3267	0.5926
Falconbridge (site 4)	2.6667	1.9750	0.1333	0.3748	0.6653
Coniston(site 5)	2.3333	1.7365	0.0667	0.3431	0.5497
Daisy Lake (site 6)	2.6667	1.7188	0.0667	0.3346	0.5914
Verner (site 7)	3.0000	1.5541	0.1000	0.3017	0.5459
Introduction 2 (site 8)	2.3333	1.7060	0.0667	0.2783	0.5041
Mean	2.6667	1.8473	0.0892	0.4606	0.9477
Standard error	±0.2520	±1.3076	±0.0941	±0.3992	±0.828

N_A = mean allele number per locus; N_{Ap} = mean number of polymorphic alleles per locus; HO = observed heterozygosity; HE = expected heterozygosity; I = Shannon's information index;

Table 11. Genetic diversity estimates for 12 *Pinus banksiana* and 8 *Pinus resinosa* populations from the Sudbury, Ontario region using microsatellite primers.

The observed heterozygosity (HO) at the population level ranged from 0.26 to 0.67 and the expected heterozygosity (H_E) varied from 0.46 to 0.72 for *Pinus banksiana* populations. The samples from INCO 3 (site 4) produced the highest HO values and the samples from Low Water Lake (site 10) used as control showing the lowest observed heterozygosity (Table 11). The degree of population differentiation (FST) was 17 % for *P. banksiana*. For *Pinus resinosa*, the observed heterozygosity (HO) at the population level, ranged from 0.07 to 0.55. Samples from site 2 located near Falconbridge produced the highest heterozygosity and the samples from nursery 2 (introduction 2) called population or site 8 showing the lowest values (Table 11). HE values ranged from 0.28 to 0.43. The degree of population differentiation (FST) was 23.9 % for *P. resinosa.*

For *Picea mariana*, the microsatellite analysis confirmed the high level of genetic diversity within each population but revealed no significant difference between wetland and upland populations for all the genetic parameters analyzed. Overall, 11% of the total genetic diversity was attributed to differences among populations. The mean number of alleles and effective number of alleles per locus were 10.3 and 5.6, respectively. The observed and expected heterozygosity values ranged from 0.425 to 0.732 and 0.584 to 0.768, respectively (Table 12).

Population	**N_A**	**N_{Ap}**	**H_O**	**H_E**	**I**
Site 1 (wetland)	5.67	5.33	0.482	0.619	1.333
Site 2 (wetland)	5.33	5.33	0.587	0.752	1.512
Site 3 (dryland)	5.67	5.67	0.652	0.768	1.572
Site 4 (dry land)	5.33	5.33	0.641	0.740	1.503
Site 5 (wetland)	6.33	6.33	0.648	0.729	1.532
Site 6 (dry land)	3.67	3.33	0.577	0.584	1.040
Site 7 (dry land)	6.00	6.00	0.559	0.744	1.541
Site 8 (dryland)	6.00	6.00	0.732	0.740	1.540
Site 9 (wet land)	5.67	5.67	0.425	0.772	1.585
Mean	5.52	5.44	0.589	0.717	1.462
Standard dev.	±0.765	±0.867	±0.094	±0.067	±0.175

N_A = mean allele number per locus; N_{Ap} = mean number of polymorphic alleles per locus; Ho = observed heterozygosity; H_E = expected heterozygosity (Nei 1973); I = Shannon's information index; F_{IS} = measure of heterozygote deficiency or excess (Wright 1978).

Table 12. Genetic diversity estimates for black spruce (*Picea mariana*) populations using microsatellite primers.

After the correction for null alleles, exact test for Hardy-Weinberg Equilibrium revealed, the majority of the populations deviated significantly from the Hardy Weinberg Equilibrium. The results revealed that the null allele frequency estimates were negligible for all populations (data not shown). The HWE deviation for these populations might be the result of other factors than null alleles. The global tests revealed significant heterozygote deficiency for most populations. Overall, the present study indicates that the long-term exposure of *P. mariana* populations to metal (more than 30 years) is not associated with the level of genetic diversity.

3.4.2 Gene flow

The gene flow estimates were considered low for both species, Nm = 1.21 for *Pinus banksiana* and Nm = 0.79 for *P. resinosa* based on Slatkin (1985). There was also no significant difference in the inbreeding coefficients among the stands within the same species. The mean inbreeding coefficients were considered high for *P. resinosa* and low *for P. banksiana*.

4. Discussion

Loss of rare alleles, lower heterozygoty and directional selection have been concerns of plant populations (Slatkin, 1985; Bergmann and Scholz, 1989). Most of the forest ecosystems within the Sudbury area have improved considerably during the last 30 years (Dudka et al., 1995; Gratton et al., 2000). Vascular and nonvascular plants such as conifers, birches and lichens have re-invaded semi-barren landscapes. More than nine millions trees mostly conifers have been planted in the Greater Sudbury Region. Genetic diversity is the foundation for forest sustainability and ecosystem stability. Bench marking genetic diversity in forest tree populations can provide resource managers with an indicator of long-term forest sustainability and ecosystem health (Mosseler and Rajora, 1998; Rajora and Mosseler, 2001a, 2001b).

For *Pinus banksiana* and *Pinus glauca*, the levels of genetic variation were low to moderate. In fact, genetic variation in *Pinus strobus* (White pine) studied varied from 24 to 40%. The newly planted populations of *Pinus banksiana* and *Pinus glauca* revealed a higher level of genetic variation compared to natural populations. The genetic distances among the pine populations growing in the Greater Sudbury area revealed that all the populations analyzed were genetically close to each other. The highest genetic diversity values were observed in new plantations being developed by the Sudbury reforestation program (Ranger et al., 2007). The level of genetic variation was low (less than 10%) for *P. resinosa*. This was attributed to other events that took place during the history of this species in North America (Mosseler et al., 1992).

Genetic variation and genetic structure of *P. mariana* (black spruce) populations growing in wet and dry lands with different levels of metal contaminations was high in all the populations analyzed with the percentage of polymorphic loci (P %) ranging from 65% to 90 %. For *Picea glauca* populations polymorphism levels ranged from 50% to 61% for ISSR markers and from 70% to 80% for RAPD markers. The level of variation in newly introduced populations of *P. mariana* and *P. glauca* from the Sudbury Reclamation program was also high. Variation within populations accounts for most of total genetic variation. Moreover, genetic tests with species-specific molecular markers revealed that all the trees from *P. mariana* and *P. glauca* planted and natural populations were pure genotypes with no introgression of other species.

In all the conifer species, metal content in soil was not associated with the level of diversity in populations analyzed. Within each species, the different populations studied were genetically closely related. Overall, the results of the present study indicate that the conifer populations from the Greater Sudbury region and other surrounding areas meet most genetic criteria of sustainability. Moreover, the levels of genetic variation observed in the targeted species were similar to data reported for other fragmented populations across Canada for the same species (Mehes et al., 2007).

Elevated accumulations of metal accumulations in soils and vegetation have been documented within short distances of the smelters in Sudbury compared to control sites (Freedman and Hutchinson, 1980; Gratton et al., 2000; Nkongolo et al., 2008). Among the sites analyzed in the present study, the highest level of metal content in soil and plant tissues were detected in samples from populations 1 and 2 located near Falconbridge Smelters in Sudbury (Gratton et al., 2000; Nkongolo et al. 2008). These populations showed the highest level of genetic variability for *Picea mariana* for example along with the control population 9 from Timmins. The same level of genetic variation was observed in parents and progenies within the same populations. This clearly indicated that the exposure to metals for more than 30 years has no effect on genetic structure and diversity of black spruce populations in Northern Ontario. This lack of association between the level of genetic variation and metal content can be attributed to the long life span of conifer species. In fact, the populations analyzed were only the first and second generations of progenies from parents exposed to metal contamination

This is in contrast to data observed in herbaceous species such as *Deschampsia cespitosa* where the level of metal accumulation reduced significantly the level of genetic variation (Nkongolo et al. 2008). Metals impose severe stress on plants, especially in the rooting zone, which has led to the evolution of metal-resistant ecotypes in several herbaceous species like *D. cespitosa* (Cox and Hutchinson 1980). Evidence of loss of genetic variation based on enzymatic analysis at the population level caused by pollution has been demonstrated in some species (Lopes et al. 2004; Prus-Glowacki et al. 2006; van Straalen and Timmermans 2002). But, plants possess homeostatic cellular mechanisms to regulate the concentration of metal ions inside the cell to minimize the potential damage that could result from the exposure to nonessential metal ions. These mechanisms serve to control the uptake, accumulation and detoxification of metals (Foy et al. 1978). This might be the case in black spruce trees exposed to certain levels of metals.

Genetic variation is the foundation for ecosystem stability and population sustainability. In tree populations this information is an indicator of long term population sustainability and health. For example, environmental stressors, such as anthropogenic factors, can affect the genetic frequencies by increasing mutation or selection. This further leads to differences among populations and increase uniformity within a population, thus increasing homozygosity and inbreeding (Dimsoski and Toth, 2001). Studies of genetic variation of impacted and unimpacted populations have defined a positive relationship between the exposure to the stressor and diversity.

Using various types of markers, several authors have reported differences in genetic structure of plants growing in contaminated areas (Muller-stark, 1985; Scholz and Bergmann, 1984). Enzymatic studies of *Picea abies* (Norway spruce) revealed genetic differences between groups of sensitive trees in polluted areas (Scholz and Bergmann, 1984). Higher heterozygosity was reported in tolerant plants of European beech in *Pinus sylvestris* (Scots pine) in Germany and Great Britain (Muller- starck, 1985; Geburek *et al.*, 1987). Berrang *et al.*, (1986) also reported a high heterozygosity in *Populus tremuloides* (Trembling aspen) and *Acer rubrum* (Red maple) populations in the USA.

No significant differences were observed among natural and planted *Picea glauca* populations. All the populations revealed high levels of polymorphic loci for the ISSR markers. This suggests that the *Picea glauca* populations are likely sustainable in long term. For *Pinus strobus*, the levels of genetic variations were in general low to moderate. The newly introduced populations revealed higher levels of polymorphic loci compared to natural populations. This confirms that the land reclamation by planting *Pinus strobus* trees and other pine species is increasing the sustainability of pine populations in the Sudbury region.

Genetic distance values were calculated according to the Jaccard similarity coefficient. In general, the genetic distance values revealed that the different *Pinus spp.* and *Picea spp.* populations were genetically closely related. Overall, the genetic distance analysis showed a high level of homogeneity among populations which could be due to the species characteristics. In fact, the relative small genetic distance values reported in the present analysis are consistent with other studies on *Picea glauca* populations in various provinces that used various molecular markers and allozymes (Rajora *et al.*, 2005; Tremblay and Simon, 1989; Alden and Loopstra, 1987). In general, the genetic similarity among the populations suggests that these populations could have originated from a common source. In addition, *Picea glauca* is an anemophilous species and its pollen is transported over great distances. The fact that *Picea glauca* populations are fairly distributed should promote the exchange of genes among populations. Hence, it is rare to find alleles that are unique to a given populations, and the frequencies of the main alleles are generally similar from one population to another (Rajora *et al.*, 2005; Tremblay and Simon, 1989; Alden and Loopstra, 1987).

In Sudbury (Canada) during the last 25 years, production of nickel, copper and other metals has been maintained at high levels while industrial sulphur dioxide (SO_2) emissions have been reduced by approximately 90% through combination of industrial technological developments and legislated controls. This has allowed for some degree of recovery to occur such as improved air quality and natural recovery of damaged ecosystems during this period of reduced emissions at Sudbury. The recovery has been further done through the reforestation program by planting over 9 million trees such as conifers in the Sudbury region. On the other hands, the African Copper belt, on the border between Zambian and DR-Congo, are among the ten most polluted areas worldwide (The Blacksmith institute, 2008; Banza et al., 2009). Like in many other regions producing heavy metals, such as Senegal, Tanzania, China, Russia, Romania, India, Philippines, Thailand, Indonesia etc.,. there are virtually no controls on the discharge of pollutants from mining and smelters. There are no land reclamation programs and environment degradations from past mining activities have not been addressed. Studies on the effect of metal contamination on genetic diversity of plant populations in those regions are limited. Prus-Glowack et al. (2006) demonstrated in a small scale study in Poland that the stress resulting from gaseous pollution and contamination of the soil with heavy metals exerts a significant effect on phenotype of individuals and on genetic structure of *Pinus sylvestris* L populations. Such data needs to be validated at larger scale using molecular markers.

5. Conclusion

The present study indicates that *Pinus spp* and *Picea spp.* populations from the Sudbury region, Ontario, are genetically variable. Metal contamination levels were not associated with genetic variation in *Picea glauca* populations. Overall, the results indicate that the conifer populations from the Greater Sudbury region and other surrounding areas meet most genetic criteria of sustainability. This conclusion was confirmed by molecular analysis using ISSR, SSR markers, and cytological studies. The effects of metals, if any, may require several generations to be detected. The reclamation of Sudbury forest lands with new populations increases the sustainability specifically for *Pinus* (Pine) species. Since Sudbury is not among the ten most polluted areas in world, a replication of this study in areas with higher soil metal content is recommended to validate the effects of metal populations in tree populations.

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Part 3

Ecosystem-Level Forest Management

15

Moving from Ecological Conservation to Restoration: An Example from Central Taiwan, Asia

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1. Introduction

The concept of “natural conservation” has been evolving since the beginning of the first efforts to preserve the natural landscape. The creation of the first national parks in the 19th century was originated by the belief that landscapes of exceptional beauty should be preserved from human influence and maintained in their current state for the enjoyment of future generations (Runte, 1997). During the first years of the establishment of national parks around the world, defining these “exceptional landscapes” was usually based on the static beauty of the area: majestic mountains, glaciers, old forests, gorges, canyons, waterfalls, etc. The protection in these areas was basically achieved through the prevention of creating human structures in the sites, reducing and controlling human activity and, in practice, maintaining the areas as they look at the time when they were declared as protected. Therefore, this protection was not based on ecological considerations, but on a human-centered view of natural sites.

The type of protected ecosystems varied widely among regions, depending on the history of human impact on them. For example, national parks in North America were created to protect largely untouched, almost pristine landscapes practically unaffected by the low populations of native peoples previous to European contact (Runte, 1997). Similarly, in South America and Africa, large natural areas could still be found during the 19th and 20th centuries were the human impact was thought to be minimal. However, in Europe or Asia, were the history of urban development can be traced back for millennia and the density of population is also higher, it was more difficult to found those untouched areas. As a consequence, national parks were created to protect landscapes of indisputable beauty but usually with a noticeable human influence on them. Ecosystems at this time of early

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conservation efforts were seen as static entities, that should not be altered or they would lose their integrity. However, with the arrival of modern ecology, this static view was gradually substituted by the classic view of gradual linear change along a continuum, arriving to a single climax state (Clements, 1916; Odum, 1969; Pickett and McDonnell, 1989). This climax state was usually identified with the state that nature reaches in absence of human influence, and therefore the efforts were oriented into maintaining it. As a consequence of this human-centered vision to define the areas to protect, regions such as oceans, deserts, swamps, shrublands and other similar ecosystems were usually considered "badlands" and unworthy of legal protection. On the other hand, very few protected areas have been established in productive landscapes with clear economical potential for agriculture or forest management (Scott et al., 2001). Even today, these regions are still underrepresented in the protected areas around the globe (Noss et al., 1995). Since the Rio Earth Summit in 1992, the global network of protected areas has continued to grow steadily, increasing yearly by an average 2.5% in total area and 1.4% in numbers of sites, and by 2006 covering more than 24 million km^2 in about 133,000 designated sites (Butchard et al., 2010). Protected areas overall remain a core element of biodiversity conservation (Andam et al., 2008; Gaston et al., 2008).

During the 20th century urban development was extended to all the regions of the world. With a booming human population and the intensification of economic development (first in Europe and North America and lately in the rest of the world) practically all the ecosystems in the world were impacted in one way or another. Therefore, it was just a matter of time that some of the iconic wildlife species of the world started to suffer from fast reductions in their populations, or even facing extinction. The danger of losing species such as whales, lions, tigers, elephants, panda bears, gorillas, brown bears, buffalos, sequoias, etc. was and still remains very real (Laliberte & Ripple, 2004; Sanderson et al., 2008). This danger was highlighted by scientists and environmental managers around the world, and the society responded with the creation of environmentalist groups, whose social pressure helped to create lists of endangered animal and plant species needing specific actions for conservation. This was the base to develop programs and activities focused on the protection of individual high-profile species. Many of these campaigns were supported by the public due to the easy sympathy or spiritual connection with some of these majestic species, and as a consequence, natural conservation was seen by the main public as "avoiding things getting worse". Some of these activities have achieved important successes, such as the halt in commercial hunting of whales (Stevick et al., 2003), the breeding programs of panda bears (Peng et al., 2001) or the increase in numbers of American buffalos (Waldman, 2001). However, in other cases the protection of the target species was not enough to prevent its decline or extinction (e.g. the Yangtze River dolphin, Turvey et al., 2007; or the Pyrenean wild goat, Folch et al., 2009), or just the species were not interesting enough for the public opinion and therefore not the main focus of protection efforts, such in the case of "ugly" species as it is amphibians, reptiles, insects, cacti, etc.

The improvement of this species-oriented conservationism from the first days of creation of protected areas is that it recognizes individual species as worth of the preservation, even if they are not in "beautiful landscapes" with some sort of legal protection. Therefore, it moves one step from the human-centered conservation of some specific favourite areas to protect species and control the factors that affect their populations. However, the main drawback of this type of ecological conservation is that it is targeted to one species, not to the ecosystem that supports that species. This species-oriented conservation followed the theory that if the causes of non-natural mortality are controlled (i.e. hunting, harvesting, poaching, poisoning, clear-cutting, etc.), and the availability of resources increased, the target species could survive or even increase its population. Therefore, actions such as banning hunting, stopping illegal logging, controlling access to the areas were the species is distributed can be part of this strategy (Folch et al., 2009). In addition, zoos, herbariums, arboretums and other centers where collections of plant and animals are kept under controlled conditions are an important part of this strategy, as they provide research insights in the biology of the species and they can specially increase the population sizes of plants and animal species (Bagarinao, 1998).

However, actions that could be beneficial for the target species are not necessary relevant for other species in the ecosystem, and they could be ineffective if the ecosystem is too altered to keep the target species, even after removing the human factors directly affecting it. Ultimately, any plant, animal or microorganism species will survive in a given ecosystem as long as the right conditions exist to support the niche that the species inhabits. Conservation paradigms, practices, and policies have shifted over time recognizing this need to preserve the ecosystem and not just the target species (Adams, 2004). As a consequence, a more holistic approach to conservation has emerged since the last quarter of the 20th century. Within this approach, the actions in the conservation effort will be directed to keep the integrity (bio-physical diversity) and the functionality of the ecosystem. This new approach is in the origin of the last trend in conservation: ecological restoration.

Ecological restoration involves assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed, typically as a result of human activities (Sala et al., 2000). Ecological restoration is based on the new view of ecosystems as biological communities established on a geophysical substrate that can develop into alternative stable states rather than into a single climax state (Lewontin 1969). As a consequence, the idea of the balance of nature has been replaced with the flux of nature (Wu & Loucks, 1995; Pickett & Ostfield, 1995; Wallengton et al., 2005), and ecosystems are thought to be mostly in non-equilibrium. Their dynamics are not only complex but also dependent on the spatial context and the history of natural disturbance and human influence (Hobbs & Cramer, 2008). The main implication of this conceptual model is that ecosystems that have been altered by human activity may not revert back to its original state if left alone. On the contrary, these altered ecosystems could just reach a different stable state defined by the actions of human management on them (i.e. soil alteration and erosion, invasive species, lost of native species, changes in hydrological regime, etc.). Examples of such alternative states are grasslands or forest dominated by invasive species or shrublands that substitute forests. The goal of ecological restoration is therefore the reestablishment of the characteristics of an ecosystem, such as biodiversity and ecological function that were prevalent before degradation (Jordan et al., 1987), and that will not be reached (or if so, in very long time scales) by the ecosystems if left alone.

Ecological restoration is different from the earlier protection of specific areas because “restoration” means human intervention to bring the ecosystem back to a state different from the one in which it is currently. Therefore, it is not a passive conservation effort in which humans are just consider outsiders that should not be “in the way” of Nature. Quite differently, ecological restoration needs direct human actions (i.e., modification of the physic-chemical environment, introduction of lost species, removal of invasive species, plantation of trees and plants, etc.). In addition, ecological restoration is different from conservation of emblematic species in that restoration targets the whole ecosystem, assuming that if the correct ecological conditions are maintained, the emblematic species (and their companion species) will be preserved in the restored area.

Ecological restoration has developed quickly since the first meetings of the Society of Ecological Restoration International in the early 1990s (Greipsson, 2011). Ecological restoration, both within and outside protected areas, is being increasingly applied worldwide (Clewell & Aronson, 2007; Nelleman & Corcoran, 2010), and it is increasingly found as part of natural resource management plans. Actions such as targeted habitat management, removal of invasive species, captive breeding, seed production and species reintroduction have yielded notable successes: among many examples, at least 16 bird species extinctions have been prevented by such means between 1994 and 2004 (Butchart et al., 2006).

Large-scale ecosystem restoration is needed to arrest and reverse the degradation of landscapes around the world (Manning et al., 2006). However, restoration efforts to date have been criticized for being ad hoc, site and situation specific (Hobbs & Norton, 1996), or focusing on small, protected nature reserves (Naveh, 1994; Soulé & Terborgh 1999). Hence, the effectiveness of restoration actions in increasing the provision of both biodiversity and ecosystem services has not been evaluated systematically. A meta-analysis of 89 restoration assessments in a wide range of ecosystem types across the globe indicated that ecological restoration increased the provision of biodiversity by 44% and ecosystem services by 25%, but values of both remained lower in restored versus intact reference ecosystems (Rey-Benayas et al., 2009). Although small-scale restoration projects can be valuable, there is an urgent need to greatly expand the scale of ecosystem restoration for both conservation and production (Naveh, 1994; Hobbs & Norton, 1996).

From these results, it is clear that detailed field research is needed to guide restoration efforts. Field experiments can be a useful guide as to which restoration practices are the most useful for achieving this goal (Kimmins et al., 2010). In this chapter we describe the field research done to guide the restoration of native conifer forests in central Taiwan. Our research has as main objective the identification of the best conditions for seedling establishment of two tree native species: the evergreen Fabaceae *Lithocarpus castanopsisifolius* and *Lithocarpus kwakamii* (stone oak) in a former plantation of Japanese cedar (*Cryptomeria japonica)*, an species alien to Taiwan. In this study, we seek to evaluate whether the combination of selective cutting, direct seeding, and understory vegetation control can be a cost-effective method to gradually restore plantation forests to native forests. We also seek to identify the potential barriers that hinder seed and seedling survival.

2. An example from central Taiwan

2.1 Historical background

Taiwan covers an area of 36,000 km^2 and is located at the fringe of the Asian continental shelf at the western rim of the Pacific Basin, and separated from the main continent by a strait of 130 km in its narrowest point. The island has a very complex terrain, with about two thirds of Taiwan's land area at slopes over 10% and almost half of the island with slopes over 40%, and with Jade Mountain (the highest peak), reaching 3952 m a.s.l. (Hsu & Agaramoorthy, 1999). As a consequence of its insularity, closeness to the continent and wide gradient of altitudes, Taiwan harbours over 4,000 vascular plants in six different forest types (Boufford et al., 1996). Wildlife resources are also abundant with 61 species of mammals, 400 species of birds, 92 species of reptiles, 30 species of amphibians, 140 species of fresh-water fish, and the estimated 50,000 species of insects including 400 species of butterflies (Hsu & Agoramoorthy, 1997). To protect this rich biodiversity, the first national park was created in 1984 in Kenting (south Taiwan). Till date, 6 national parks, 18 nature reserves and 24 nature protected areas have been designated to ensure protection for wildlife and their habitats. The protected area covers 12.2% of the total land area of Taiwan (Hsu & Agoramoorthy, 1999).

The history of forest conservation and restoration in Taiwan is closely linked to the economic development of the island. Timber harvesting peaked during the Japanese colonial period and immediately following World War II. Large areas of valuable timber, primarily cypress, spruce, and camphor, were cut and shipped primarily to Japan. Economic pressures led to an aggressive management, with plantations of native species and timber harvesting program through the 1950s to the 1970s, with an average of 1,552,600 m^3 harvested from 1965 to 1975, corresponding to about 18,000 ha cut annually (Lu et al., 2001). These levels of harvesting brought petitions from citizens and environmental protection groups urging forest protection. This intensive level of exploitation was essentially halted with the national forestry management policy of 1976 (Wang, 1997). Since then, the emphasis of forest management in Taiwan has shifted almost entirely from timber production to forest protection. After 1977, timber was harvested mainly from forest plantations with an annual cut of about 100,000 m^3 and by 1990, 99% of Taiwan's timber supply was imported (Wang, 1997; Lu et al., 2001). Currently, national forest lands are managed almost exclusively for the purposes of streamflow regulation, erosion control, and conservation of biological diversity. Under this new approach, the harvesting-reforestation approach is no longer viable and alternatives need to be devised.

The interest on conservation is not limited to natural forests, but it is also extending into plantation forests, especially in the marginal plantations created during the 50s and 60s, at the peak of exploitative management in the island. To restore and promote biodiversity, the current management directives mandate the restoration of plantations no longer serving for timber production back to native forests, in a gradual manner. One example is the important number of existing Japanese cedar (*Cryptomeria japonica* D. Don) plantations that were established in sites now considered as unsuitable for harvesting, mainly due to soil and slope protection concerns. This species was introduced from Japan with the start of the Japanese colonial rule at the end of the 19th century. It has become the most widely planted tree species in Taiwan, covering about 1.1% (41,132 ha) of the island's total land area (Taiwan Forestry Bureau, 1995). However, due to increasing production costs and declining timber prices, most of Taiwan's Japanese cedar plantations either are approaching or have passed the prescribed rotation age.

Knowledge on how to use current forestry practices to accelerate and support the conversion from plantations into native forests is needed to design successful restoration plans in these plantations. Among other concerns, it is necessary to understand the best ways of promoting native trees establishment. Seed and seedling survival are limited by multiple biotic and abiotic factors (Beckage et al., 2000; Fenner & Thompson, 2005), making these stages the bottleneck of ecological restoration (Fenner & Thompson, 2005; Leck et al., 2008). Drought, herbivory, and light are the three most important causes for seedling mortality (Leck et al., 2008)

To improve seed establishment rates, seedling planting and direct seeding are two common tools used in forest restoration. The former has the advantage of high success rate, but it is also more expensive than the later (Bullard et al., 1992). Direct seeding has the advantage in term of cost, but it usually has low success rates. Thus, the creation of an environment that enhances the survival of tree seeds and seedlings is a key element of a successful gradual forest restoration strategy. Selective cutting and thinning are common forestry practices that can also be used for restoration. During these procedures, only a portion of trees is removed, and the overall stand abiotic environment is not greatly altered. Therefore, partial removal of trees can enhance local light availability and create physical environments similar to natural gaps that are essential for seedling survival (Augspurger, 1984; Brokaw & Busing, 2000; Masaki et al., 2007). In addition, the presence of understory vegetation may reduce seedling survival by reducing light availability or increasing competition between seedlings and understory vegetation (Leck et al., 2008). On the other hand, understory vegetation may reduce seedling predation by providing protection (Smit et al., 2006). Therefore, understory vegetation control may cast both positive and negative effects on the survival of seeds and seedlings (Beckage et al., 2000; Fenner & Thompson, 2005; Leck et al., 2008).

2.2 Material and methods

2.2.1 Experimental site

This study was carried out in a 10-ha Japanese cedar plantation in the Heshe District of the National Taiwan University Experimental Forest, central Taiwan (120° 52′ E, 23° 37′ N, 1442-1602 m a.s.l.; Fig. 1). Mean annual temperature of the study site is 19.8°C, with a mean annual rainfall of 1500 mm (NTUF, 2011). Originally an evergreen broad-leaf forest dominated by *Fagaceae* and *Lauraceae* species, the site was clear-cut in 1958 and planted with

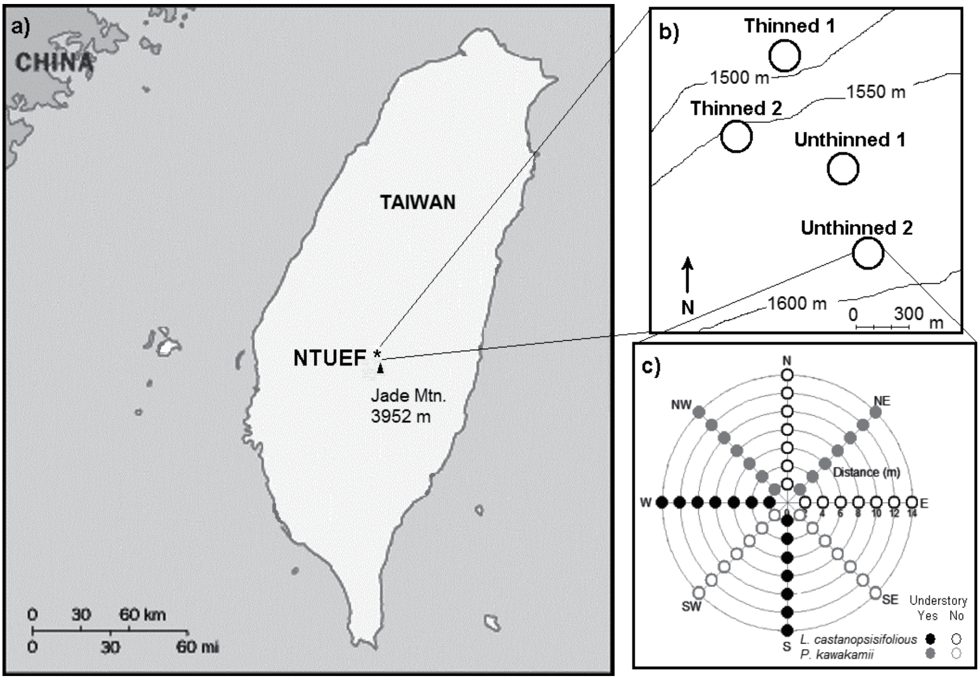

Fig. 1. Location of the experimental site, National Taiwan University Experimental Forest – NTUEF (a), spatial arrangements of the treatment combinations (b), and seed transects (c).

Chinese fir (*Cunninghamia lanceolata*). Due to typhoon damages in 1969, the stand was re-planted with Japanese cedar in 1971. In 2005, the plantation was selected as a demonstration site to study how to gradually restore Japanese cedar forests back to native vegetation communities. Within 500-m from the edges of the plantation, remnants of the original vegetation can still be found. We regard those edge areas as the reference for the restoration project and to set the initial restoration goal: the successful establishment of late succession components of the reference stands in the plantation.

2.2.2 Materials and experimental design

An initial inventory found that while the saplings of late succession *Lauraceae* species (mainly dispersed by birds) were relatively abundant, only a few saplings of *Fagaceae* species were present. Thus, we focused only on the reintroduction of the main *Fagaceae* species. *Lithocarpus castanopsisifolius* (Hayata) Hayata and *Pasania kawakamii* (Hayata) Schottky were selected as the target species for reintroduction as they are late succession species and relatively abundant in the surrounding areas from were collected seeds. All fresh seeds used in this study were collected between October and November 2008 from the reference stands in the edges of the Japanese cedar plantation, and they were stored at 4 °C until they were used in January 2009.

As a part of the experiment, 20% of the standing volume was harvested to create gaps of different sizes. We established four plots, two thinned and two unthinned, within the plantation (Fig. 1b). The canopy openness of the two thinned plots was 27% and 29%, whereas canopy openness of the two unthinned plots was 13% and 11%. For each plot, a 10-meter transect was set at each of the 8 cardinal and inter-cardinal directions (Fig. 1c). The seeds of *L. castanopsisifolius* were placed along the cardinal direction transects, whereas the seeds of *P. kawakamii* were placed along the remaining four transects (Fig. 1c). For each group of transects in each plot (cardinal or inter-cardinal), we randomly selected two transects from where we removed the ground vegetation in a strip of 1-m wide along the entire transect (devegetated transects), whereas the ground vegetation of other two transects was left untouched (vegetated transects, Fig. 1c). Thus, the entire experiment consisted of 4 treatments for each species.

In January 2009 we placed 30 fresh seeds every 2.5 m along each transect, starting and ending at the 2.5-m and 10-m marks, respectively, for a total of 120 seeds per transect and 1920 seeds per species for the entire experiment. After placing the seeds, the number of seeds still present was counted every day during the first 35 days. After that, we went back on day 140 as the final checking time. At day 140, almost all the seeds were removed or consumed, therefore the experiment ended at that time.

Eight infrared automatic cameras, one for each species-treatment combination, were also set up to capture how the seeds were removed or consumed and by which animal species under different treatment conditions.

2.2.3 Data analysis

Cox regressions were used to analyze the survival and seedling establishment, with the hazard defined as the instantaneous mortality risk of a seed (Cox, 1972). The thinning and understory vegetation removal treatments were used as the explanatory variables. Species were analyzed separately. We used R to conduct all statistical analyses, with survival analysis using the R package Survival (R Core Team, 2010).

2.3 Results

2.3.1 Field observations

Seeds were first removed from transects with no ground vegetation cover (Fig. 2). Twenty days since the beginning of the observation, 82% and 48% of *L. castanopsisifolius* seeds were missing in the unthinned and thinned plots, respectively. These results were similar for the *P. kwakamii* seeds, with 95% and 48% seeds disappearing in the unthinned and thinned plots, respectively.

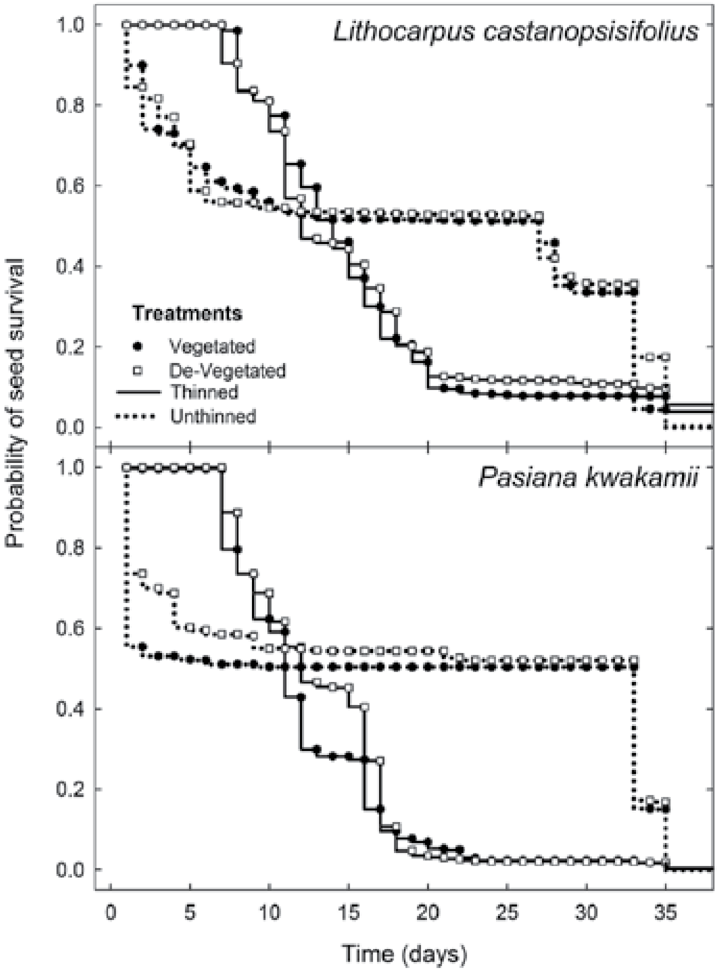

Fig. 2. Seed removal rates over a period of 61 days in different thinning and understory vegetation treatments for *Lithocarpus castanopsisifolius* (upper panel) and *Pasania kawakamii* (lower panel). Solid lines indicate thinned treatment, and dotted lines represent unthinned treatment. Solid black dots indicate ground vegetation intact, whereas opened squares represent without ground vegetation.

Seeds of *P. kwakamii* were removed more slowly from the devegetated plots for both thinned and unthinned treatments, but this effect disappeared after 23 days of exposure. This pattern was not clearly identified for *L. castanopsisifolius* seeds, but after 15 days there seemed to be a tendency for a slightly higher probability survival in devegetated plots for both canopy types. Ninety-four percent of *L. castanopsisifolious* seeds had disappeared from the vegetated plots after 35 days, versus 91% from devegetated plots. However, the treatment producing the biggest differences after 35 days for *P. kwakamii* was thinning, with 98% of seeds disappearing from thinned, a much lower probability of survival than in close canopy plots (84% seeds disappeared after 35 days).

From the images captured by the automatic cameras, we identified two mammal species as the acorn consumers/removers during the observation period. These two species were red-bellied squirrel (*Callosciurus erythraeus*) and Owslon's long-nosed tree squirrel (*Dremomys pernyi owstoni*). These two species can be seen as potential dispersers of large seeds in the late succession period.

2.3.2 Seed removal

The results from Cox regressions indicated that, for both species, removing part of the canopy significantly influenced seed removal (mortality risk) in the study site (Table 1, Fig.2). Results indicated that, for *P. kwakamii,* seeds in the thinned treatments suffered the highest removal risk (Table 1). Similar results were found for *L. castanopsisifolius* (Table 1). In addition to the main effects, the interaction between canopy type and understory vegetation cover was non-significant (Table 1).

Treatment	**df**	**Hazard ratio**[1]	***Z***[4]	***P***
Lithocarpus castanopsisifolius				
Thinning[2]	1	0.70	-5.11	<0.001
Understory removal[3]	1	1.05	0.73	0.466
Thinning × Vegetation	1	1.18	1.69	0.091
Pasania kwakamii				
Thinning	1	0.65	-6.18	<0.001
Understory removal	1	1.04	0.66	0.509
Thinning × understory removal	1	1.09	0.93	0.351

Table 1. Effects of thinning and ground vegetation treatments on the seed hazard (instantaneous mortality risk) based on Cox regressions. Notes: 1) Hazard ratio is defined as the ratio of mortality risk between two factor levels. If hazard ratio = 1, it indicates equal mortality risk; 2) Risk ratio of thinned relative to unthinned treatment; 3) Risk ratio of devegetated relative to vegetation treatment; 4) Cox regression coefficient.

2.3.3 Seedling establishment

Probabilities of successful seedling establishment at day 140 differed among species and treatments. For *P. kwakamii, s*eedlings only successfully established in the unthinned plots (Fig. 3 left panel). For *L. castanopsisifolious,* there was a small seedling establishment probability in thinned plots, but the success rate was much higher for unthinned plots. (Fig. 3 right panel). No significant difference was detected between vegetated and devegetated plots.

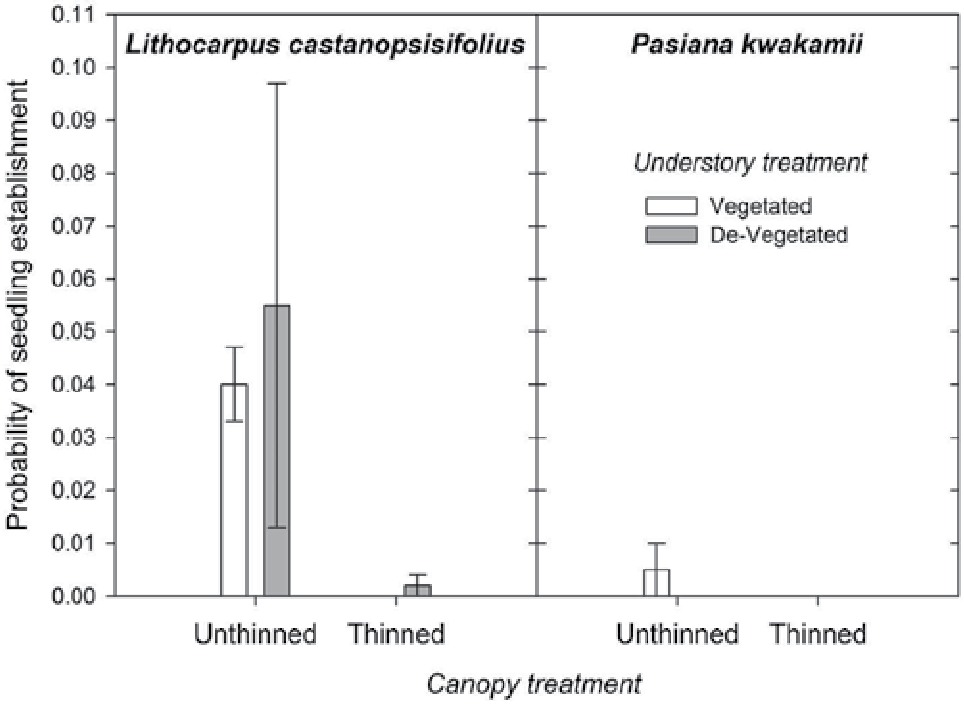

Fig. 3. Probabilities of successful seedling establishment after 140 days of seed planting for *Lithocarpus castanopsisifolius* (left panel) and *Pasania kawakamii* (right panel). Error bars represent the mean ± standard error.

2.4 Discussion

Differential seed survival and seedling establishment among species, canopy and ground vegetation conditions were observed. The thinning treatment reduced seedling establishment in both species and significantly reduced seedling survival in both species. In addition, seedling establishment was not significantly affected by removing ground vegetation.

Despite that our results are species-specific, they suggest that keeping canopy vegetation intact may be more effective than removing understory for the two species studied. Survival rates for the unthinned plots were consistently higher than for the thinned plots in either vegetated or devegetated after two weeks of seeding (Figure 2). In contrast, differences in seed survival between the two vegetation types did not show consistent patterns and the difference was rather small. Such results suggest that removing the understory layer may not be as effective as keeping the canopy cover, although understory removal showed a tendency to increase seed survival in *L. castanopsisifolius*, although statistically not significant.

The observed differences in seed survival may arise from changes in foraging behaviours of seed predators as a result of the forest management treatments. The understory vegetation was rather dense in the study site, especially in the thinned plots. The understory grew rapidly after selective thinning was conducted in 2005. The improved light conditions due to thinning were believed to facilitate the rapid growth, which was mostly composed by broadleaf species, such as *Schefflera actophylla,* and *Machilus thunbergii*, which are shade-tolerant but can take advantage of increased light levels (C.-W. Yu, personal observation). Therefore, thinning could reduce seed survival by favouring understory growth and then providing more protection for seed predators.

In addition, the openness of the canopy layer can also influence the behaviour of seed predators (Boman and Casper, 1995; Schnurr et al., 2004), as well as the effects of understory vegetation (Chambers and MacMahon, 1994; Fenner and Thompson, 2005). The effect of both canopy structure or understory vegetation density on seed survival, however, is somewhat context-dependent (den Ouden, 2004; Hulme & Kollmann, 2004; Tamura & Katsuki, 2004). Seed predation may increase or decrease among different microhabitats depending on the composition of seed predators (Schupp et al., 2002; den Ouden, 2004; Hulme & Kollmann, 2004; Tamura & Katsuki, 2004). For instance, seed predation by squirrels is reduced in canopy gaps, while predation rates by field mice, *Peromyscus mexicanus* are higher in canopy gaps (Tamura & Katsuki, 2004). This may be the case in our study, which showed increases in seed predation in conditions with higher canopy openness after thinning. To try to understand the relationship between seed predators and seedling establishment, the movements of mammals were monitored in a nearby plantation.

Mammalian activities were decreased immediately after thinning treatments (Lin & Bridgman, 2010). In addition, the photos taken from our automatic cameras in our plots also suggested that major seed predators in the study sites were granivorous animals, including red-bellied Squirrel and Owslon's long-nosed tree squirrel. These animals may also become seed dispersers via scatter-hoarding behaviour. Therefore, they can be reducing the seed survival but increasing seed dispersal rates at the same time. Scatter-hoarding behaviour has been widely observed in squirrels and jays in various forest ecosystems, where instead of consuming the seeds, they moved seeds away and cached the seeds (Vander Wall, 1994; Forget et al., 2004; Zhang et al., 2004). The cached seeds may germinate at later dates. Some of the animals observed by the automatic camera may also function as seedling predators. For example, many rodent species, such as red-bellied squirrels or the Formosan field mouse have been observed to eat seedlings (Young, personal observation). Seed tracking techniques are required to study the details of scatter-hoarding behaviours (Forget et al., 2004), and they could be a future research line at these sites.

In addition of these two species, we are carrying similar experiments for other tree species at the same plots, and our preliminary results indicate that for other species the effects of thinning and understory removal can be the opposite (data not shown). Our experiments are the first ones of these kind in Taiwan, and the species-specific responses of seedling establishment to management activities provide a clear indication of the need to shift from a static conservation in which the "no human action" approach is favoured into a more active restoration strategy. If no action were taken, it can be expected that *L. castanopsisifolious* will successfully regenerate, and in a lesser way *P. kwakamii.* Under this scenario, the future tree composition of these stands could be a multi-story canopy in which the Japanese cedar (an alien species) dominates the canopy, with lower layers of *L. castanopsisifolius* and other similar native species, but in which *P. kwakamii* will remain mostly suppressed. As a consequence, the new state of this forest under a conservation-only strategy would not be either the Japanese cedar plantation or the original mixed forest, but a hybrid of both. Only after a major natural disturbance (i.e. a typhoon or a stand-replacing wildfire) this hybrid stand could be transformed into the original mixed forests. Therefore, if this "new ecological state" is to be avoided and the recovery towards the original mixed forest is needed, a program of seeding combined with additional research to improve the regeneration of *P. kwakamii* should be implemented in these stands to ensure that *P. kwakamii* finds favourable conditions to regenerate. However, these activites should be localized and not general through the stands to avoid the inhibitory effect that close canopy or exposed forest floor could have for the regeneration of other important native species.

3. Conclusions

The native forests within the elevational range in this experimental area were dominated by *Fagaceae* and *Lauraceae* species. These families were, however, rare in the seed rain of the planted forest after thinning (Sun, 2010). Such results suggested a high degree of recruitment limitation in the plantation. Therefore, to facilitate the transition from planted forest to native forest, it is essential to develop management strategies to overcome recruitment limitation of native species in the plantation forest. Our study indicated that for the two species studied, keeping the canopy cover could be an effective management tool to overcome recruitment limitation, suggesting an easy and inexpensive mean for forest restoration. With extensive plantation forests in Taiwan, the management practices could be widely applied to facilitate the regeneration of native species. The next step is to apply such treatments to a broader area to assess the operational costs of such management techniques. The efficiency of these management techniques, however, seems to be species-specific. Other research has shown opposite effects of thinning and vegetation removal in other species at the same sites (data not shown). Therefore, we warn the readers from assuming that the results presented here could be applied to other forests types or regions. The interaction between light availability, soil moisture and species-specific factors for trees (seed size, seed dispersal) and seed predators (foraging behaviour, seed preference) can make the same management have very different results in restoring different sites.

All things considered, our research shows how the shift from passive ecological conservation towards a more active ecological restoration can be successful if enough ecological information on ecosystem structure and function is available. Also, if no active restoration is implemented, the ecological barriers for seedling establishment could prevent these ecosystems from recovery for a long time, generating a new "hybrid" state with elements from both the human-altered (plantation) and original (mixed forest) ecosystems. We suggest that other similar programs monitoring seed survival and seedling establishment should be enacted in other forest regions around the world, especially in tropical forest where little is known about many of the native tree species.

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16

Restoration of Forest Ecosystems on Disturbed Lands on the Northern Forest Distribution Border (North-East of European Russia)

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1. Introduction

Since the second half of the 20th century, due to active growth of minerals extraction in the European North of Russia, the area of disturbed forest ecosystems is steadily enlarges. It is known that disturbance of forest ecosystems leads to environmental unsteadiness and biodiversity decrease. It is vital to mention, that forest destruction negatively affects the traditional way of life of local people who depend on forest resources.

Natural forest destruction is a global problem. According to Losev K.S. et al. (2005) it is noticed that intensive growth of cultivated areas in the world is generally connected with forest destruction. About 63% of land on the planet is developed, what leads to infringement of balance stability if elements biogens (biological circulation of substances) and infraction of biosphere steadiness – habitat of human beings. It is noticed that in present time it is essential "to stop the destruction of this the most important ecological resource and then start natural restoration of forest ecosystems" (p. 78). It is vital for northern conditions, where forest ecosystems are particularly vulnerable to technogenic impact. Taiga forest ecosystems are easily disturbed and slowly self-recover after technogenic impact. This phenomenon was thoroughly surveyed by V.V. Ponomareva (1970, 1980). She wrote that forests are adjusted to strongly expressed eluvial conditions, "…forests minimize leaching of biophil elements from soil by accumulation them not in soil but in their huge always-living phytomass; (forests – ed.) exist from the autonomous above-soil circulation of elements between living organisms and their dying remnants which concentrate on soil surface" (Ponomareva, Plotnikova, 1980; P. 188). Thus, soils under taiga forests are characterized with high moisture content and so biological circulation in such ecosystems is nearer to an autonomous and close type. Huge perennial phytomass of tree plants holds organic elements it has assimilated from the upper earth's crust layer and partly gives them back with tree waste; then dead leaves and branches on soil surface are decomposed and provide for a new portion of nutrient for roots in soil litter. In this connection, forest soils have a very thin organic (productive) layer underlain by almost non-productive mineral layers with low absorbing capacity and containing practically none of plant nutrients. Technogenic interference easily destroys a thin organic soil layer and bares biologically inert mineral soil horizons which are not appreciated for plants. Restoration of disturbed forests on poor and strongly moist substratum is kind of difficult. In consequence, formerly forested areas undergo quick erosion and so their restoration further slows down.

The above-said information evidences a necessity for man-induced maintenance of ecosystem restoration on disturbed lands. In this article the results of investigation method are presented in comparative way. Method that accelerates the process of taiga forest ecosystem restoration is compared to traditional ways of forest cultivation.

2. Objects and investigation methods

We have studied different restoration modes of forest ecosystems in the Usinsk region of the Komi Republic (Russia). This particular region is characterized by severe climatic conditions. Annual air temperature is -3.2 ˚C. The coldest month is January with mean temperature -18.4 ˚C. Snow cover holds 200 days and is 48 cm high. The period with mean daily temperatures over +5˚C is 110 days. Mean air temperature in July, the warmest month, is +13.8 ˚C. Annual precipitation is 474 mm, among them 159 mm precipitate during vegetation period (June-August) (Scientific-applied reference book…, 1989).

Principal vegetation of the study region, which is located in far north taiga subzone, is forests that intermixed with large marshes; 10% of the area is covered by tundra vegetation (Yudin, 1954). Dominant are forest stands sparse spruce and spruce-birch forests with crown density of 0.3-0.5, height of trees 8-15 m, quality (bonitet) classes of tree stands V-Va. Forest composition mainly includes *Pinus sylvestris* and *Larix sibirica*. Most popular are long-moss forests, less represented are green-moss and sphagnum forest types.

The typical soil types of the region are boggy-podzolic, gley-podzolic, tundra-boggy, and boggy peaty soils (Podzolic soils…, 1981). Soil-forming rocks are moraine loams and sandy deposits formed in the glacier period. Sandy rocks are overlain by differently-moist soils as illuvial-humus-iron podzols, weakly peaty-podzolic-gley illuvial-humus soils; fine-textured loams are overlain by gley-podzolic soils and weakly peaty-podzolic-weakly gley soils.

The base of region's economy is oil-gas extracting and processing industries. Expansion of those industries leads to enlargement of the area of disturbed lands, including forest ecosystems. Sand pits are the most common technogenic objects within the Usinsk region. Sandy material excavated from pits is used for building roads, making bore sites and bore drills, etc. Restoration of vegetation cover in severe climatic conditions on sandy technogenic substrata, poor in nutrients, proceeds extremely slowly. Consequently, the restoration method of forest ecosystems on such lands is very much required for development.

Experimental plots were used in order to study the efficiency rate of forest ecosystems' restoration. Particularly, vegetation cover was studied using common geo-botanical methods (Field geo-botany, 1964), tree species that are planted on experimental plots were monitored by common study methods of forest cultures (Ogievskiy, Khirov, 1964). Soil type's description and soil samples' analysis (soil pH, organic C, exchangeable Ca, Mg, hydrolysable N, P_2O_5, K_2O) were done by the general methods (Agrochemical methods…, 1975; Theory and practice of soil chemical investigation, 2006). Humus composition was evaluated by the Tyurin method in Ponomareva-and-Plotnikova modification (1975).

3. Results and its discussion

Investigations of new ways of forest ecosystem were done in a way of comparative analysis with traditional methods of forest recultivation.

Traditional restoration methods of forest ecosystems in the North The main methodological position of traditional restoration methods of disturbed forest ecosystems is the resource approach aiming at planting forest cultures of the principal forest-forming species as spruce and pine. In other words, the task of traditional technology is to create forest plantations and not to restore earlier destroyed forest ecosystem of previous quality (Losev et al., 2005). Coniferous cultures are planted at the age of 1-3 years and have open roots; no ground treatment is meant.

First forest cultures in the Usinsk region were planted in 1958 by the personnel of the Usinsk leskhoz. From 1991 to 2007 forest cultures were planted on area of 1020.8 ha. Among this figure, the share of *Pinus sylvestris* made 53.6%, that of *Picea obovata* 27.6%, and that of *Pinus sibirica* 1.5%. Willow young trees were also planted for ground fixing with portion of 17.3%. Most forest cultures (44.8%) were planted on pits.

We have observed the sites being reforested by common restoration methods. The sites are located on the most usual sample of technogenic disturbance, in our case on 8 b technogenic pit (N 66°16´, E 57°16´).

Sandy material on 8 b pit is characterized by low content of clay (sum of particles <0.01 is less than 6%) (Table 1). This is responsible for low absorption and moisture content values; ground can be easily water- or wind-eroded.

Sampling depth (cm)	Hygroscopic moisture, %	HCl ignition losses	Number of particles (%) with diameter of:						Sum of particles >0.01	Sum of particles <0.01
			1.0-0.25	0.25-0.05	0.05-0.01	0.01-0.005	0.005-0.001	<0.001		
0-20	0.39	0.00	11.35	81.88	0.66	1.47	0.30	4.34	93.89	6.11
20-40	0.43	0.37	11.94	80.59	2.11	0.04	0.64	4.67	94.64	5.36

Table 1. Texture composition of technogenic material on 8 b pit.

The 8 "b" pit was partly planted with 3-year-old pine trees in 2001 without previous ground treatment.

On the second year after planting, the content of nitrogen, an important biogenic element, made 0.2 mg / 100 g a.d.s. which corresponded with low organic carbon content (Table 2). On the eighth year, no significant quantitative changes in composition of nutrients and absorbed bases were observed; content of organic carbon resisted low.

Seven years after planting the survival rate of plantings made 50%, tree height 53 cm, and crown diameter 43 cm. Above presented data is general. Pine plantings were underdeveloped because of poor concentration of nutrients in substratum and so were susceptible to the (snow) Schütte disease which stroke 60% of remaining pines. This disease additionally inhibits the growth of pines and often causes their depth. Soil cover was underdeveloped with total projection cover under 1%. 7 plant pioneers were identified (*Festuca ovina, Chamaenerion angustifolium, Hieracium umbellatum, Equisetum arvense, Carex* *arctisibirica, Rumex acetosell),* also in microdepressions mosses of the genus *Polytrichum* and *Ceratodon purpureus,* lichens of the *Stereocaulon* genus.

Year	Sampling depth, cm	pH_{water}	$C_{org.}$, %	$N_{hygr.}$	P_2O_5	K_20	Ca^{2+}	Mg^{2+}
				mg /100 g a.d.s.			mM/100 g a.d.s.	
2002	0-10	5.9	0.1	0.2	8.4	2.5	0.3	0.2
	10-20	5.9	0.3	0.3	8.0	2.8	0.2	0.2
2008	0-10	6.0	0.3	0.1	9.4	2.3	0.3	0.2
	10-20	5.9	0.4	0.4	7.9	3.1	0.2	0.2

Table 2. Agrochemical indices of substratum planted with 3-year-old pine cultures.

Thus, unfavorable properties of ground material did not provide for the active self-restoring process.

The other common restoration method of disturbed area is planting willow. Willow cultures were planted on the above-mentioned 8 "b" pit under the leadership of the ecologist of the OSC "Northern Oil" V.I. Parfenyuk in 1991 without previous substratum treatment. The distance between plantings in a row was 25 cm and between rows 2 m. On the twelfth planting year (2002) only 20% of planted trees remained alive and were about 1 m high. Single herbaceous plants *Festuca ovina, Chamaenerion angustifolium, Hieracium umbellatum, Equisetum arvense* were observed between rows. Those plant species are typical of the initial stage of self-restoring succession (Table 3). Herbaceous layer projective cover made less than 1%.

Species	Availability, %			Projective cover, %			Height, cm
Herbaceous plants:	2002	2006	2011	2002	2006	2011	
Carex arctisibirica (Jurtz.) Czer.	-	7	5	-	<1	<1	15
Chamaenerion angustifolium (L.) Scop	16	29	20	<1	<1	<1	20-30
Equisetum arvense L.	48	56	50	1	<1	<1	10
Festuca ovina L.	25	53	60	<1	<1	<1	10-25
Hieracium umbellatum L.	24	29	20	<1	<1	<1	20-30
Leucanthemum vulgare Lam.	4	-	-	<1	-	-	10
Rumex acetosella L.	36	14	5	<1	<1	<1	15-20
Solidago virgaurea L.	-	17	10	-	<1	<1	10-25
Tripleurospermum perforatum (Merat.) M.Lainz	8	7	-	<1	<1	-	10
Avenella flexuosa L.	-	-	5	-	-	<1	25
Mosses:							
Bryum sp.	-	7	5	-	<1	<1	1
Ceratodon purpureus (Hedw.) Brid.	-	7	10	-	<1	1	1
Polytrichum piliferum Hedw.	-	7	60	-	<1	5	1
Lichens:							
Stereocaulon paschale (L.) Hoffm.	-	7	15	-	<1	<1	1-2
Cladonia sp.	-	-	7	-	-	<1	1-2

Note: «-» - not found.

Table 3. Species composition of soil cover at site planted with willow trees.

20 years after planting (2011), the health status of shrubby layer did not practically change; soil cover remained thin (Table 3). The surface of ground material was partly covered with algae film and protonema of mosses. Microdepressions hosted mosses of the *Polytrichum* genus and *Ceratodon purpureus*. Totally, 8 species of herbaceous plants and 3 mosses were identified at the area.

Chemical analysis of ground material samples on the twelfth willow planting year revealed a low content of biogenic elements and organic matter. On the sixteenth planting year the agrochemical parameters did not practically change (Table 4). As the herbaceous layer was very thin, sandy ground was susceptible to erosion. On the twelfth planting year we observed washed-out erosion hollow 2.5 m wide, 1 m deep, 5 m long. On the sixteenth planting year it increased in size with a depth of 1.5 m and a length over 10m.

Year	Sampling depth, cm	pH_{water}	$C_{org.}$, %	$N_{hygr.}$	P_2O_5	K_20	Ca^{2+}	Mg^{2+}
				mg /100 g a.d.s.			mM/100 g a.d.s.	
2002	0-10	5.9	0.2	0.1	9.4	2.3	0.3	0.2
	10-20	5.9	0.2	0.4	7.8	3.1	0.2	0.2
2005	0-2*	5.9	1.2	1.7	9.7	0.7	1.4	0.2
2006	0-5	5.8	0.2	0.1	7.9	6.5	0.8	0.6

Note: * - crust of algae and protonema in a small depression.

Table 4. Agrochemical parameters of ground material planted with willow trees.

Consequently, there was almost no positive effect from willow planting for post-technogenic substratum restoration.

The above-sited data allow for the following conclusion. While using the traditional restoration methods of disturbed forested areas, soil and vegetation cover formation is slow, what hampers restoration of the forest ecosystem as whole. To speed up restoration there is a need to apply complex methods aiming at development plant biogeocenosis, i.e. maintenance plant matter biological cycle, ensuring conditions for intensive plant cover formation on ground surface and organic matter accumulation in substratum. So, restoration the technogenically disturbed forest ecosystem in the North cannot be efficient without development the basic system components, first of all plant community including not only tree layer but also ground plant cover.

4. Main principles of the "nature restoration" conception and the complex of methods aimed at accelerated restoration of forest ecosystems on technogenically disturbed lands

The "nature restoration" conception was developed at the Institute of Biology Komi SC UrD RAS under the leadership of Dr. I.B. Archegova. This conception means restoration of forest ecosystems including their initial structure and "functions" which, finally, ensures the integrity of the biosphere (Archegova, 1998). The "nature restoration" methodological conception operates forest as a system and ecosystem self-restoration as a succession process. From this point of view, ecosystem presents a system of the three main components as plant community, fauna-microbe complex that processes plant remnants and soil that is a productive (biogenic-accumulative) layer. These three components are integrated into ecosystem by means of organic (plant) matter biological cycle. In practice, the "nature restoration" system aims at restoration the ecosystem as a whole, not its single components, tree layer in particular. The "nature restoration" methods should correspond with the regional climatic conditions, also taking into consideration regional economy, traditional regional nature management.

Northern ecosystems poorly resist technogenic impacts and slowly self-restore because of not only severe climatic conditions together with the presence of permafrost rocks but also because of a thin productive organic-accumulative layer (soil) which hosts the majority of nutrition elements, plant roots, and active microbiota. Mineral layer becomes visual after organic-accumulative layer disturbance. Mineral layer is unfavorable for biota self-restoration and so hampers the process of nature self-restoration, first of all plant community restoration. Consequently, any organic layer technogenic disturbance always has total nature ecosystem destruction as an aftereffect. The absence of vegetation cover for a long period of time speeds up erosion processes that only aggravate self-restoration of plant-soil cover. This situation requires development an active and up-to-date approach to restoration of disturbed forest ecosystems.

Based on the "nature restoration" conception we have developed the two-stage system of rapid (managed) "nature restoration" practical methods (Fig. 1). At the first "intensive" stage, we form herbaceous ecosystem and corresponding biogenic-accumulative layer in a short period of time, namely in 3-5 years, using complex agrotechnical treatments as applying organic and mineral fertilizers and sowing local perennial herbs. In the other words, this way reduces the usually long (up to 30-40 years) initial self-restoration succession stage. At the second "assimilation" stage, no agrotechnical treatments are used. The previously formed herbaceous community is gradually self-replaced by a zonal type of plant community or generally by forest ecosystem.

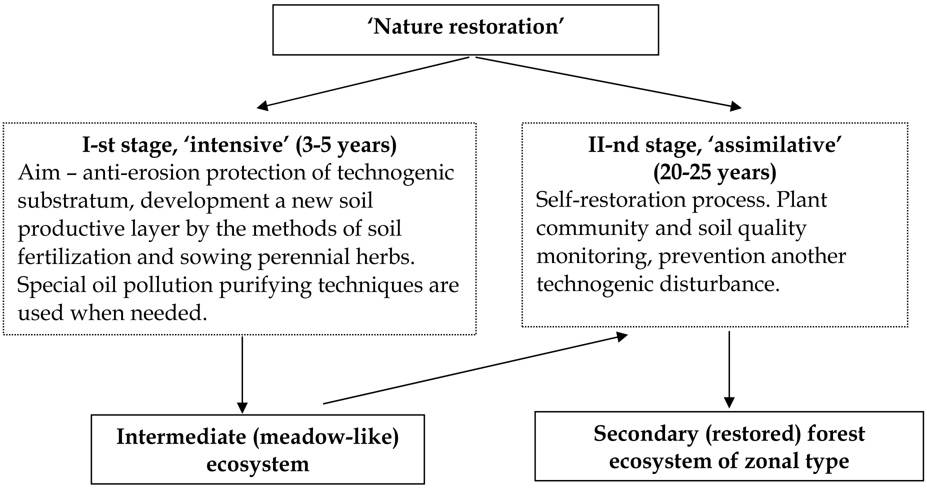

Fig. 1. The scheme of complex 'nature restoration' methods.

According to this sketch in 1991 we initiated the experiment on the 8 "b" pit located near the above discussed plots being restored by traditional methods. Intensive "nature restoration" methods included soil surface fertilization with peat in a 15-cm layer and with mineral fertilizers ($N_{60}P_{60}K_{60}$), sowing the herbaceous mixture of *Alopecurus pratensis* and *Poa pratensis* in a dose of 20 kg seeds/ha with proportion of seeds 1:1. Initial sandy substratum contained 0.2% organic carbon, 0.1 hydrolysable nitrogen, 6.7 phosphorus and 2.0 mg/100 g a.d.s. potassium oxides. Sawn grasses were annually given a complex mineral fertilizer in a rate of 30 kg each mineral element/ha.

Three years later the plot grew into an intermediate herbaceous community (TPC 100%) of meadow type with corresponding meadow-like soil constituted of typical soddy horizon and humus horizon. Later there was no any kind of treatment. It was the beginning of the second restoration stage thereby tree plants inhabited the plot with gradual replacement of herbaceous ecosystem to forest ecosystem.

After intensive agrotechnical treatments, already the first ten years saw formation of woody-shrubby layer with a crown density of 0.1 of *Betula pubescens*, *Larix sibirica, Salix* species 1.5-2.5 m high (Table 5). Ground cover (TPC 100%) 10 years after restoration start was considerably composed of sawn *Alopecurus pratensis* (PC 44%) and less by *Poa pratensis.* At the same time, 19 new non-sown herbaceous species were observed. Among them, *Festuca ovina, Chamaenerion angustifolium, Erigeron acris,* and *Solidago virgaurea* had highest projective cover figures (Table 8). Ground cover was largely composed of synanthropic species (*Rumex acetosella*, *Chamaenerion angustifolium*, *Crepis tectorum*, *Tripleurospermum perforatum*, *Tussilago farfara*, *Equisetum arvense*), characteristic of initial restoration stages of disturbed lands. The plot was inhabited by mosses and single *Cladonia* and *Peltigera* lichens; 5 mosses were totally identified dominated by polytrichum mosses (16%) (Table 8). Consequently, the first ten years after the experiment start there is an active replacement of intermediate herbaceous ecosystem by forest ecosystem with formation of woody layer of quickly-growing tree species. Ground cover was identified for numerous non-sown vascular plant species and still numerous sawn grasses and mosses.

Species	Quantity, inds./100 m^2		Height, m	
	2002	2011	2002	2011
Developing tree story:				
1st layer:				
Betula pubescens Ehrh.	2	13	2.5-3	4-6
Larix sibirica Ledeb.	9	15	1.3-1.5	4-5,5
Salix caprea L.	2	2	2.5	6
Salix dasyclados Wimm.	2	1	3	4
2nd layer:				
Betula pubescens Ehrh.	-	16	-	2-3
Larix sibirica Ledeb.	-	6	-	2-3
3rd layer:				
Betula pubescens Ehrh.	-	13	-	0.5-1.5
Larix sibirica Ledeb.	-	3	-	0.5-1.5
Picea obovata Ledeb.	-	1	-	0,5
Developing tree understory:				
Betula nana L.	1	1	0.7	1-1.5
Ribes rubrum L.	1	1	0.7	1
Salix phylicifolia L.	11	6	1.5	1-3
Salix hastata L.	1	-	0.9	-
Salix lapponum L.	1	-	1.3	-

Table 5. Species composition and structure of tree story and tree understory on the experimental plot.

Species	Abundance, %			Projective cover, %			Height, cm
	2002	2006	2011	2002	2006	2011	
Shrubs:							
Arctostaphylos uva-ursi (L.) Spreng.	5	7	5	<1	<1	<1	10
Empetrum hermaphroditum (Lange) Hagerup	5	7	10	<1	<1	<1	10
Vaccinium uliginosum L.	-	-	5	-	-	<1	10
Vaccinium myrtillus L.	-	-	5	-	-	<1	10
Herbaceous plants:							
Agrostis tenuis Sibth.	-	7	35	-	<1	5	20-50
Avenella flexuosa (L.) Drey.	-	-	70	-	-	25	20-50
Alopecurus pratensis L.	100	80	75	44	46	25	80
Antennaria dioica (L.) Gaertn.	-	-	5	-	-	<1	15
Calamagrostis epigeios (L.) Roth	10	7	-	<1	<1	-	60-80
Calamagrostis lapponica (Wahl.) Hartm.	-	-	15	-	-	1	50-60
Carex brunnescens (Pers.) Poir	5	-	5	<1	-	<1	25
Chamaenerion angustifolium (L.) Scop.	100	67	65	9	5	7	40-80
Crepis tectorum L.	5	7		<1	<1		20-25
Deschampsia cespitosa (L.) Beauv.	30	7	25	2	1	7	40-80
Epilobium palustre L.	10	7	-	<1	<1	-	20
Equisetum arvense L.	10	7	15	<1	<1	<1	20
Equisetum sylvaticum L.	5	-		<1	-	-	25
Euphrasia frigida Pugsl.	-	-	5	-	-	<1	15
Erigeron acris L.	70	40	40	4	<1	1	35-45
Festuca ovina L.	100	67	40	23	18	16	15-30
Festuca rubra L.	-	7	15	-	<1	1	40-45
Hieracium umbellatum L.	40	33	25	1	1	1	40
Hieracium vulgatum L.	10	20	10	<1	1	<1	40
Omalotheca sylvatica (L.) Sch.Bip.	60	33	70	2	1	2	10-30
Phalaroides arundinacea (L.) Rausch.	-	-	5	-	-	<1	50
Poa pratensis L.	30	20	30	1	4	5	60
Rumex acetosella L.	10	7	25	<1	<1	<1	20-25
Solidago virgaurea L.	80	60	80	3	3	10	10-45
Taraxacum officinale Wigg.	40	20	5	1	<1	<1	15-20
Tripleurospermum perforatum (Merat.) M.Lainz	5	7	-	<1	<1	-	15
Tussilago farfara L.	20	7	5	<1	<1	<1	10-15
Trientalis europaea L.	-	-	5	-	-	<1	5-10
Lycopodium annotinum L.	-	-	5	-	-	<1	10
Lathyrus pratensis L.	-	-	5	-	-	<1	30-40
Orthilia secunda (L.) House	-	-	5	-	-	<1	15
Mosses:							
Brachythecium campestre (Bruch) B. S. G.	-	-	20	-	-	5	3-5
Brachythecium reflexum (Starke) Schimp.	-	-	10	-	-	5	3-5
Brachythecium salebrasum (Wed et Mohr) Bryol.	-	-	20	-	-	5	3-5

Species	Abundance, %			Projective cover, %			Height, cm
	2002	2006	2011	2002	2006	2011	
Brachythecium sp.	20	20	-	1	15	-	3-5
Ceratodon purpureus (Hedw.) Brid.	20	20	5	<1	<1	<1	2-3
Dicranum polysetum Sw.	-	-	10	-	-	1	3-4
Plagiothecium denticulatum (Hedw.) B. S. G.	-	-	10	-	-	1	1-2
Pleurozium schreberi (Brid.) Mitt.	-	20	80	-	1	10	3-5
Polytrichum commune Hedw.	20	20	20	2	1	2	5-7
Polytrichum juniperinum Hedw.	60	40	90	11	11	30	5-7
Polytrichum piliferum Hedw.	30	33	15	5	5	3	3-5
Sciurohypnum oedipodium (Mitt.) Ignatov et Huttunen.	-	-	10	-	-	1	3
Sciuro-hypnum starkei (Brid.) Ignatov et Huttunen *(Brachythecium starkei*(Brid.) B.S.G.)	-	-	65	-	-	30	3-5
Lichens:							
Cladonia anomaea (Ach.) Ahti & P.James	-	-	4	-	-	<1	1-3
Cladonia arbuscula (Wallr.) Flot.	-	7	10	-	<1	<1	1-3
Cladonia borealis Stenroos	-	-	4	-	-	<1	1-2
Cladonia botrytes (Hag.) Willd.	-	-	4	-	-	<1	1
Cladonia carneola (Fr.) Fr.	-	7	-	-	<1	-	1-2
Cladonia cervicornis (Ach.) *Flot. ssp. verticillata* (Hoffm.)	-	-	4	-	-	<1	1-2
Cladonia chlorophaea (Florke ex Sommerf.) Spreng.	-	-	4	-	-	<1	1-2
Cladonia cornuta (L.) Hoffm.	-	7	20	-	<1	<1	1-4
Cladonia crispata (Ach.) Flot.	-	-	4	-	-	<1	1-2
Cladonia deformis (L.) Hoffm.	-	7	-	-	<1	<1	1-3
Cladonia fimbriata (L.) Fr.	-	7	10	-	<1	<1	1-3
Cladonia gracilis (L.) Willd.	-	7	20	-	<1	<1	1-3
Cladonia phylophora Hoffm.	-	-	20	-	-	<1	1-2
Cladonia pleurota (Floerke) Schaer.	-	-	4	-	-	<1	1-2
Cladonia rangiferina (L.) Web.	-	7	20	-	<1	<1	1-3
Cladonia subulata Weber.	-	-	4	-	-	<1	1-2
Cladonia sp.	10	7	-	<1	<1	-	1
Peltigera didactyla (With.) Laundon	-	-	10	-	-	<1	1-2
Peltigera leucophlebia (Nyl.) Gyeln.	-	-	4	-	-	<1	1-2
Peltigera rufescens (Weis.) Humb.	-	-	4	-	-	<1	1-2
Peltigera sp.	10	7	-	<1	-	<1	1-2

Table 6. Composition and structure of ground plant cover on the experimental plot.

The newly-formed 10-year-old soil had the following morphological structure. Loose layer of weakly-decomposed plant waste (dead grass) was penetrated with rare moss stems.

AOA1 0-8(12) cm	Well-decomposed plant waste with inclusions of mineral particles, moist, abundant roots.
A1 layer 8(12)-21 cm	Sandy, dark-grey (humus color), structureless, loose, moist, many roots. Transition to the next horizon is abrupt by color.
III-rd layer 21-29 cm	Sandy, light-yellowish with whitish and dark-ochre spots, loose, moist, rare roots.
IV-th layer 29-45 cm	Sandy, grey-yellowish, lighter than the previous horizon, loose, moist, without roots.

In the first ten years there is a soil profile formation with organic horizons with features of soddy layer, typical for meadow ecosystems. The upper biogenic-accumulative layers (A0A1, A1) had weakly-acid medium reaction and accumulated the maximum of nitrogen, humus, and exchangeable bases (Table 7).

Year	Horizon, sampling depth, cm	pH_{water}	C, %	N_{hydr}.	P_2O_5	K_20	Ca^{2+}	Mg^{2+}
				mg/100 g a.d.s.			mM/100 g a.d.s.	
11th year (2002)	A0A1 0-8(12)	5.4	5.0	2.9	8.5	7.9	7.1	1.1
	A1 8(12)-21	5.7	3.3	1.6	10.1	4.3	5.9	0.8
	III 21-29	5.7	1.6	0.8	9.9	3.8	1.7	0.5
	IV 29-45	5.6	0.2	0.8	10.0	2.5	1.2	0.4
20th year (2011)	In group of trees							
	A0 0-5	5.4	6.7	11.5	10.0	29.0	17.7	3.6
	A1 5-15	5.2	4.9	9.0	9.9	9.0	10.0	1.6
	$A0_{buried}$ * 15-21	5.0	7.2*	5.9	8.3	8.9	14.8	2.1
	BC 21-35	5.3	0.2	7.8	14.0	8.6	2.3	0.6
	Open area							
	A0 0-2(4)	5.3	5.7	9.5	13.3	36.0	10.6	2.2
	A_1 2(4)-13,5(14)	4.9	5.4	5.9	11.1	11.4	10.1	1.6
	$A0_{buried}$ 13,5(14)-21	4.9	14.8*	5.5	5.3	14.9	17.5	2.2
	BC 21-24	4.8	0.3	2.4	12.8	5.5	2.5	0.6
	BC/ 24-35	5.1	0.2	1.1	13.2	3.8	2.4	0.6

Note: * – buried organic residues (peat).

Table 7. Agrochemical indices of newly-formed soil on the experimental plot.

The forest community was structurally formed on the 20th year after restoration start. The first tree story consisted of *Betula pubescens* and *Larix sibirica* with few tree-like willow species (*Salix dasyclados*, *Salix caprea*); tree height was 4-6 m, stem diameter 4-6(9) cm (Table 5). Crown density increased to 0.4. Since 2002, tree re-growth (with a height of less than 50 cm) was clearly dominated by *Betula pubescens*, 40 individuals per 100 m^2, for contrast only 5 individuals of *Larix sibirica*. *Betula pubescens* was also a dominant species in the second and third tree stories which were formed on the 20th restoration year. The plant waste accumulation dynamics of woody plants evidenced the active development of tree layer (Tables 8, 9). Thus, the community on its 20th restoration year was at the stage of quickly-growing woody plants, typical of self-restoration succession in the taiga zone (Shennikov, 1964). Low-height young growth of *Picea obovata* and *Pinus sylvestris* appeared in amount of 1-3 individuals / 100 m^2.

Plant waste sampling period	Plant waste weight
June 2002 – September 2002	8.5±1.7
October 2002 – May 2003	27.5±2.0
Year total:	36.1
June 2007 – September 2007	15.0±6.5
October 2007 – May 2008	52.2±8.6
Year total:	67.2
June 2008 – September 2008	13.6±5.4
October 2008 – May 2009	53.05±10.2
Year total:	66.65
June 2009 – September 2009	11.9±2.8
October 2009 – May 2010	73.3±15.3
Year total:	85.2
June 2010 – September 2010	14.7±3.2
October 2010 – May 2011	106.01±31.2
Year total:	110.71

Table 8. Plant waste weight by years on the experiment plot (air-dried weight, g/m^2).

	October 2008 – May 2009		June 2009 – September 2009		October 2009 – May 2010		June 2010 – September 2010		October 2010 – May 2011	
Fraction	Weight g/m^2	Share %	Weight g/m^2	Share %	Weight g/m^2	Share %	Weight g/m^2	Share, %	Weight g/m^2	Share, %
Branches	0.45	1	0.498	4	0.604	1	0.756	5	1.96	2
Betula pubescens leaves	30.68	58	2.263	19	35.88	49	1.028	7	68.59	65
Herbs	2.17	4	0.169	1	3.664	5	0.412	3	2.80	3
Salix leaves	2.48	5	4.421	37	1.972	3	0.780	5	2.95	3
Bark	0.43	1			0.14	0	0.132	1	0.37	0
Larix sibirica needles	8.46	16	1.046	9	21.352	29	9.792	67	20.50	19
Dust of rotten wood	8.38	16	3.54	30	9.736	13	1.848	13	8.72	8
Inflorescences	-	-	-	-	-	-	-	-	0.11	0

Note: «-» - not found.

Table 9. Plant waste fraction composition on the experiment plot (air-dried weight, g/m^2).

At the end of the second decade of experimental years the TPC of herbaceous-dwarfshrub layer comprised 85%. This retreat in TPC was related to woody plants' shadowing. Forest dwarfshrubs increased in species number, among them *Arctostaphylos uva-ursi*, *Empetrum hermaphroditum*, *Vaccinium uliginosum, Vaccinium myrtillus* (Table 6). Among 24 herbaceous species found on the experimental plot, the forest species *Avenella flexuosa* and *Solidago virgaurea* had essential PC, 25 and 10%, correspondingly. The sawn meadow grass *Alopecurus pratensis* significantly reduced its PC (25%). Mosses counted 11 species on the 19th experimental year. The highest shares in PC belonged to *Sciuro-hypnum starkei* (30%), *Polytrichum juniperinum* (30%) and the common forest species *Pleurozium schreberi* (8%). Lichens were highly diverse with 17 species, mainly from the *Cladonia* genus. Thus, the end of the second experimental decade saw formation the forest community where sown plants of the first "intensive" restoration stage were normally replaced by forest species together with mosses and lichens.

On the 20th experiment year, soil pits on open area and in group of trees were excavated.

Soil pit №1 was dug in a group of trees (Betula pubescens, Larix sibirica). Ground cover (TPC 75%) was found for the herbs (Avenella flexuosa, Solidago virgaurea, Alopecurus pratensis, Chamaenerion angustifolium, Orthilia secunda) and the mosses (Sciuro-hypnum starkei, Pleurozium schreberi). Moss cover was well developed (PC 60%) with practically full-formed mossy litter.

A0 0-5 cm	Loose layer of mossy litter, upper part contains weakly-decomposed and lower part stronger decomposed plant remnants with inclusions of sand, abundant roots.
A1 5-21 cm	Sandy, grey-black, loose, inclusions of weakly- to well-decomposed plant remnants from outside peat (brought at the 1st restoration stage), many roots, transitional boundary is abrupt by color.
BC 21-35 cm	Sand, grey-yellowish, with whitish spots, structureless, few roots, moist.

Soil pit №2 was made on open area. Herbaceous cover (TPC 100%) was dominated by *Alopecurus pratensis*, *Solidago virgaurea*, *Omalotheca sylvatica.* There was a 2-cm-thick layer of dead grass on surface. Dead grass was the development base for the *Brachythecium* mosses and *Sciuro-hypnum starkei*.

A0 0-2(4) cm	Loose layer of weakly-mean-decomposed plant remnants, dark-grey, sand inclusions in lower part, abundant roots.
A1 2(4)-21 cm	Sandy, dark-grey to black, structureless, moist, abundant roots, inclusions of decomposed peat remnants brought at the 1st restoration stage, many rain worms, transitional boundary is abrupt by color.
BC 21-36 cm	Sandy, grey-yellowish, with whitish spots, moist, upper part with single roots.

Agrochemical parameters of the studied soils (Table 7) provide evidence that the biogenic-accumulative layers (litter and humus horizons) have been formed on the 20th restoration year. Those horizons were marked through high content of organic carbon, nitrogen, exchangeable bases, and other biogenic elements. Humus of the biogenic-accumulative layer was dominated by humic substances (Table 10).

Horizon, depth, cm	$C_{org.}$ total, %	Humic acids				Fulvic acids					Non-soluble residue	C_{HA} / C_{FA}
		1	2	3	∑	1a	1	2	3	∑		
A1 3-13	4.2	20.94	11.76	20.7	53.4	3.18	14.7	6.24	9.88	34.0	12.6	1.57
A1 13-23	2.4	10.98	14.22	14.4	39.6	4.88	12.6	6.5	6.1	30.08	30.32	1.32
23-28	0.2	9.52	1.91	4.76	16.19	28.6	9.5	17.17	7.14	62.41	21.4	0.26
28-45	0.1	7.7	0.76	4.61	13.07	15.38	2.32	22.29	1.51	41.5	45.43	0.31

Table 10. Fraction-group humus composition of organic-accumulative layer of the newly-formed soil on the 18th experiment year (% of total content).

Consequently, the biological cycle of organic (plant) matter started at the "intensive" stage resulted in forest ecosystem formed to the 20th year as the integrity of two components, plant community (or biotic complex) and soil. Organic (plant) matter biological cycle restoration initiated active soil restoration visualized by formation of the biogenic-organic-accumulation layer. This layer's structure depends on plant community type. It determines the significance of soil as a system structure, capable of holding and accumulating plant nutrition elements and ensuring stable conditions for self-restoration of ecosystem. These properties are formed during the transformation processes of plant waste called humus formation, the main soil formation process (Ponomareva, Plotnikova, 1980).

Restoration of nature medium components is a complete process that functionally unifies biota with its habitat. Soil can be formed when technogenic substratum reaches some "critical" mass of plant material to start the biological cycle, including humus accumulation.

In the North, the process of self-restoring succession is a long-term process. To speed up (manage) the self-restoration process on post-technogenic bare areas, is to apply a complex of agrotechnical methods, i.e. fertilization, sowing perennial grasses, that is called an "intensive" restoration period. Accumulation of organic matter (plant remnants of perennial herbs etc.) in substratum, its transformation (humus formation) with help of zoo-microbe complex, accumulation and consequent assimilation of biogenic elements by plants provide favorable conditions for the next stage, forest ecosystem development.

The conducted study has evidenced the efficiency of agromethods ("intensive" stage) for speeding up the restoration process of forest ecosystem. It was demonstrated that the first experimental decade was already indicated by the most advanced restoration succession stage, i.e. formation the herbaceous community and its transition to forest community of quickly-growing woody species under whose canopy conifers started growth. Transformation of herbaceous community and corresponding soil type during self-restoring succession in taiga zone into quickly-growing woody species stand is a normal process (Shennikov, 1964).

Acceleration in forest ecosystem formation becomes more prominent when comparing the study plot with the near self-restoring plot. On its 28th restoration year the TPC figure remained under 1 % without woody plants and with active erosion signs.

5. Optimization the "nature restoration" methods

As said above, the preliminary "intensive" stage ensures favorable substratum conditions for acceleration of woody layer self-restoration, replacement of herbaceous ecosystem by forest ecosystem. However, restoration of conifers proceeds slowly and under the canopy of quickly-growing deciduous (birch, asp) species. To further accelerate restoration of forest ecosystem on the second restoration stage, complex of methods was developed. These methods are to optimize restoration of conifers in woody layer of forest ecosystems in north taiga zone and consist in planting conifers simultaneously with agrotechnical treatments on the first ("intensive") restoration stage.

Another experiment on the territory of 8b sand-pit was started, where *Pinus sylvestris* two-year-old trees, traditionally used for restoration purposes, with open root system were planted with a planting density of 5000 individuals/ha. Herb mixture composition being sown on "intensive" stage included *Poa pratensis*, *Festuca rubra*, *Festuca pratensis*, *Bromopsis inermis*, *Phleum pratense* in proportion 1:1:1:1:1. Annual additional fertilization with complex mineral fertilizer was done during 4 years. By our data, only 30-40% of pine plantings remained alive on the second year and resisted few for the whole study period. The two-year-old *Pinus sylvestris* plantings did not develop well on the "intensive" restoration stage with a height of 12-17 cm at the fifth year. Herb stand was already 90 cm high at that period of time with 80-90% TPC. So, the study has identified two-year-old *Pinus sylvestris* plantings with open root system not a promising material to be used on the "intensive" restoration stage of the "nature restoration" experiment. Herbaceous layer developed quicker than *Pinus sylvestris* plantings. Low growth rates did not allow the plantings to overgrow herb layer in a short period of time which was particularly responsible for their future underdevelopment.

Absolutely other results were obtained on usage the high-growth material, *Pinus sylvestris* wildlings about 50 cm high with a ground clot 30x30 cm. Planting density was 2500 individuals/ha. The same herb species as sown in the trial with two-year-old plantings were used. Additional fertilizing with complex mineral fertilizer (N45P45K45) was done every spring for 4 years.

By the observation results, the planted wildlings remained alive by almost 100% 5 years afterwards (Table 11). High surviving rate of the plants was related to their sufficient height, planting with ground clot, and caring for 5 years.

Year(s) after planting	Survival rate, %	Height, cm	Stem diameter, cm	Crown diameter, cm
1	100	59.1±2.4	1.1±0.1	32.9±1.4
2	100	60.9±2.8	1.5±0.2	37.3±1.6
3	100	68.8±3.1	1.7±0.1	46.5±2.1
4	96	79.5±3.1	1.8±0.1	48.7±3.1
5	96	100.3±4.3	2.1±0.2	55.4±4.5

Table 11. Biometric parameters of *Pinus sylvestris* plants in optimization experiment (autumn observations).

Beginning from the third planting year, *Pinus sylvestris* steadily increased in height and was over 20 cm high on the fifth year (Fig. 2).

On the fifth year the mean height of planted trees was about 1 m, consequently, the trees showed high survival rate and well development.

Herbaceous cover on the experimental plot actively developed. On the third year TPC of herb layer was 30% and already 70-75% to the fourth-fifth year (Table 12). Herb layer practically lost such sown herbs as *Festuca pratensis*, soil moisture-dependent, and *Trifolium pratense*. The rhizome grasses *Bromopsisinermis*, *Poa pratensis* and the rhizome loose-bunch *Festuca rubra* remained. The latter species as least dependent of soil richness and moisture had the highest projective cover among sown herbs. New non-sown herbs appeared and were prevailed by *Festuca ovina* that normally grows in lichen pine forests. There were species typical of anthropogenically disturbed areas as *Chamaenerion angustifolium*, *Equisetum arvense*. The species *Solidago virgaurea*, *Deschampsia cespitosa*, *Avenella flexuosa,* usual for forest and meadow were fixed but were few in number. Forest sub-shrubs (*Empetrum hermaphroditum*, *Vaccinium vitis-idaea*) transported there within ground clot were identified. Moss cover started formation and included pioneer species (Table 12). The majority of newly-appeared species were single in number. The vivid species composition on the study plots characterized the plant community as young and unstable.

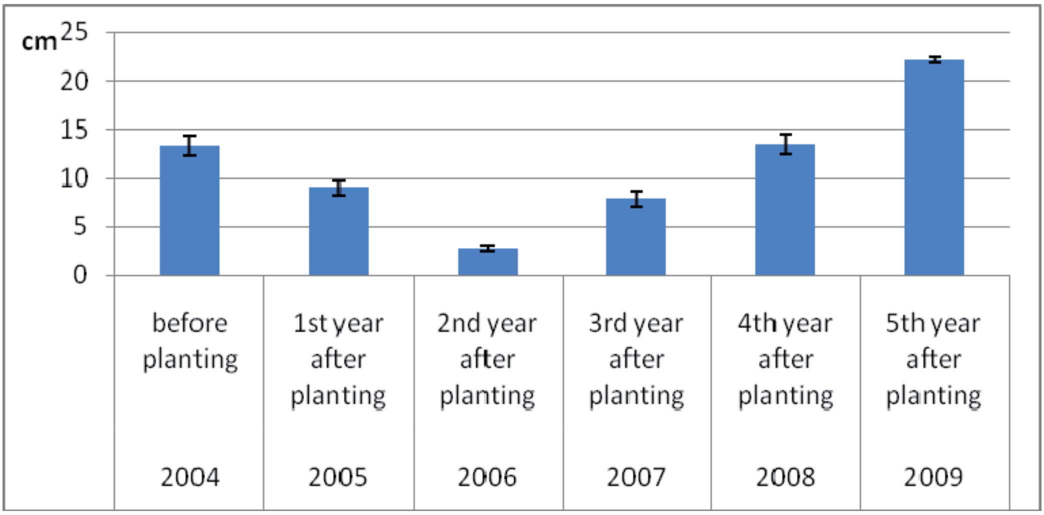

Fig. 2. Increment dynamics of *Pinus sylvestris* wildlings in optimization experiment.

Species	Number of years after experimental start			
	2	3	4	5
Sown herbs:				
Bromopsis inermis (Leyss.) Holub	2	6	10	7
Festuca pratensis Huds.	1	3	<1	2
Festuca rubra L.	2	3	7	26
Phleum pratense L.	4	7	5	5
Poa pratensis L.	2	5	8	6
Trifolium pratense L.	1	1	<1	1
Invasive species:				
Avenella flexuosa (L.) Drey.	-	-	-	1
Agrostis tenuis Sibth.	<1	<1	-	-
Carex arctisibirica (Jurtz.) Czer.	-	<1	<1	<1
Chamaenerion angustifolium (L.) Scop	3	2	4	1
Chenopodium album L.	-	<1	-	-
Crepis tectorum L.	-	-	1	-
Dactylis glomerata L.	-	-	<1	1
Deschampsia cespitosa (L.) Beauv.	-	-	<1	<1
Empetrum hermaphroditum (Lange) Hagerup	<1	<1	<1	<1
Equisetum arvense L.	3	2	1	<1
Festuca ovina L.	10	16	41	20
Hieracium umbellatum L.	1	3	<1	2
Solidago virgaurea L.	<1	<1	<1	<1
Tripleurospermum perforatum (Merat.) M.Lainz	<1	<1	-	-
Vaccinium uliginosum L.	-	<1	-	-
Vaccinium vitis-idaea L.	<1	<1	<1	<1
Mosses				
Ceratodon purpureus (Hedw.) Brid	<1	<1	<1	5
Polytrichum juniperinum Hedw.	<1	<1	1	<1
Polytrichum piliferum Hedw.	<1	<1	1	1
Moss protonema	-	21	32	30
Total projective cover	**30**	**48**	**75**	**70**
Number of herb species	**18**	**18**	**17**	**17**
Number of moss species	**3**	**3**	**3**	**3**

Table 12. Development characterization of herbaceous cover in the optimization experiment (projective cover by years, %).

The changes in ground vegetation cover provoked changes in substratum. Substratum surface was identified for a loose layer of dead plant remnants (litter). On the fourth-fifth restoration year it became underlain by a weakly-compact soddy layer up to 3(5) cm thick. Slow dead plant material decomposition in the North causes slow organic carbon accumulation in substratum (Table 13, Fig. 3). This fact was proven by other scientists (Abakumov, 2008). There is an existed positive trend in content of biogenic elements (Figs. 4,5,6) related to the already started organic matter biological cycle.

Plot, №	Sampling depth, cm	pH_{water}	C, %	$N_{hydr.}$	P_2O_5	K_20	Ca^{2+}	Mg^{2+}
				Mg/100g a.d.s.			mM/100g a.d.s.	
initial substratum								
control	0-10	5.7	0.1	0.2	6.6	2.1	0.6	0
	20-30	5.7	0.1	0.4	8.1	2.2	0.5	0.1
trial	0-10	6.5	0.2	0.3	5.7	2.9	0.9	0.0
on the second year after planting								
control	0-5	5.8	0.2	0.3	6.3	3.8	1.1	0.5
	5-10	5.7	0.2	0.3	6.5	3.2	0.9	0.3
trial	0-5	6.1	0.3	1.3	5.6	3.0	1.1	0.1
	5-10	6.1	0.2	0.3	3.4	1.8	1.0	0.4
on the fourth year after planting								
control	0-5	5.8	0.1	0.4	10.5	4.7	0.6	0.1
	5-15	5.9	0.1	0.3	9.5	2.7	0.8	0.1
trial	0-3	6.1	0.3	1.0	16.2	7.4	0.8	0.1
	3-15	6.0	0.1	0.2	5.7	3.9	1.3	0.2
	15-30	6.4	0.1	0.5	5.6	2.5	1.3	0.4
on the fifth year after planting								
control	0-5	5.3	0.1	0.4	7.2	5.1	0.4	0.3
	5-10	5.2	0.1	0.3	7.9	5.4	0.3	0.2
	10-20	5.2	0.2	0.4	6.9	5.5	0.3	0.2
	20-30	5.2	0.1	0.3	7.0	5.3	0.3	0.2
trial	0-5	5.1	0.2	1.5	11.1	13.4	0.7	0.2
	5-10	5.5	0.1	0.7	5.0	4.7	0.9	0.3
	10-15	6.0	0.1	1.0	6.5	4.1	0.9	0.3
	15-30	6.0	0.1	0.7	5.0	3.4	0.7	0.3
on the sixth year after planting								
control	0-5	5.2	0.1	0.4	7.2	2.2	0.6	0.2
	5-10	5.2	0.1	0.2	7.9	2.9	0.8	0.2
	10-20	5.2	0.1	0.2	8.8	3.2	0.8	0.3
	20-30	5.3	0.1	0.3	9	2.9	0.8	0.4
trial	Ад 0-2	5.2	0.2	2.2	32.1	10.2	0.6	0.3
	АдА$_1$ 2-5	5.4	0.1	2.5	13.8	12.3	0.4	0.1
	А// 5-10	5.4	0.2	0.7	9.5	10.1	0.6	0.2
	АВ 10-20	5.6	0.2	1.9	12.1		0.8	0.2
	В 20-30	6.1	0.1	0.3	9.1	2.9	1.3	0.3

Table 13. Changes in substratum agrochemical parameters in the optimization experiment.

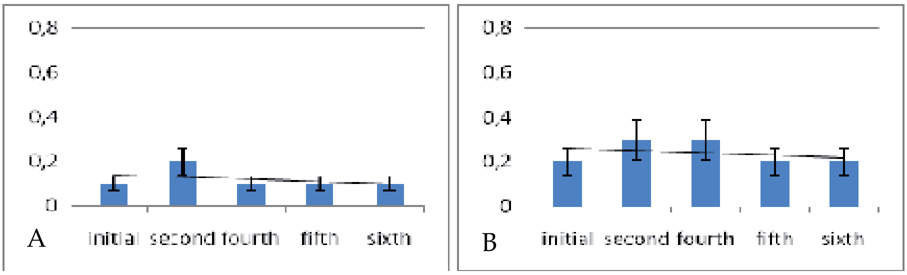

Fig. 3. Organic carbon content dynamics (%) by years in upper substrata layer in the background (A) and experimental (B) plots.

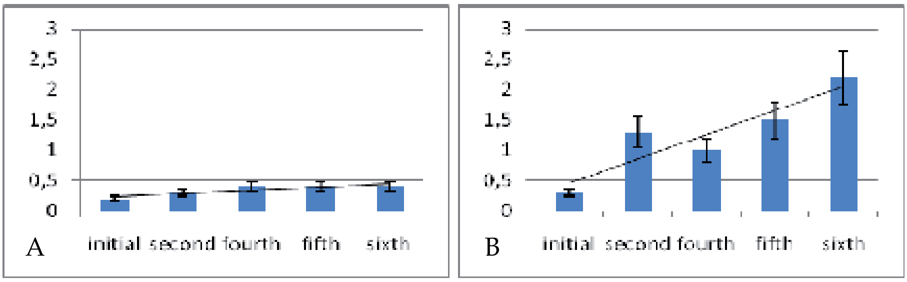

Fig. 4. Hydrolizable nitrogen content dynamics (mg/100 g a.d.s.) in upper substrata layer in the background (A) and experimental (B) plots.

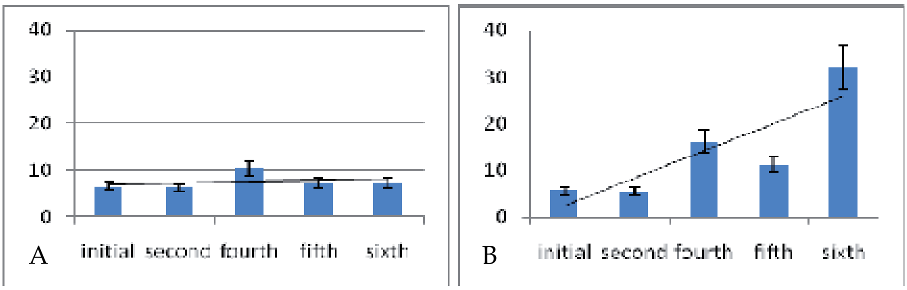

Fig. 5. Phosphorus oxide content dynamics (mg/100 g a.d.s.) in upper substrata layer in the background (A) and experimental (B) plots.

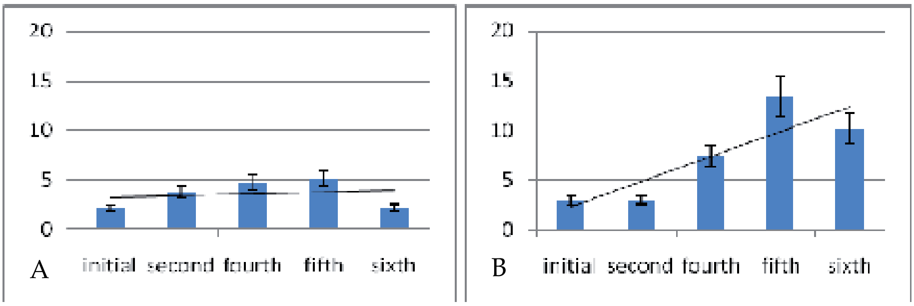

Fig. 6. Potassium oxide content dynamics (mg/100 g a.d.s.) in upper substrata layer in the background (A) and experimental (B) plots.

By the obtained experiment results, usage of intensive agromethods combined with high-quality planting material, big-size *Pinus sylvestris* plantings with ground clot, ensures the high survival rate and active growth of the planted conifers together with herbaceous layer formation. This is important because it causes simultaneous transformation of technogenic substratum and formation of soil as a forest ecosystem component. Soil development is behind plant community development; soil formation in morphological and chemical senses can be only after accumulation of some "critical" plant mass and its transformation products (humus) in substratum.

The popular opinion about the necessity of herb cover destruction while planting of trees in order to improve their growth (competition for nutrients) appeared to be questionable, especially on usage of big-size plantings.

This experiment has shown possibility of accelerated formation of forest ecosystem already on the first ("intensive") restoration stage. Further observations will allow for more recommendations on the optimized experiment.

6. Conclusion

The usage of two-stage "nature restoration" approach ensures active self-restoration of forest ecosystem in far-north taiga (on forest distribution border). It is vital to mention that "nature restoration" conception and its application in practice widen the traditional sense of the term "recultivation" not only by geographical point but also by understanding the functional interdependence between ecosystem components linked together by organic matter biological cycle.

Taking into consideration the serious ecological situation not only in the North, very significant is to revise our opinion on recultivation. Common sense of recultivation is returning lands into repeated agricultural usage. But nowadays there is the need to revise this term. In this view, "nature restoration" conception has a deep sense with its system approach aiming at accelerating restoration of nature ecosystems on disturbed areas exerting important biosphere functions. The system of "nature restoration" can be widely used, including tropical forests, however with some corrections in respect to particular climatic conditions. It is important to mention that oil-polluted lands' restoration at "intensive" stage requires usage of special purifying preparations followed by agrothechnical methods. In view of progressive development of economics, intensive "nature exploitation" should be accompanied by full-scale accelerated (managed) restoration of zonal ecosystems on disturbed areas, proportional to disturbance extent. Imbalance in "human-nature" system produces ecological critical situations (Ecological principles…, 2010).

In relation to the above-said, in newly-published work of K.S. Losev (2010) it says that only some part of natural ecosystems on Earth can be replaced by artificial ecosystems (agrarian or technogenic) without hampering the biological regulation mechanism, responsible for biosphere balance. He calls territories under such artificial ecosystems as ecological (economic) biosphere parts. The importance of natural ecosystems as a biosphere stability factor is now underestimated. The aftereffects cause a row of nature medium changes visualized in climate change, progressive environmental pollution, soil poorness, poor human's health, etc. There is a need of changing the understanding and treat the nature with more responsibility for conservation the environment and wild world in its initial diversity. One simple rule should be followed – whatever we took from nature (disturbed) we are to recover by means of additional work and financial expenses. This is the closest link between ecology and economics.

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17

Close to Nature Management in High-Mountain Forests of Norway Spruce Vegetation Zone in Slovakia

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1. Introduction

The Slovak Republic is one of the most forested countries in Europe. Forest covers about 20,000 km^2 (41%) of the total area of the country, a substantial part of which is occupied by the mountains of the Carpathian Arch (highest peak: Gerlachovsky Peak, 2655 m). Forests in Slovakia have commercial functions as well as functions of benefit to the public, for example: timber production, water management, soil erosion control, avalanche control, nature conservation, tourism, and aesthetic value. Many rivers that are important for neighbouring countries spring from the Slovak mountains; Slovakia is therefore sometimes called the roof of Central Europe.

The Slovak forests are classified according to dominating tree species into eight vegetation zones: 1. Oak (located on altitudes below approximately 300 m), 2. Beech–oak (about 200–500 m), 3. Oak–beech (300–700 m), 4. Beech (400–800 m), 5. Fir–beech (500–1000 m), 6. Spruce–beech–fir (900–1300 m), 7. Spruce (1250–1550 m) and 8. Mountain pine (over 1,500 m). One of the most important forest ecosystems in terms of benefit to the public is Norway spruce forests, located at an altitude of 1250–1550 m in the so-called Norway spruce vegetation zone (SVZ).

Mission of these forests is fulfilment of their important protective functions and specific social needs which govern also the way of their management. A substantial part of them are situated in protected territories pursuant to the Act on nature and landscape conservation in national parks or protected landscape areas. Thus forests of the SVZ fulfill in addition to ecological functions (water management, soil protective, avalanche control functions) also significant social functions, especially nature protective function and recreational function. By Greguš (1989) the mentioned forests with prevailing ecological and social functions fulfill in the best way all required functions in such a state, which corresponds to the state of stands not affected by human activity. The aim of management should be regeneration and preserving sustained forest existence with functionally effective stand structure of natural or primeval character with preserved self-regulating capabilities and good health condition. In this way the management and care about such forests is very effective as the treatments of manager are not required or they are minimal.

On the other side forest stands with substantially changed tree species, age and spatial structure, usually artificially established or disintegrating and disintegrated stands without natural regeneration cannot be retained for self-regulating processes without intervention. Required functionality can be secured in an acceptable time horizon only by means of reconstruction management measures with resultant creation of desired differentiated structure. In the forests with partially changed structure (semi-natural and natural) according to criteria of Zlatník (1976) only necessary correction measures should be carried out to direct their development toward target state.

According to Korpeľ (1990) we have only little experience with regulating the structure of forest stands with prevailing ecological and environmental functions, so there prevail considerable caution to complete passivity in this approach. Only few authors have been dealing with forest management of protection and special purpose forests in Slovakia. Because of such reasons, there is an urgent need for gathering of objective knowledge about the functionally desirable condition of these forests, patterns of their existence, development, risk factors that damage its stability and functionality as well as deepening the connections between forest management planning and work on patterns of dynamics of natural forests and nature friendly silviculture. This need led to the development of proposal presented in this paper focused on objectified practice of framework and detailed forest management planning depending on the degree of conservation of natural structure (naturalnee class) in forests with prevailing ecological or social functions.

The knowledge about the naturalness class of forest ecosystems is therefore of great importance. Its objective assessment is essential in the decision-making process dealing with forest utilisation and subsequent forest management. According to Hoerr (1993) and Schmidt (1997), naturalness is the most significant and widely applied criterion for the evaluation of nature conservation, and serves as a key tool in analyses and as a support in planning nature conservation measures. Unfortunately, the assessment of the forest naturalness class lacks the application of the complex objective procedures and methods not only in Slovakia, but also in other countries. This situation results from the facts that research has not provided the practice with any suitable methodological mechanisms that would enable its scientifically based and statistically provable determination. The same fact has been reported by Bartha and others (2006) who mentioned that in the last decades, a number of authors developed procedures for the assessment of forest naturalness. However, in all these schemes subjective elements have been included. The assessed values of the indicators depend partially on the expert judgement and partially on their estimation. In addition, the experts make decisions, which attributes are to be assessed and what their weight is. The classification of forest naturalness proposed by Zlatník (1976) for Slovakia is also primarily based on subjective expert evaluation of the extent of human influence on forests (Table 2).

In Slovakia, several authors dealt with the evaluation of forest naturalness using typological surveys (Šmídt 2002; Glončák 2007; Viewegh and Hokr 2003; Bublinec and Pichler 2001; Polák and Saxa 2005). These works are characterised by insufficiently complex evaluation of forest naturalness, since the authors primarily assess the suitability of tree species composition. For example, Glončák (2007) identified areas which require active management of forest ecosystems in protected areas by comparing real tree species composition with model using GIS tools. The disadvantage of this method is a high level of subjectivity needed for the development of the model of natural tree species composition. On the other hand, precise distribution of the values of naturalness of tree species composition in GIS environment is a practical advantage of this method. The proposal of the network Natura 2000 in Slovakia was based on the assessment of qualitative attributes of forest ecosystems using numerical quantifiers (Šmelko ex Polák and Saxa 2005; Šmelko and Fabrika 2007). However, this system assessed also features which were not directly connected to forest naturalness (e.g. forest health status, adverse external influences), and when evaluating the majority of attributes, artificial securing of forest status needed from the point of nature conservation was accepted. Hence, this system was more likely aimed at the assessment of nature conservation values than at naturalness of ecosystems.

Naturalness is also a pan-European indicator of sustainable forest management (SFM) belonging to the set of criteria and indicators for sustainable forest management (No. 4.3) proposed within the framework of the Ministerial Conference on the Protection of Forests in Europe (MCPFE (Ministerial Conference on the Protection of Forests in Europe) 2002). In this context, forests are divided into forests undisturbed by man, which encompass forests with least human interventions; modified natural forests, seminatural forests and plantations (productive and protective), which cover man-made (artificial) forests. According to the Global Forest Resources Assessment 2010 (FAO 2007), forests are distinguished into primary forests defined as naturally regenerated forests of native tree species with no clearly visible indications of human activities and with not significantly disturbed ecological processes; other naturally regenerated forests which are also regenerated naturally but the indications of human activities are clearly visible; and planted forests, where the trees established through planting or seeding prevail.

The degree of forest naturalness is assessed through various indicators, mainly: nativeness of species and genotypes, differentiation of stand structure (e.g. diameter frequency distribution, vertical and age structure, occurrence of deadwood, natural regeneration of forests and coverage of ground vegetation), as well as the existence and extent of human influence in particular forest ecosystems (e.g. occurrence of timber felling and forest re-establishment and the applied methods, soil scarification, existence of forest roads, recreational activities, grazing, forest damage). (e.g. McComb and Lindenmayer 1999; Müller-Starck 1996; Peterken 1996; Scherzinger 1996; Frank 2000). Some European countries assess forest naturalness at a sample plot level within the framework of their national forest inventories. However, such an assessment provides summary information on individual forest naturalness classes only at national or regional levels.

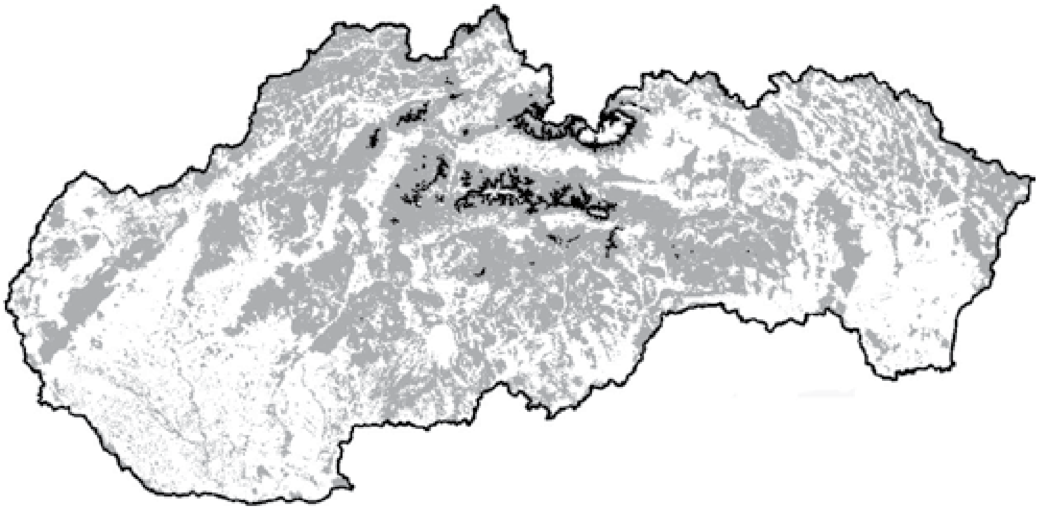
Since the assessment of forest naturalness is very demanding from the points of methodology, applied techniques and funding, its realisation is reasonable if this indicator is an essential element in a specific decisionmaking process. In forestry, forest naturalness is of the greatest significance in the decision-makings that deal with the designation of forests as protected areas, and as a tool for determination the need and the urgency of management (cultivation, tending) in such a way, which will secure the protection of biological diversity, ecological stability and other natural values in forest with prevailing ecological and social functions – protective and protected forests. For these purposes, it is required to perform detailed surveys of forest naturalness.

In contrast to the above-mentioned methods, our proposal (presented in this chapter) is based on more precise data gathering methods, it deals with exclusive relationship with forest naturalness, and allows to account for the specifications of particular biotopes. And above all, it presents the proposal of mathematical and statistical assessment, formulation and presentation of results. In this point the significance of this work has a great international value. It can be used as a basis for efficient application of differentiated methods of utilisation and subsequent forest management. It fits also for application of Assessment Guidelines for Protected and Protective Forests and Other Wooded Land in Europe (MCPFE 2003) which can be regarded as one tool for differentiated management of protected forests. In Guidelines, three classes of forests, in which biodiversity is the main management objective, were defined. Class 1.1 comprises the forests where no active direct human interventions can take place. In class 1.2, only minimum human interventions are permitted. Class 1.3 comprises the forests designated for biodiversity conservation through active management.

2. Characteristics and main problems of forests in the Norway spruce vegetation zone

In the SVZ, total annual precipitation ranges between 1000 and 1300 mm, mean annual temperature ranges between 2°C and 4°C, and the vegetation period lasts 70–100 days. The SVZ forests cover about 40,000 ha or 2% of the total forest area and are located in the central and northern parts of the country, some of them in national parks.

The original SVZ forests were made up mostly of sparse stands or groups of trees with Norway spruce as a dominant species. Some forests also have European larch, European beech, mountain ash, and individual stands of dense mountain pine. Silver fir, cembra pine, and sycamore maple can also be found. The most frequent forest type groups (original species composition before human influence) are *Sorbeto-Piceetum* (mountain ash-spruce) and *Lariceto-Piceetum* (Larch-spruce).



Similar forest types occurred in other European mountain ranges (e.g. Alpine and Carpathian regions in Romania, Ukraine, Poland, Austria, Germany, Switzerland, France and Czech Republic.

Fig. 1. Distribution of spruce vegetation zone over the area of Slovakia.

The age, diameter, and height structure of the forests in SVZ should be highly (horizontally and vertically) diversified to ensure the fulfillment of important ecological and social functions. Their static stability and the continuous influence of forest stand structure on forest functions are significant. Some authors (Korpeľ 1978, Turok 1990, 1991) stated that in spite of the existence of the trees that live to a greater age, the upper age of the mountain Norway spruce primeval forests is approximately 250 years. Almost identical forest types are spread over the whole Alpine and Carpathian region, less frequently they can be found also in other European mountain ranges (Palearctic habitat 42,21: Alpine and Carpathian subalpine spruce forests).

In spite of significant ecological and social functions of these forest ecosystems, their actual condition is not favourable. Moravčík and others (2005) presented the following reasons of the current, not always favourable state of the forests:

- Natural conditions: the SVZ forests are situated at an elevation from approximately 1250 up to almost 1600 m above sea level on long and steep slopes; growing in shallow, skeletal, drying-out (mainly due to the climate change), and nutrient-poor soils; on the sites with high potential and real soil erosion; on remote and technologically inaccessible locations.
- Climatic conditions: extreme temperature, moisture, and wind conditions; frequent intensive precipitation with occurrence of storm rainfalls, which is in the last years intensified by the climate change; and short vegetation season (70 to 100 days).
- Another negative ecological factor significantly influencing the health of high-mountain forests is unfavourable climatic conditions (lack or unsuitable distribution of annual precipitation, temperature extremes, etc). Formerly, the Slovak high-mountain forests were considered to have sufficient precipitation and favourable soil moisture. However, recent studies showed a dramatic change in the water regime in mountain forest soils, especially in sparse spruce stands. Soil acidification and lack of soil moisture are considered the most negative factors — worsening, or on some sites even disabling, natural regeneration of high-mountain forests.
- Monitoring of forest health in certain areas within the SVZ showed that about 90% of SVZ forest can be considered to be affected by air pollution. A rise in ozone concentration with altitude has been proven within the SVZ. Furthermore, a significant decrease of soil pH values was recorded (0.5–1.0 unit since the 1960s). Although sulphur and nitrogen emissions were considerably reduced during the past two or three decades, these substances are still accumulated in the soils.
- Age, vertical and horizontal stand structure of a large proportion of these forests is altered and little/unsufficiently differentiated. This state is the result of the strong colonisation pressure and clear-cutting management in the past.
- A significant proportion of these stands are over-mature (average age 105 years), disintegrating or disintegrated; average stocking 0.63 is significantly lower than the target stocking (0.7).
- Influence of injurious agents. The forests of SVZ are exposed to a complex of negativelly influencing factors, particularly at the upper limit of their occurence. This refers to the influence of air pollution in conjunction with natural factors (insects, fungi, wildlife), with climatic effects (windthrows and snow breakage), and with the impact of tropospheric ozone.

- These forests have been seriously damaged by storms. Trees damaged by wind or physiologically weakened by climatic extremes create suitable conditions for bark beetle outbreaks. Whereas in the past such outbreaks occurred only up to 1000 m, presently this limit is at 1300 m and in certain areas even at the timberline. All these factors cause weakening or even collapse of forest ecosystems. Forest stands become sparse and fragmented. This phenomenon is most evident on mountain ridges at 1300–1600 m.
- Long-term tendency of leaving forests in SVZ without any treatments (since the first half of the last century), which was caused by the fact that their management was unprofitable if assessed solely from the point of management costs and returns obtained from selling the wood. Considering lower wood quality and long extraction distances, both tending and regeneration measures are loss-making.
- Lack of objective knowledge about the functionally desired state of forests in SVZ and about the regulation or management of the structure of the stands with prevailing ecological and social functions. This has resulted in considerable cautiousness or even in passivity in their management (Korpeľ 1989).
- The attitude of state administration of nature conservation and some organisations of nature conservationists, who support a so-called passive conservation, i.e. against any treatments of these forests regardless their altered origin and their actual state.

3. Objectives, materials and methods

The purpose of this scientific paper is to improve the practices of forest management and tending of forests with particularly ecological and social functions on the example of SVZ. It contains development of objectified processes of forest tending according to their naturalness. The primary instruments of systematic forest tending in Slovakia are models of forest management (Fig. 2) that determines for specific natural conditions and stand conditions: management targets, basic management decisions and forest management principles. Our primary objective was to develop differentiated models of forest management for conditions in SVZ forests with added differentiating measure – naturalness class, which has not been applied systematically in the models so far.

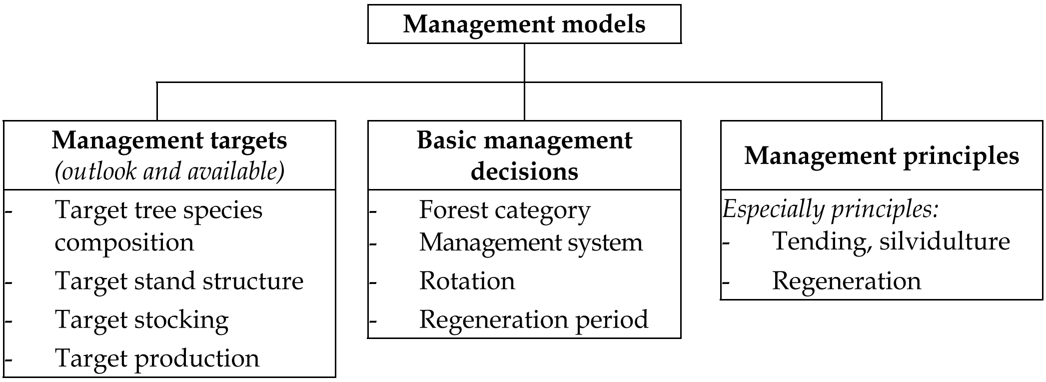


Fig. 2. Framework classification and content of management models.

For mentioned research we selected the SVZ ecosystem because of these reasons: 1) This forest community is very valuable but also vulnerable with significant ecological and social functions including nature-conservation functions. 2) Current condition of these forests (see previous section) is characterized by inappropriate structure of forest stands on a considerable part of them, exposure to harmful agents and adverse changes of the environment, which cause the urgent need to implement the measures to restore and improve their functional efficiency. 3) Because extensive national and international scientific activities have been carried out in the forests of SVZ (e.g. 4-year research project at the Zvolen Forest Research Institute dealing with methods for high-mountain forest management based on principles of sustainable development; S4C Initiative, Mountain Research Initiative, International Scientific Committee on Research in the Alps ISCAR).

Greguš (1989) formulated the general principles of forest management as follows: The mission of forest management should be: (1) achieving the maximum benefits from forest, (2) their permanent provision, (3) minimum risk, and (4) efficiency of providing these benefits. Once formalized these principles to the conditions of SVZ forests, in terms of the forest tending it is essential to achieve:

- The maximum observation of ecological and environmental functions, in particular through the functionally efficient forest stand structure, equivalent or approaching the state of natural anthropicly unaffected stands.
- Ensuring the permanent existence of the forest with good health condition and with corresponding forest stand structure according to which stands are capable of self-regulatory processes.
- Minimal risk of benefits in the given natural conditions through healthy, statically and ecologically stable forests with high-differentiated structure.
- Effectiveness of provision of benefits, through conservation and cultivation of natural forests to primeval forests with preserving their self-regulating features, which will reduce intervention of the forest manager to a minimum.

From the above-mentioned principles, the passive approach for SVZ forests with changed forest stand structure is unacceptable, respectively retaining them without the intervention (the self-development), because there is a risk of their subsequent destruction in large areas. The time horizon of the natural return into the stage of climax forest with the desired functionality through the stages of pioneer and intermediate forests is as a result of the passive approach unacceptable.

Proposing the methodology of solving the problem area was based on the following principles:

- Due to variety of natural conditions and the SVZ stand conditions, forest management models should be differentiated according to:
  - The naturalness class of forest stands (primeval forests, natural and semi - natural forests, man-made forests) and development stages of nature friendly forests.
  - Specific natural conditions characterized by present groups of forest site types (GFT) *Sorbeto-Piceetum* (SP) *Lariceto Piceetum* higher degree (LP hd) *Cembreto-Piceetum* (CP) *Acereto-Piceetum* higher degree (AcP hd) *Fageto Piceetum* higher degree (FP hd) and *Pineto-Laricetum* higher degree (PiL hd).

  - Height zones of SVZ (lower zone – to an altitude of about 1400 m and high zone – from about 1400 m up to the upper limit of tree vegetation).
- With regard to the mission of SVZ forests, the basic objectives of management are the following: the target tree species composition, target stand structure and the target stocking.
- Available management targets should be proposed for man-made forests in which the target status can not be achieved during one rotation period.
- Identify the need and urgency of the implementation of forestry measures in forests with different naturalness.

To achieve planned objectives the following procedure was chosen:

- To obtain and evaluate own empirical material from the permanent research plots (PRP) established, so that:
  - each of the PRP represents a particular naturalness class,
  - PRP represents significant typological units: groups of forest site types and the both vertical zones (hight zones) (upper and lower) in SVZ,
  - they were etsablished in the forest areas with a significant presence of SVZ.
- To find a detailed information on natural conditions on PRP and on forest stand condition of SVZ forests using indicators appropriate for expression of condition of structurally differentiated forests – according to their naturalness.
- Deduce the average values of the indicators on forest condition in the PRP classified by the aggregated naturalness classes and development stages so that they could be used retroactively in forest management practice to identify the given forest types and to precise and add the existing management models.
- To use and to process data available from literature and documents of Forestry Information Centre.

We used data of detailed analysis of SVZ forest relized on the basis of data from 122 PRP and published knowledge from authors dealing with the issue of mountain forests as a background material to provide the above-mentiond activities. Empirical material was collected in PRPs by preferential and non-random sampling. The PRPs were established as circle plots of a size of 100-1,000 m^2 in order to meet the prerequisite that a minimum of 25 trees occur within each plot. The PRPs were localized using the global positioning system (GPS). The methodological intention was to establish PRPs in such a manner that detailed information about the natural and stand conditions (inclusive of forest naturalness) of forests in SVZ could be obtained. In the process of the methodology preparation, indicators suitable for the description of the state of structurally differentiated forests that were assumed to be related to the forest naturalness class were identified and proposed.

To find out natural conditions we monitored on PRP the status of these indicators: exposure, slope, altitude, relief, geological parent rock, thickness and form of humus layer, surface skeleton, forest type, soil type and the soil was also sampled. To characterise the state of the forest stocking and canopy were monitored, basic mensurational parameters were taken and development stage and naturalness class were determined on each PRP. All trees were localised as regards position and visualised by means of *Stand Visualisation System* (SVS), version 3.36. Then damage to trees, loss of assimilatory organs and social status were determined, crown length was measured and a necessary number of bores for age analyses was taken. Assimilatory organs were sampled for laboratory analyses. Ground vegetation was assessed as well as conditions for natural regeneration of Norway spruce and existing natural regeneration. The database system *„Mountainous Forests“* was constructed in MS Access 2000 for the processing and assessment of empirical material. An overview of the classification of 122 PRP according to natural and stand conditions under which they were established (forest eco-region, group of forest site types, naturalness classes and elevation) is given in Table 1.

Aggregated naturalness classes, n / %							
Primeval forest			*Natural forest*			*Man-made forest*	
17/13.9			94/77.1			11/9.0	
Of it the stage of			Of it the stage of			Of it the phase of	
Growth	Optimum	Decline	Growth	Optimum	Decline	Tending	Regeneration
2	9	6	32	36	26	2	9

Forest eco-region, n / %							
Veľká Fatra		Poľana		Nízke Tatry		Vysoké Tatry	
7/5.7		12/9.8		85/69.7		18/14.8	

Group of forest site types, n / %			
SP, LP hd	AcP hd	FP hd	CP
84/68.9	22/18.0	9/7.4	7/5.7

Elevation (meters above sea level), n / %					
Up to 1,350	1,351–1,400	1,401–1,450	1,451–1,500	1,501–1,550	1,551 and above
14/11.5	21/17.2	29/23.8	32/26.2	19/15.6	7/5.7

SP – *Sorbeto-Piceetum*, LP hd – *Lariceto-Piceetum* higher degree, AcP hd – *Acereto-Piceetum* higher degree, FP hd – *Fageto*
Piceetum higher degree, CP – Cembreto-Piceetum.

Table 1. Data structure with regard to natural and stand conditions.

The classification of forest into forest naturalness classes in each PRP in the field was based on the categorisation of Zlatník (1976) (Table 2). The assessed forest naturalness classes resulted from the detailed, though subjective evaluation of the forest status. Naturalness was assessed as a rate of human influence on a forest on the base of visual features that indicate human interventions (inclusive of forest management), which affect tree species, spatial and age structure (Fleischer 1999) of forests in SVZ. Each PRP was assigned one of forest naturalness class from the scale A to G (Zlatník 1976).

Forest naturalness classes (NC) by Zlatník (1976) were further aggregated into three degrees: Primeval forest, Natural forest, Man-made forest (Moravčík and others 2003; Moravčík and others 2005; Moravčík 2007a, b) prior to data processing. This was done due to insufficient number of plots in the degrees of the finer scale from A to G, and also from the reason of the need their practical application. The aggregated degrees of naturalness were complemented by the classification according to basic development stages defined by Korpeľ (1989) (Table 3).

NC	Name	Signs of anthropic effect; signs of stand structure
A	Primeval forest	without any effect of human activity
B	Natural forest	appearance of primeval forest without obvious signs of anthropic activity, possible selective felling in the past, natural forests affected by natural disasters left to natural development are included as well
C	Semi-natural forest	natural tree species composition, altered spatial structure due to extensive human activity
D	Predominantly natural forest	natural signs predominate over anthropic signs
E	Slightly altered forest	forest with natural as well as anthropic signs, the latter ones prevail
F	Markedly altered forest	forests only with anthropic signs but of natural appearance
G	Completely altered forest	forest stand only with anthropic signs of its origin or formation

Table 2. Criteria for the classification of stands by the naturalness classes.

1 – primeval forests (A)	2 – natural and semi-natural forests (B, C)	3 – man-made forests (D-G)
11 – in the stage of growth	21 – in the stage of growth	34 – tending phase
12 – in the stage of optimum	22 – in the stage of optimum	35 – regeneration phase
13 – in the stage of decline	23 – in the stage of decline	–

Table 3. Overview of aggregated naturalness classes and their classification by development stages.

These development stages of naturalness classes 1 and 2 in SVZ can be characterized as follows:

- Stage of growth – this stage is characterized by the largest diameter, height and area (vertical and horizontal) differentiation of stands. Canopy is graded to vertical, with a significant participation of trees in the middle and lower layer. There is characterized high vitality of trees and slight tree mortality in upper layer. Smaller gaps as results of tree falling from the previous cycle or accidental death of a strong tree from a new cycle are rapidly canopying.

- Stage of optimum – due to a longer life than height growth, the forest adjusts in height despite the large all-age. The maximum growstock is reached. Characteristic is: small number of trees per area unit and loss of foliation. Construction of stand is graded in height
- Stage of decline – overaged trees in good health condition begin to die in numbers at the end of stage of optimum and the forest is getting to the stage of decline. Growing stock rapidly decreases due to mortality of numerous large trees and is distributed very irregularly. Squads and groups of trees from the old generation are altered by gaps or incoming forest regeneration. Individuals of natural regeneration from the end stage of optimum merge into a continuous regeneration. Usually, there is regeneration of climax (target) tree species, only after fast (calamity) damage also the regeneration of preparatory tree species.

Characteristics of the development stages of man-made forests in SVZ:

- Forests in a period of forest tending - Horizontal involved, even-aged mostly spruce stands in the growth phase of cultures, providing cultures, youg wood, pole young forest and pole mature forest that require forest tending interventions.
- Forests in the regeneration period – even-aged spruce stands in various stages of thinning, or even locally disrupted, in different ages and unstocked areas that require regeneration.

Considering the structure and the type of data stored in the database system ''Mountainous forests'', a number of indicators that were assumed to be related to a degree of forest naturalness were proposed. In total, 25 different indicators of naturalness of forest ecosystems in SVZ were quantified, while tree species diversity was represented with 10 indicators, and structural diversity with 15 indicators (Table 4a, 4b). Tree species diversity was quantified with five indices of species richness, two indices of species heterogeneity, and three indices of species evenness. The indices of species heterogeneity were calculated from the proportion of basal area of particular tree species from the total basal area in a sample plot. The indicators of structural diversity reflect the diversity of structural elements of a forest ecosystem in horizontal and vertical directions. From 15 proposed structural indicators, two characterise vertical diversity (number of tree layers determined on the base of the sociological position of trees, and ''*Arten Profil*'' (species profile) index (Pretzsch 1996), while horizontal diversity is quantified by an aggregation index (Clark and Evans 1954). The remaining structural indicators are relatively simple and easy to be quantified, and are also related to static stability, stand density, and site quality. The average ratio of crown length to tree height, and the average ratio of tree height to tree diameter were calculated from the trees ranked in 1st to 3rd sociological layers. The indicators describing the coverage of herbs, grasses, mosses and lichens, shrubs and subshrubs; the coverage of phases describing the conditions for natural regeneration (juvenile, optimal, senile); the coverage of natural regeneration were visually estimated in the field and are given in relative values (%) (Moravčík and others 2005).

Structural diversity			
Indicator	**Formula**	**Units**	**Reference**
Number of tree layers (*Z*)	$Z = j$	DIM	
Arten profil index (*A*)	$A = -\sum_{i=1}^{S}\sum_{j=1}^{Z} p_{ij} \cdot \ln p_{ij}$	DIM	Pretzsch 1996
Aggregation index (*R*)	$R = \frac{\frac{1}{M} \cdot \sum_{i=1}^{M} r_i}{0.5 \cdot \sqrt{\frac{M}{A}}}$	DIM	Clark and Evans 1954
Coefficient of variation of tree diameter (*CV_D1.3*)	$CV\_D1.3 = \frac{\bar{d}}{SD_d}$	%	Šmelko 2000
Coefficient of variation of height (CV_H)	$CV\_H = \frac{\bar{h}}{SD_h}$	%	Šmelko 2000
Average ratio of crown length to tree height (*AM_K*)	$AM\_K = \frac{\sum_{i=1}^{M} \frac{cl_i}{h_i}}{M}$	%	Šmelko 2000
Average height / diameter (*h*/*d*) ratio (*AM_HDR*) (Slenderness quotient)	$AM\_HDR = \frac{\sum_{i=1}^{M} \frac{h_i}{d_i}}{M}$	DIM	Šmelko 2000
Coverage of grasses (*PK_T*)	$PK\_T = p_i$	%	
Coverage of herbs (*PK_B*)	$PK\_B = p_i$	%	
Coverage of mosses and lichens (*PK_M*)	$PK\_M = p_i$	%	
Coverage of shrubs and subshrubs (*PK_K*)	$PK\_K = p_i$	%	
Coverage of juvenile regeneration stage (*PK_JS*)	$PK\_JS = p_i$	%	
Coverage of optimum regeneration stage (*PK_OS*)	$PK\_OS = p_i$	%	
Coverage of senile regeneration stage (*PK_SS*)	$PK\_SS = p_i$	%	
Coverage of natural regeneration (*PK_NR*)	$PK\_NR = p_i$	%	
Deadwood volume (*MOD*)	$MOD = \frac{\sum_{i=1}^{m} v_i}{A / 10000}$	m^3/ha	

Table 4a. Calculated indicators of structural diversity of forest ecosystems.

Tree species diversity				
Category	**Indicator**	**Formula**	**Units**	**Reference**
Species richness	Index N0 – living trees	$N0 = S$	DIM	Hill 1973
	Index N0 – mosses and lichens	$N0 = S$	DIM	Hill 1973
	Index N0 – shrubs and subshrubs	$N0 = S$	DIM	Hill 1973
	Index R1	$R1 = (S\text{-}1)/\ln(M)$	DIM	Margalef 1958
	Index R2	$R2 = S/\sqrt{M}$	DIM	Menhinick 1964
Species heterogeneity	Index λ	$\lambda = 1 - \sum_{i=1}^{S} p_i^{2}$	DIM	Simpson 1949
	Index H´	$H` = -\sum_{i=1}^{S} p_i \cdot \ln(p_i)$	DIM	Shannon and Weaver 1949
Species evenness	Index E1	$E1 = H`/ln(S)$	DIM	Pielou 1975, 1977
	Index E3	$E3 = (e^{H`}-1)/(S-1)$	DIM	Heip 1974
	Index E5	$E5 = ((1/\lambda)-1)/(e^{H`}-1)$	DIM	Hill 1973

Legende for Tables 4a and 4b:
S – number of species; M – number of individuals, number of living trees in a sample plot; m – number of deadwood individuals (stumps, lying deadwoood); pi – probability, proportion of ith species or category in a sample plot; pij– proportion of trees of ith tree species in jth stand layer; Z – number of layers – stories of the stand; ri – distance between ith tree and its closest neighbour (m); A – area of a sample plot (m2); d – tree diameter; SDd – standard deviation of tree diameters in a sample plot; cl – crown length; h – tree height; v – volume.

Table 4b. Calculated indicators of tree species diversity of forest ecosystems.

4. Results and discussion

4.1 Management targets

4.1.1 Target stand structure

To derive the target structure we used data from literature and the values of selected indicators of spatial structure obtained from the assessment of empirical material, namely from PRP classified into the highest naturalness class (primeval forests) for the derivation of outlook target structure and into the 2nd naturalness class (natural and semi-natural forests) for achievable target structure. The results of testing statistical significance of the differences in diameter variability, height variability, slenderness quotient, crown length (in %) between individual naturalness classes showed to be statistically significant (*) up to highly significant (**). But mostly no statistical significant differences were confirmed between individual altitudinal zones (lower zone – *lz* and upper zone – *uz)* in the same naturalness classes.

The objective is to achieve and keep the structure of forest stands with markedly differentiated age, diameter and height (horizontal and vertical), which ensures the fulfillment of their significant protective (ecological and social) functions. Static stability of these forest stands is of primary importance. Their target structure is not connected with a single moment of the forest stand life. A permanent effect of target structure mainly on soil protective function (soil erosion control, avalanche control) and water management function is desirable.

The threshold values of selected indicators for target stand structure were derived from data collected on the PRP classified in the 1st naturalness class (primeval forest). They characterize the most original SVZ forest stands and were therefore considered as a benchmark for the desired outlook stand structure. Primeval forests have 3 developmental stages—growth, optimum, and disintegration—characterized by adjusted average values of the following indicators: degree of diameter dispersion (to assess tree diameter variability); share of canopy level (to assess tree height variability); ratio between crown length and tree height, and tree height and tree diameter; and mosaic of stand clusters.

Indicator		**1st natural-ness class**	**Development stage (adjusted average values)**		
			Growth	**Optimum**	**Decline**
Tree diameter variability (Sx%)		50 ± 15	60	45	50
Degree of diameter dispersion		3	3	2–3	3
Tree height variability (Sx%)		40 ± 20	50	30	40
Share of canopy level (%)	Upper	55 ± 15	45	65	60
	Middle	25 ± 15	30	25	20
	Downer	20 ± 15	25	15	20
Crown length / tree height (%)		75 ± 10	80	75	75
Tree height / tree diameter (slenderness quotient)		0,6 ± 0,1	0,55	0,60	0,55
Texture:	mosaic of stand clusters and groups of the area 0.5 hectare max.				

Table 5. Model of outlook target structure derived from the values of indicators of forest state on permanent research plots classified into the 1st naturalness class.

However, it will not be possible to reach the desired stand structure even in the next generation because of large areas of artificially formed stands where management has been neglected. The characteristics of a realistic (achievable) target stand structure were therefore derived from the data representing the 2nd degree of naturalness (natural forest).

Indicator		2nd naturalness class	Development stage (adjusted average values)		
			Growth	Optimum	Decline
Tree diameter variability (Sx%)		35 ± 15	45	30	35
Degree of diameter dispersion		2	2-3	2	2
Tree height variability (Sx%)		30 ± 15	40	20	30
Share of canopy level (%)	Upper	65 ± 20	50	75	65
	Middle	20 ± 15	30	15	20
	Downer	15 ± 15	20	10	15
Crown length / tree height (%)		70 ± 10	75	67,5	72,5
Tree height / tree diameter (slenderness quotient)		0,6 ± 0,1	0,65	0,6	0,55
Texture:	area form of structural types mixture (above 0,5 ha)				

Table 6. Model of achievable target structure derived from the values of indicators of forest state on permanent research plots classified into the 2nd naturalness class.

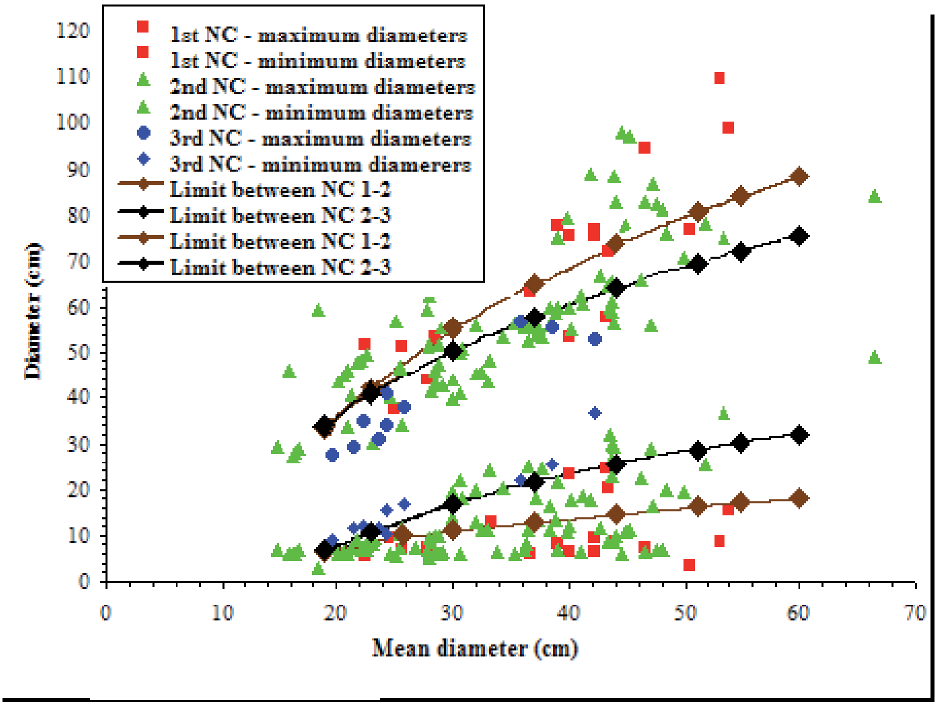


Fig. 3. Graph of diameter variance for Norway spruce in the SVZ in dependence on the naturalness classes.

To simplify the evaluation of diameter variability it is possible to use the degree of diameter variance as a practically usable indicator. In dependence on the mean diameter given on *x* axis the values of minimal and maximal diameter (*y* axis) of each PRP were illustrated. Minimal and maximal values of diameters were separately equalled graphically for all three naturalness classes. Equalling was made by means of logarithm curves. As the obtained curves represented only average values for the naturalness classes, the curves of limit values between the 1st and 2nd naturalness class, and the 2nd and the 3rd naturalness class were put between them. In this way 4 limit curves were constructed (Fig. 3) determining the variances of diameters for all three naturalness classes. The highest degree of variance 3 corresponds to the 1st class of naturalness, the 2nd degree of variance corresponds to the 2nd class of naturalness and the lowest degree of variance 1 corresponds to the 3rd class of naturalness.

4.1.2 Target stocking

As a rule stocking is defined as an indicator of the growth space utilization by a forest stand. Traditional way of its determination is the share of considered trees and the sum of considered trees and missing trees to the full stocking. According to Greguš (1976) target stocking is the stocking when the stand fulfils the determined functions in the best way. In commercial forests it is mainly production of wood and simultaneously fulfillment of other functions; in protective forests mainly fulfillment of publicly beneficial (ecological and social) functions (Midriak 1994). Greguš (1989) considered target stocking as an important component of management objectives especially because it informs us, though indirectly, but clearly about the fulfillment of desired functions and about the phase of regeneration. Especially by a change in stocking the manager can influence the development in forests. Derivation of target stocking is therefore a significant prerequisite to ensure professional care of forests, including those in the SVZ with the objective of achievement of their maximum functional utility. Assmann (1961) defined these concepts: optimum stocking with optimal stand basal area in which the forest stand produces maximum volume increment; maximum stocking with maximum stand basal area formed by living trees; critical stocking with critical stand basal area in which the forest stand still produces 95% of its maximum increment. In Slovakia mainly these authors dealt with issues related to target stocking: Halaj (1973, 1985), Faith and Grék (1975, 1979), Korpeľ (1978, 1979,1980), Šmelko et al. (1992), Korpeľ and Saniga (1993), Kamenský et al. (2002), Fleischer (1999), Moravčík et al. (2002).

Target stocking in the forests of the SVZ was derived on the basis of an original procedure as optimum stocking with harmonization of the requirements for the fulfillment of ecological functions, securing static stability and the existence of adequate conditions for formation and development of natural regeneration. To achieve this objective our own empirical material (122 PRP) was analyzed. Research was aimed at the investigation of relations between stocking and indicators (Table 4a) of static stability (slenderness coefficient and ratio of crown length to tree height), conditions for the formation and development of natural regeneration, coverage of natural regeneration and coverage of ground and non-wood vegetation in natural and semi-natural stands of the SVZ.

- *Ground vegetation* was found out as the percent of coverage of non-wood and shrubby vegetation on PRP; percent of coverage was determined in the groups: grasses, herbs, mosses and lichens, shrubs and semi-shrubs and total coverage.
- *Young regeneration and thicket* on PRP were found out as the percent of coverage by tree species in respective development stages; current year seedlings, natural seeding being high 50 cm, advance growth being high 1 m and thicket within diameter $d1.3 < 6$ cm were distinguished.

- Conditions for natural regeneration of the Norway spruce were evaluated according to Korpeľ (1990), Vacek et al. (2003) in three phases (juvenile, optimal and senile).
  - *Juvenile (early/premature) phase* – it is characterized by the almost closed canopy of stand with a marked microclimate buffering climatic extremes and by low coverage of ground vegetation. In the forests of the SVZ the soil is usually covered by a layer of forest floor, and low herbs and mosses with total coverage 30–40% prevail in the ground vegetation. The parent stand is capable to ensure natural seeding of the plot being regenerated by a sufficient amount of seeds that can germinate but the conditions of the stand environment are not suitable for the growth of natural seeding and formation of advance growth.
  - *Optimal phase* – it is characterized by the relatively open canopy, and thus by an increased access lof light, warmth and moisture to the soil surface. Climatic extremes are alleviated by the stand. Thin ground vegetation with prevalence of herbs over grasses occurs on the whole plot. In the forests of the SVZ this phase is frequently characterized also by the whole-area occurrence of mosses (more than 20%). Conditions of the stand environment enable the stages of germination, natural seeding, as well as advance growth on the same plot.
  - *Senile (late) phase* – it has the markedly open canopy of parent stand that enables almost a full access of light, warmth and moisture to the soil surface. In the dense ground vegetation grasses and high herbs prevail markedly. Ferns can be dominant in the stands of the SVZ at northern exposures as well. Conditions for the stages of seedling germination and their growth are not favourable any more. Providing there are natural seedlings or advance growth in the stand they can develop successfully.

Actual stocking on PRP was analyzed in the forests of the SVZ in relation to the degrees of naturalness classes, development stages, altitude and groups of forest site types. Average stocking on PRP established in primeval forests reached the value 0.61, in natural and semi-natural forests 0.62 and in artificial man-made forests 0.76. The lowest values of stocking were found in the decline stage (0.52 in NC 1 and 0.45 in NC 2). In the growth stage these values are 0.55 in NC 1 and 0.65 in NC 2. In the stage of optimum the values 0.69 and 0.72 were found. In average data on stocking there were not any statistically significant differences between stocking in the upper and lower altitudinal zone. Forests of the SVZ are permanently naturally open and thin by their appearance, towards the timberline the stands are thinner. Along the timberline they have a character of thin park forests.

In extreme site conditions the density of stands is lower. Trees in extreme conditions need a relatively greater growth area. Using the traditional way of stocking determination we estimate its value to be lower than 1.0 though it is frequently only the result of natural growth processes not influenced by man or injurious agents and its higher value under the given conditions (with regular spacing of trees) is not possible. In this case reduced clearing is unproductive clearing. Its reforestation is impossible. It is a part of the natural growth process and natural stocking of stands below the timberline also according to Assmann (1961).

Optimal stocking in the forests of SVZ was derived so as it would correspond in the best possible way to requirements for the fulfillment of ecological functions (soil protection, hydrological function), securing static stability and the existence of conditions for the formation and development of natural regeneration. It follows from the analysis of the relation between the ratio of crown length to tree height and stocking that with lower stocking the ratio is increasing, up to stocking about 0.7. Further drop of stocking is not reflected significantly in the increase in the ratio (Fig. 4).

It follows from the analysis of the relation between slenderness coefficient and stocking that with lower stocking the value of slenderness coefficient is lower as well. It drops to the value about 0.7. Further drop of stocking is not reflected significantly in the drop of the slenderness coefficient (Fig. 5).

It follows from the analysis of the relation between the conditions for natural regeneration and stocking that the most suitable combination of all three phases of preconditions for natural regeneration (juvenile, optimal, senile) is with stocking 0.7 (Fig. 6). At this value there are the most suitable conditions for the formation and development (advance) of natural regeneration as well as adequate coverage of ground and non-wood vegetation (Fig. 7).

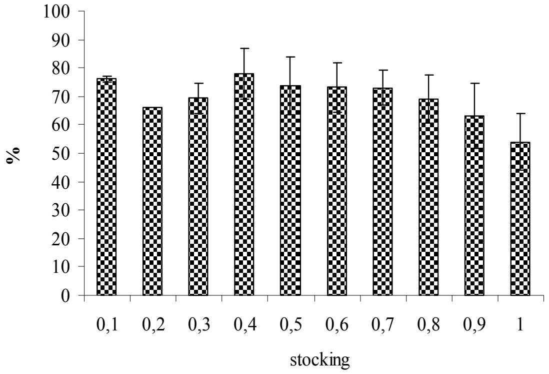


Fig. 4. A relation between the ratio of crown length to tree height (%) and stocking.

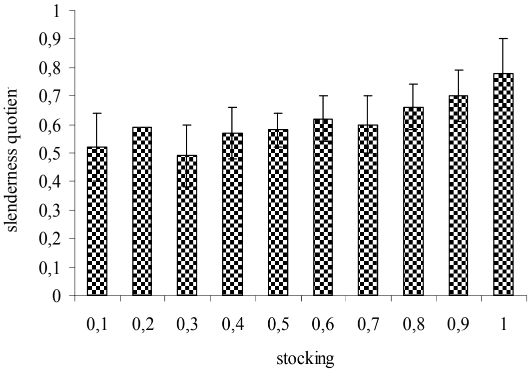


Fig. 5. A relation between slenderness coefficient and stocking.

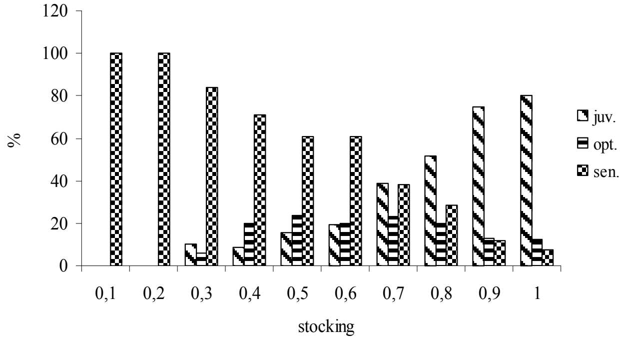


Fig. 6. A relation between natural regeneration phases (%) and stocking.

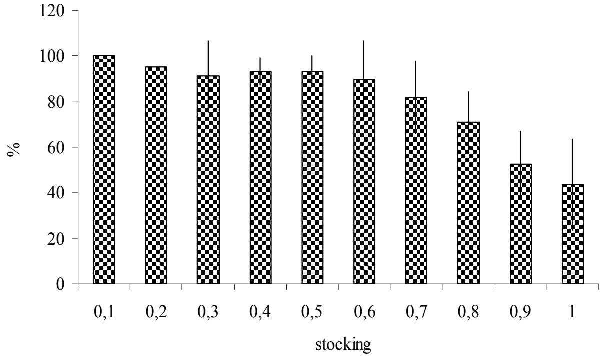


Fig. 7. A relation between ground and non-wood vegetation coverage (%) and stocking.

The optimum values of stocking with regard to the state of evaluated indicators are for stocking 0.7 or 0.7+. It follows from this finding that on average target stocking is about 0.7 for the forests of SVZ. It can differ slightly in dependence on the altitudinal zone or group of forest site zones. More significant differentiation can occur in dependence on the development stage but the objective of the care of forests of SVZ is to prevent the occurrence of the development stage "decline" on large areas. It is a desirable permanent (continuous) effect of this indicator of stand structure on forest functions. We can consider the given stocking rounded to 0.7 as Assman's natural stocking of the stands of SVZ below the timberline being evaluated by a practical manager with a traditional attitude. The values of stocking lower than 0.7 but within 0.7 determine the area share to complement or regenerate the stand.

4.1.3 Target tree species composition

Norway spruce has an absolute dominante in autochtonous stands of SVZ. It is the only tree species, which bears the harsh and extreme existential conditions of this vegetation zone. Therefore, spruce is the doninant tree species in current stands. Current tree species composition in groups of forest site types does not differ from the desired target tree species composition (such as in the sixth vegetation zone, or in other); on the contrary, it is very similar in the main tree species.

In neighbour lower sixth vegetation zone in the original stands of individual forest site type groups tree species as spruce, fir and beech (possibly along with other coniferous and broadleaved tree species such as pine, larch, sycamore maple, ash, elm) formed various mixtures. Currently, tree species composition is altered in a large part of these forests. It consists of spruce monocultures and often is different compared to desired target diverse tree species composition. This has led to introduction of the so-called achievable tree species composition into forest management planning (achievable target), which reflects the current, altered tree species composition and it disintegrates (into the phases) the complex process of a desired target status into shorter periods, respectively to the possible achievable change in the current rotation period. This process is not necessary in SVZ with respect to closely existing and target tree species composition.

Table 7 shows the target tree species composition for groups of forest site types of SVZ. Selection and shares in forest site type groups is based on the original tree species composition as introduced by Zlatník (1956, 1957, 1959). There is an expected arborescent growth of spruce, in LP also of larch and swiss pine. Other tree species may have a height of a tree or shrub, according to altitude and locality conditions of a specific site. Desirable are all original, also rarely growing shrub tree species. Representation of mixed tree species can be provided by permanent, constant cluster and individual natural regeneration, or filling, in the emerging stand spaces.

Forest site type groups	**Target tree species composition, %**	**Detailed specification considering the height degree**
SP	Spruce 70 – 90, rowan, Silesian willow, betula carpatica, sallow, dwarf pine 10 – 30	In the higher degree towards the upper forest limit (which is mostly irregular and continuous), dwarf pine should be more applied in tree species composition for a continuous transition to 8. vegetation zone.
LP hd	Spruce 70 – 90, larch, swiss pine, rowan, rowan, Silesian willow, betula carpatica, sallow, dwarf pine 10 – 30	In the higher degree towards the upper forest limit (this has a continuous transition), individually and cluster mixed swiss pine, larch and dwarf pine should be more applied in tree species composition.
AcP hd	Spruce 70 – 90, sycamore maple, rowan, beech, Silesian willow, dwarf pine 10 – 30	Beech can be applied in a lower degree (referring to 6. vs), there is a lack in higher degree, to apply more dwarf pine towards the upper forest limit.
FP hd	Spruce 70 – 90, beech 0 – 10, white beam, rowan, larch, Silesian willow, dwarf pine 10 – 30	Beech mainly in a lower degree, there is a lack in higher, to apply more dwarf pine towards the upper forest limit.
PiL hd	Larch, dwarf pine, spruce, fir, pine, white beam, Silesian willow (individual tree species on rocks and cliffs)	Small areas of extreme localities of different tree species composition.

SP – *Sorbeto-Piceetum*, LP hd – *Lariceto-Piceetum* higher degree, AcP hd – *Acereto-Piceetum* higher degree, FP hd – *Fageto Piceetum* higher degree, PiL hd - *Pineto-Laricetum* higher degree.

Table 7. Target tree species composition by groups of forest types and height degree.

4.2 Basic management decisions

Basic management decisions in the Slovak forest management practice concern forest category (forests: commercial, protective, special purposes), silvicultural system (clear-cutting, shelter-wood, selective cutting), rotation, and regeneration period.

4.2.1 Functional focus

In terms of significance of SVZ forests when carrying out the environmental and social functions, their current categorization as protective forests is correct and there is no need to change it. Highly functional potential in providing natural and protective functions is in many cases seen in their declaration as a special purpose forests.

4.2.2 Rotation period (non-production rotation maturity)

The derivation of rotation period in SVZ forests was based on rotation maturity of the main tree species – spruce, life of forest stands and functions that are provided by these forests. Rotation period in protective forests results from their ability to carry out the required functions and it should not be higher than life of forest stands. Life of forest stand is deemed as the maximum age to which the stand retains in the given tree species composition and structure the character of canopy forest, not weedy by foreign species of forest phytocoenoses, preventing the forest regeneration.

These principles were the basis for evaluating the backround material with aim to derivate the rotation perion of SVZ forests. If the rotation period does not to exceed the life of forest stand, it must be determined in the age before the onset of stage of decline, i. e. at the end of the stage of optimum. Because the life of man-made stands is shorter due to faster culmination of growth processes compared to stands growing under cover of parent stand (Pliva, 2000), we researched the life of stand with regard to naturalness classes. We selected among the PRP those that are characterized by natural, semi-natural and man-made forests. Forest stand in a stage of optimum were set apart in and natural and semi-natural forests. Despite the fact that in different locality conditions (group of forest site types), altitude and forest area the life of stands may be different, in the framework feature of rotation period are these differences negligible. Therefore, we suggest differentiating the rotation periods only generally by aggregated naturalness classes.

Rotation period should be seen as a benchmark variable set near the maximum life of stands in natural and semi-natural forests. Maximum age of stands in the stage of optimum in these forests is about 180 to 210 years, so we recommend indicating the rotation period at the age of 200 years. Rotation period is only symbolic in the forest stands with a structure corresponding to the state of primeval forests with preserved self-regulatory process and should be close to the maximum physical age of the main tree species – spruce. Based on literature data and own findings, we suggest indicating the age of 250, respectively 300 years in these best-preserved SVZ forests. In man-made forests with the density 0.7 to 1.0 can be found the oldest stands mainly in the age of only 100 to 110 years. There were found no stands of age that exceeded 150 under the given stages of density. Man-made stands in age over 150 years can be usually found only in the advanced stage of decline. Based on these findings, we proposed to indicate the rotation period at maximum of 150 years in man-made forests.

4.2.3 Regeneration period

Stand structure in SVZ forests should be improved, we should prevent its levelling and create conditions for natural regeneration. It is therefore necessary to maintain the current practice of applying a continuous regeneration period in natural and semi-natural forests, when applying the fine methods and regeneration felling of shelter management method, in particular special purpose selection. In man-made forests, which are intended to restructure to more nature friendly forest types, we should bear in mind with respect to the largely neglected forest tending and difficult natural conditions the early onset, low intensity and slow process of regeneration. Therefore, there is also a well-founded application of a continuous regeneration period. The advantage of a continuous regeneration period is that it allows carrying out interventions with aim to improve the functional efficiency of stands and promotion of forest regeneration any time. An excception from these introduced processes are stands with poor health condition and high degree of threat, often thinned and weedy. Felling-regeneration procedures can not be applied in these stands that require a long-term regeneration periods.

4.2.4 Silvicultural methods

The aim of forest management in SVZ forests is to maintain or achieve such condition of stands, when they can carry out the best of the desired ecological and social functions and are able to exist and evolve through their internal self-regulatory abilities, without or with minimal human intervention. In natural and semi-natural forests of SVZ with partly altered structure, this status can be achieved by applying the finest forms and regeneration felling of shelterwood system, mainly special purpose selection. Selection system can be used only in stands with selection structure. The current state of man-made stands does not allow using special purpose selection. Their reconstruction requires using group, respectively marginal shelterwood cutting which will enable to achieve structurally differentiated stands.

Intensified management use of SVZ

In the issue of use of SVZ forests can be noticed an effort to enforce the passive protection by some interested groups of nature protection. However, there are also proponents of more intensive management use, for example Mráz (2001). In assessing the requirements of more intensive management use, we were looking for conjunction between the limit attributes of production capacity of stands and the need to meet the primary protection functions. The suitability of stands for their management use is limited by locality conditions, relief characteristics (slope, sceleton, regularity of micro-relief), transport accessability and an acceptable height stand quality. Locality conditions in SVZ are expressed by five groups of forest site types (SP, LP hd, AcP hd, FP hd, PiL hd). We should exclude from economic use all those forest site types in groups of forest site types FP and PiL becasue of terrain condition resulting from the following conditions:

- Slope should not exceed 40%, in larger slope there is an increased need to realize the soil protection functions, especially erosion and in higher altitudes also avalanche functions.
- Soil and surface sceleton should not exceed 50% for potential management use. SVZ forests are situated on hard sceleton soils. Sceleton directly affects also production capabilities of the site that decrese in greater representation of the sceleton.
- Forests used for the production of wood requires more management measures, so there should be regular slopes with an balanced gradient of slope and micro-relief should not be bouldered or rised.
- With regard to the possibility of use the ecological techniques and technologies, it is essential to provide accessibility to the given localities. This is essential requirement also in terms of preventing the subsequent damage to stands and soil.
- An important indicator of the possibility of management use of stands is the middle height, respectively the absolute height quality. Hančinský (1972) Stands in SVZ groups of forest site types SP, LP a AcP are considered to be possible economically used when they achieve the absolute height quality 24-25 m. Vološčuk (1970) In AcP and its bottom limit in the absolute height quality. According to our results, it could be from the absolute height quality of 24 m. According to this reason, potential economic conditions for management use can be limited by altitude up to about 1400 m, because there is a significant decrease of height quality over this limit and cluster stan structure with a loose canopy.
- With regard to the above conditions and requirements, these forest site types are potential for the management use:
  - 7106 – fertile rowan spruce wood - SP, LP hd
  - 7401 – fertile maple spruce wood – AcP hd
  - 7404 – irrigated maple spruce wood – AcP hd

Based on the analysis of natural, stand and economic conditions of SVZ forests, we concluded that these forests could be increasingly used for timber production after fulfilling the following conditions and criteria:

- They must be situated on forest site types with the potential of economic use (7106, 7401, 7404), indicated by acceptable absolute height quality of 24 meters or more.
- They must be located in the lower zone of SVZ, up to approximately 1400 m.
- They must meet criteria of micro-relief, limited to a maximum allowable slope up to 40% and the proportion of soil and surface skeleton up to 50%.
- They must be accessible by transport and there must be created such conditions for a minimum damage to stands and soil.
- There shall be no deterioration in carrying out the primary ecological and social functions.
- To assign particularly stands with lower naturalness class for intensified economic use (man-made, respectively natural forests).

4.3 Management principles

Until recently, mountain forests were rather domain of natural scientists. With regard to the inefficiency of their management from the momentaly short-term view, they apply a conservative approach. They were retained to self-development regardless of their structure and closely related stability. Reducing of vitality and decline of mountain stands, however, drew the attention of foresters. Extreme climatic and soil conditions along with an unstable structure, which is a natural consequence of the lack of silviculture treatment, create from mountain forests complexes with a low resistance to stress factors and a high probability of catastrophic decline. In cases where this process has already begun, remedial measures are extremely difficult to apply from a technical and economic point of view. Using an appropriate silviculture measures may lead to growing of stands with significantly differentiated structure, which substantially increases their stability. Implementation of silviculture measures under these conditions is very difficult mainly due to their "un-profitability", unaccessability of stands and discrepancies between forestry legislation and environmental legislation.

Aggregated Naturalness Classes / Forest Type Groups	**Forest category**	**Management system**	**Rotation, year**	**Regeneration period, year**
1 – Primeval forests				
SP, LP, AcP, FP hd, PiL hd	Protective	Retained for self-regulating processes without intervention	Symbolic 250 – 300	Permanent natural regeneration
2 – Natural forests				
SP, LP, AcP, FP hd	Protective	Shelterwood system	200	Continuous
PiL hd		Retained for self-regulating processes without intervention		
3 – Mand-made forests in reconstruction				
SP, LP, AcP, FP hd	Protective	Shelterwood system	150	Continuous
Forests of the SVZ determined for more intensive commercial expolitation				
SP, LP (7106), AcP (7401, 7404)	Protective	Shelterwood system	120 – 130	50 – 60

Table 8. Review of chosen basic management decisions in Norway spruce vegetation zone.

The aim of management in protected forests, including SVZ forests is not the quantity of production as in production forests, but the quality of stands, expressed by target tree species composition, target structure, target stocking and other indicators. It is necessary to focus primarily on use and direction of natural forces towards a low need for additional energy in all phases of management, from establishment through tending and regeneration of stands. Therefore we also propose to differentiate the management principles for the stands with various naturalness classes and development stages. Moreover procedures must be also differentiated with regard to health condition, static stability and the state of natural regeneration of forest stands. From this aspect only preserved forest stands or their parts with parameters corresponding to primeval forests including stand texture, which should be by Plíva (2000) formed of a mosaic of stand clusters, groups and small stands with the area the most 0.5 ha can be retained for self-regulating processes.

Predisposition of mountain forests to forming large-scale horizontal structure Korpeľ (1989, 1995) considers a significant risk factor. Mayer & Ott (1991) state that immediately as there appears a tendency of formation of one-layered stand the spruce stand can be maintained in the state of optimal functional effectiveness only by permanent silvicultural tending. Based on the results of owns research as well as experience from abroad Korpeľ (1990) also notes that high effective differentiated structure cannot be maintained in the altitude below 1400 m for a longer period without intentional silvicultural-logging treatments (with except for extreme soil conditions). He also says there is little experience with regulating desirable structure of stands with prevailing protective (ecological) functions and therefore a very careful almost passive attitude prevails in this field. Korpeľ (1980) evaluated the development and structure of Slovakian natural spruce forests in the SVZ. In the stage of optimum one-layered, height-balanced structure with horizontal canopy is being formed in these forests with long lasting (about 100 years) low resistance potential against wind. Due to fear of weakening the stands are left their natural development frequently, which is ended by calamity.

Due to the mentioned reasons we propose to carry out in the forests with partially altered structure (natural and semi-natural forests) if necessary inevitable correction measures to direct their development towards target state. By KORPEĽ (1980) the most effective and least risky are regulatory treatments through so called purposeful selection felling in advanced phase of growing up or in the initial phase of optimum. Purposeful selection must be aimed at increasing (maintaining) individual stability of trees. Shelterwood regeneration should start in advance on small areas in clusters or groups or in small cleared gaps. The procedure is similar to slow natural disintegration / declina but going on in still resistant stand. In Norway spruce natural forests, where development stages and structurally different parts of stand interchange in a mosaic on plots smaller than 1 ha, regulatory silvicultural-felling treatments are not urgent (especially treatments similar to regeneration felling).

Later when there are still suitable conditions for the germination of seed, survival and growth of spruce seedlings (prior to old-age phase of the conditions of natural regeneration) it is purposeful by Korpeľ (1980) to try to start intentional regeneration. Trees with reduced stability (intermediate with short crown) are removed and the most stable trees as bearers of stand resistance are preserved. By cutting of instable trees concentrated into clusters or groups an irregular regeneration elements rise. It is desirable to use permanently silvicultural and regeneration opportunities for creating strongly differentiated structure of stands and improvement of their static stability, mainly in lower part of the SVZ within the altitude about 1400 m. A great individual stability of trees is conditioned by slow decline of individual trees and thus markedly small-scale regeneration and small area forest texture (Korpeľ 1992). By Míchal (1995) the greater is the area of optimum stage with one-layered stands, little differentiated what concerns height and diameter the faster is their decline and on the greater area. In opposite to that markedly uneven-aged groups decline slowly on a small area.

The difference between actual value of stocking lower than 0.7 and stocking 0.7 determine area proportion to complement or regenerate the stand providing the area has continuous round shape, not very elongated, of minimally 300 m^2, e.g. 17x18 m, 20x15 m etc., which appears as a marked stand gap after missing trees. Fleischer (1999) states he found only for the plot with area 300 m^2 more stable progress of natural regeneration. In this sense also Saniga (2000) give the area of 200-300 m^2 as sufficient also for larch. He states the best conditions for natural regeneration are in the stands with stocking about 0.7 without herbaceous cover (herbs and mosses occur only sporadically). In some places there are small plots with almost 50 about two-year old spruce seedlings per m^2 but the conditions for survival are not suitable and therefore seedlings die (insufficient heat and light).

In structurally altered forests it is impossible to secure in an acceptable time horizon required functionality through retaining the forests for self-regulating processes. Therefore there must be applied reconstruction management measures according to actual state in forest stands with substantially altered age and spatial structure, formed usually as a result of artificial regeneration or in declining and declined stands without natural regeneration. A principal shortcoming is late time of regeneration and state of advanced decline of stands without securing regeneration. In such cases the regeneration can be realized only through artificial or combined regeneration; however only stands with little differentiated age and spatial structure are again created in this manner.

With all this in mind, we propose to plan and carry out any measures in these forests only on the basis of their actual "naturalness" class, which has to be the decisive criterion for determining the urgency of proposed measures. Additional criteria should include an assessment of static stability, natural regeneration, health condition, and stocking, as an indicator of fulfilment of ecological functions (mainly soil and water protection). Basically, it can be stated that the forest stands classified in the 1st naturalness class can be left as is. In such stands, natural regeneration usually fully corresponds to the actual stand structure, and both static stability and health condition are excellent. Forest stands that do not meet these criteria—mostly man-made, even-aged, vertically and horizontally little-differentiated forests, but also natural forests with various development stages whose natural regeneration ability is insufficient—require concrete measures. These measures can be classified according to the degree of urgency, based on the forest's actual status.

Better management of high-mountain forests SVZ will also require building a comprehensive net of forestry roads that are ecologically adapted to the terrain. It will be necessary to adapt all forestry activities in these forests to ecological standards and to introduce the most recent techniques and technologies. Clear-cutting is forbidden in the SVZ and has been fully replaced by shelter-wood and selection (purposefull) systems. On sites with deteriorated soils, recovery measures such as area-wide application of dolomitic limestone by airplane or helicopter, addition of dolomitic limestone and NPK fertilizers in holes, or application of mulching cloths when planting will create suitable growth conditions for subsequent forest stands.

Generally, natural regeneration is preferable. However, on certain sites tree species diversity will be enhanced by planting desired tree species. Mixed stands (especially of Norway spruce, European beech, silver fir, Scots pine, sycamore maple, European larch, and mountain ash) will gradually substitute pure spruce plantations, thus enhancing the ecological stability of the forests (including resistance to ongoing climatic change). The health status of forests and occurrence of harmful agents will continue to be monitored. In the field of forest protection, preventive methods will be given preference over suppressive methods.

4.3.1 Need and urgency of management measures

On the basis of the status of stand structure indicators, the conditions and the state of natural regeneration, static stability, health condition as well as after considering the requirements and conditions being given in basic management decisions and the management targets the manager will decide about the need and urgency of management measures with applying the management principles. The manager will decide whether the stand or its part requires a concrete management measure as well as about the degree of the urgency of management measure based on the fact how the state of stand corresponds to the criteria listed in following table.

Forest stand or its part doesn´t require any measures	*Forest stand or its part requires measures in the 1st degree of urgency (within 3 years)*
1st naturalness class Static stability – excellent Health condition – excellent Natural regeneration – fully corresponding	3rd (2nd) naturalness class Static stability – unsatisfactory Health condition – caduceus or died forest Natural regeneration – slight or minimal
Forest stand or its part requires measures in the 2nd degree of urgency (within 10 years)	*Forest stand or its part requires measures in the 3rd degree of urgency (postponable)*
3rd or 2nd naturalness class Static stability – satisfactory Health condition – mediumly declined Natural regeneration – slight or minimal at the age of forest less than 50 years under rotation	2nd (3rd) naturalness class Static stability – good Health condition – slightly declined Natural regeneration – slight or minimal at the age of forest more than 50 years under rotation

Table 9. Criteria for determination of the need and urgency of the measures.

Stand or its part will be classified into respective naturalness class on the basis of evaluation of diameter and height variability (especially by means of the degree of diameters dispersion and the share of canopy level – Fig. 3 turned into table), crown length and stand texture. Age range may be as an auxiliary indicator. In the following tables (10, 11) are given orientation values of the indicators. They can be used as an aid for assignment of the aggregated naturalness class and development stages of the 2nd NC of respective forest stands or their parts. The values listed in the following tables were derived from empirical material of 122 PRP.

Indicator		**Aggregated naturalness classes**		
		1	**2**	**3**
Degree of diameters dispersion		3	2	1
Share of canopy level; %	1	55 ± 15	65 ± 20	90 ± 10
	2	25 ± 15	20 ± 15	5 ± 5
	3	20 ± 15	15 ± 15	5 ± 5
Crown length; %		75 ± 10	70 ± 10	55 ± 10
Stand texture; ha		> 100	40 – 100	< 40
Age range; years		< 0,2 – 0,5	> 0,5	> 0,5

Table 10. Values of chosen indicators of forest status in naturalness classes 1, 2 and 3.

Indicator		**Development stages of naturalness class 2**		
		21	**22**	**23**
Degree of diameters dispersion		2-3	2	2
Share of canopy level; %	1	50 ± 20	75 ± 15	70 ± 15
	2	30 ± 15	15 ± 10	15 ± 10
	3	20 ± 15	10 ± 5-10	15 ± 10
Crown length; %		75 ± 10	67,5 ± 7,5	72,5 ± 7,5

Table 11. Values of chosen indicators of forest status in development stages of naturalness class 2.

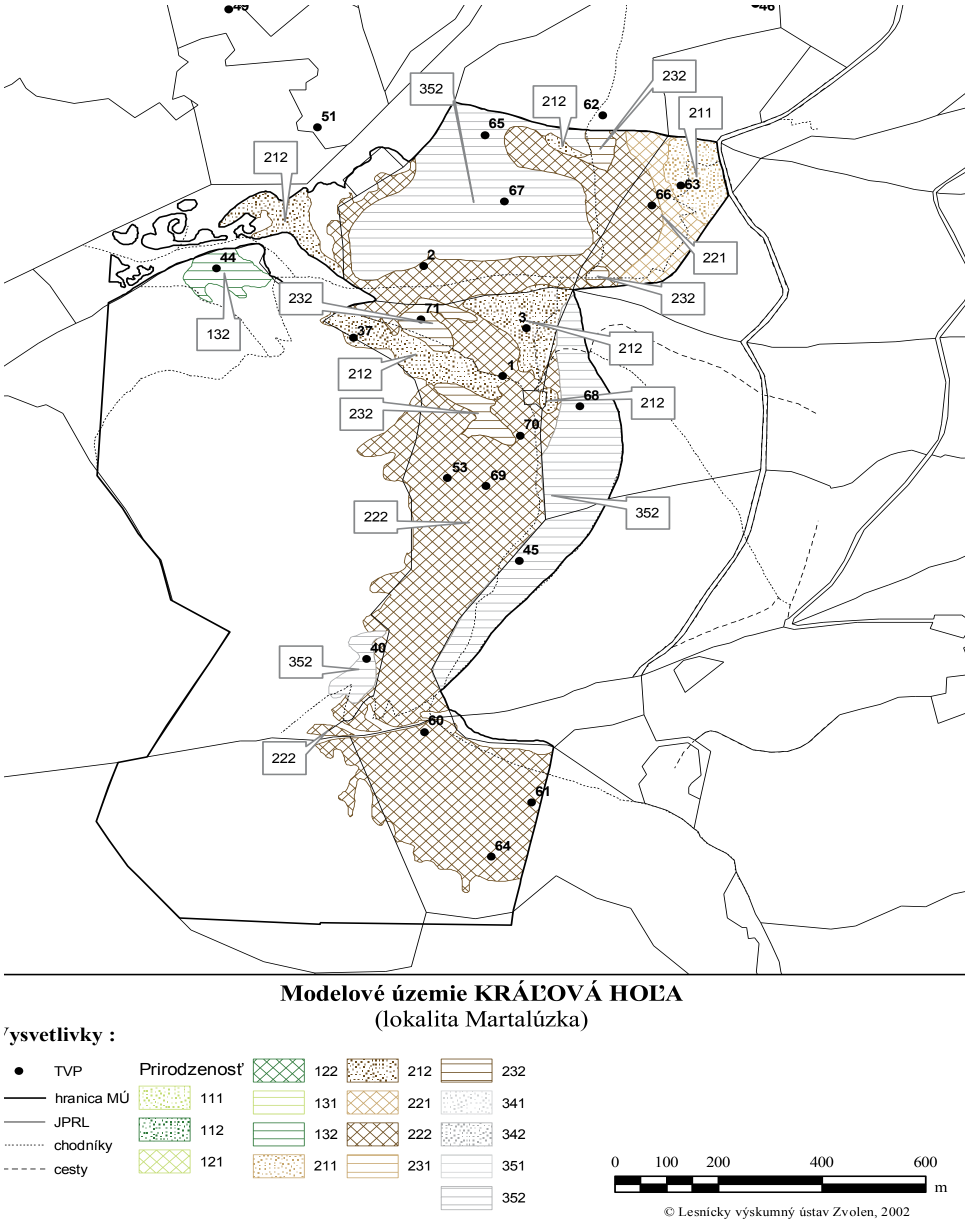
The evaluation of static stability (Konôpka, J., 2002) will be made on the basis of the value of slenderness coefficient, which will be calculated as the proportion of tree height and tree diameter $d_{1,3}$ multiplied by 100. Slenderness coefficient of the stand or its part will be determined as mean value of slenderness coefficients found on respective standpoints. The assessment will be done in four degrees in the dependence on mean diameter and yield class.

Yield class	**Degree of static stability**	**Slenderness coefficients by mean diameter, cm**						
		10	**15**	**20**	**25**	**30**	**35**	**40**
≤ 16	1-excellent	0,63	0,60	0,57	0,55	0,52	0,49	0,46
	2-good	0,64-0,73	0,61-0,70	0,58-0,67	0,56-0,64	0,53-0,61	0,50-0,58	0,47-0,55
	3-suitable	0,74-0,82	0,71-0,79	0,68-0,76	0,65-0,73	0,62-0,70	0,59-0,67	0,56-0,64
	4-unsuitable	0,83	0,80	0,77	0,74	0,71	0,68	0,65
18-22	1-excellent	0,67	0,65	0,63	0,60	0,58	0,55	0,53
	2-good	0,68-0,77	0,66-0,74	0,64-0,72	0,61-0,69	0,59-0,67	0,56-0,64	0,54-0,62
	3-suitable	0,78-0,86	0,75-0,83	0,73-0,81	0,70-0,78	0,68-0,76	0,65-0,73	0,63-0,71
	4-unsuitable	0,87	0,84	0,82	0,79	0,77	0,74	0,72
≥ 24	1-excellent	0,68	0,66	0,64	0,62	0,61	0,59	0,57
	2-good	0,69-0,78	0,67-0,76	0,65-0,74	0,63-0,72	0,62-0,70	0,60-0,68	0,58-0,67
	3-suitable	0,79-0,87	0,77-0,85	0,75-0,83	0,73-0,81	0,71-0,79	0,69-0,77	0,68-0,76
	4-unsuitable	0,88	0,86	0,84	0,82	0,80	0,78	0,77

Table 12. Criteria for evaluation of static stability by mean diameter and site classess.

Health condition (Konôpka, J., 2002) is being evaluated according to the damage by identifiable injurious agents (wind, snow, frost, bark beetles, fungal diseases, it means rots, damage by game) and the evaluation of the state of crown, it means the loss of assimilatory organs. Co-dominant and dominant trees are evaluated by means of 5 degree scale – excellent or slightly disturbed, moderately disturbed, heavily disturbed, very heavily disturbed and dying or died stand.

In the assessment of the state of natural regeneration (Jankovič, 2002) actual state of natural regeneration will be estimated and on the basis of actual spatial and age structure of the stand or its parts there will be determined percentage of the area where natural regeneration should occur. It follows from the comparison of actual and required state of natural regeneration that the state being evaluated can be fully corresponding – suitable in 91-100 %, sufficient – 61-90 %, average – 41-60 %, weak – 11-40 % and minimal within 10 %. Only natural regeneration being in accordance with regeneration tree species composition is taken into account.



Explanation notes: 1st number – naturalness class, 2nd number – development stage, 3rd number – altitudinal zone.

Fig. 8. Example of forest distribution by naturalness classes and developmet stages in Nature Reserve of Martalúzka.

5. Classification model of a forest naturalness class

Because of the above-mentioned reasons it is required to know the actual forest naturalness class in the forest ecosystems since it can be taken as an objective criterion for decision-making about forest use and consequently about forest management (Hoerr 1993; Schmidt 1997). This is a generally applicable requirement and a need for achieving the optimal and the most effective use of forests. Hence, our goal was to prepare and propose a generally applicable method for the derivation of an integrated indicator and a model of forest naturalness class. Our requirement was to obtain unit values of the indicator and the variability of such a magnitude, that the differences between the individual degrees of forest naturalness would be significant. In order to examine the practical applicability of the proposed method, it was developed for a case of forest ecosystems located in SVZ.

Two variants of the classification model of forest naturalness were proposed, one based on the principles of discriminant analysis, while the second one uses an additive approach to derive the integrated indicator of the forest naturalness class. The discriminant model is derived as an application of multivariate statistical analysis, so-called predictive discriminant analysis (Cooley and Lohnes 1971; Huberty 1994; StatSoft 1996; Merganič and Šmelko 2004). Its role is to classify the sampling unit on the base of several quantitative variables into one of the pre-defined qualitative classes, in our case into one of the three forest naturalness classes. Using the data from the database, three discriminant equations were derived, each for one class of forest naturalness. These discriminant equations serve for the classification of an evaluated forest stand into one of the three forest naturalness classes. Secondly, we proposed an integrated indicator of forest naturalness class. This indicator belongs to complex indicators that combine several diversity components into a single value (Merganič 2008). The indicator is based on an additive approach, while the partial components are given in real measurement units. Mathematical formula of the integrated indicator of the forest naturalness class (IISP) is as follows:

$$IISP = ID_1 + ID_i + \ldots ID_n$$

where ID partial indicator of the forest naturalness class.

5.1 Data adjustment to meet the needs for the derivation of the classification model of the forest naturalness class

The relation between a diversity indicator and an area, for which the indicator was assessed, is known from a number of theoretical and practical studies. Due to the varying area of our sample units, we tested the relationship between the values of the partial indicators of forest naturalness and the area of the sample plot. The analysis revealed that 9 indicators (R1, R2, the average ratio of crown length to tree height, the average ratio of tree height to tree diameter, coverage of herbs and grasses, coverage of juvenile and senile phases and deadwood volume per hectar) had a significant relationship with the plot area ($p<0.05$). This result is logical and is mainly coupled with the effect of the development stages. The significant influence of the development stage on the indicators of forest naturalness was found in 16 out of 25 cases. Since the plots were distributed among the development stages, the varying area of the sample plots should not have a negative influence on subsequent analyses and on the creation of the classification model of the forest naturalness classes. On the contrary, the estimates of the average values and the variation of the indicators derived from tree data (the average ratio of crown length to tree height, aggregation index atc.) are even more representative, since they always represent a similar group of trees (approx. 25 trees).

Numbers of the PRP in individual forest naturalness classes, as well as the numbers of the plots in individual development stages (growth, optimum, decline) within the naturalness classes are imbalanced. Due to this and the above-stated facts, it was required to equalise the number of the sampling units in individual development stages and in individual forest naturalness classes. The missing plots were added by random replication of the existing sample plots using bootstrap technique (Chernick 2008; Yu 2003) until the number of the plots in the most abundant development stages was reached in other stages, too. In this way, the numbers of the plots in less abundant development stages and 1st, 2nd, and 3rd naturalness classes were set to 9, 36, and 9 plots, respectively.

Subsequently two different variants of the integrated complex indicator and the model of the forest naturalness class were proposed, one as a discriminant model, while the other one as an additive model.

Discriminant Model

From a great number of the examined combinations of the indicators (Table 4a, 4b), the best results of the correct classification of the forest naturalness class were obtained using the combination of the following six indicators: the arithmetic mean of the ratio between crown length and tree height (AM_K), the deadwood volume (MOD), the coverage of grasses (PK_T), the coverage of mosses and lichens (PK_M), the aggregation index (R), and the coefficient of variation of tree diameters (CV_D1.3). The general formula of the final discriminant model looks as follows:

$$\text{Discriminant score } j = AM\_K \cdot b_{j1} + MOD \cdot b_{j2} + PK\_T \cdot b_{j3} + PK\_M \cdot b_{j4} + R \cdot b_{j5} + CV\_D1.3 \cdot b_{j6} + b_{j7}$$

where: J = 1st to 3rd forest naturalness class.

The classification of the forest naturalness class is performed in several steps. First, the discriminant score of each naturalness class (1–3) is calculated from the particular discriminant equation using the real values of the partial indicators. An evaluated location, a stand, or in our case a sample plot, is assigned such a forest naturalness class, for which the calculated discriminant score is a maximum.

Forest naturalness class	**Correct classification in %**	**Degree of forest naturalness according to the model**			
		1	**2**	**3**	**Total**
		Number of plots			
1	85.2	23*	4	0	27
2	68.5	15	74*	19	108
3	94.4	0	1	17*	18
Total	74.5	38	79	36	153

** indicates the cases with correctly classified forest naturalness class.*

Table 13. Classification matrix of the discriminant model.

The results of the classification matrix of the parameterisation data set are presented in Table 13. As can be seen in this table, the overall correctness of the classification of the forest naturalness class using the proposed discriminant model is 74.5%. The highest probability of correct classification is in marginal classes (classes 1 and 3), while the lowest probability is in the middle class (class 2, 68.5%).

Following Table 14 presents the statistical characteristics of the model. According to the values of Fischer F and Wilks′ Lambda statistics we can, with 99.9% probability, say that the proposed discriminant model is highly significant. The Willks′ Lambda can be interpreted in the following manner: if its value is close to 0, the model is appropriate; if, on the other hand, the value approaches 1, the model is not suitable. The partial Lambda values given in the third column of Table 13 provide us with the information about the contribution of each independent variable to the discrimination of the dependent variable. Five out of six selected indicators are significant, which means that their contribution to the discrimination of the forest naturalness class is significant. Although the sixth indicator, the coefficient of variation of tree diameters, was insignificant, its presence in the model improved the classification. The indicators AM_K and MOD have the largest influence on the discrimination of the forest naturalness class.

Discriminant model				
Number of variables: 6			Number of groups: 3	
Wilks' Lambda: 0.43676			$F_{(12,290)}$= 12.401***	
Input variables				
Indicator	Wilks' Lambda	Partial Lambda	$F_{(3,935)}$ **95%, ***99.9%	
Arithmetic mean of crown length / tree height ratio (*AM_K*) [%]	0.587	0.744	24.944	***
Deadwood volume (*MOD*) [m^3/ha]	0.491	0.889	9.062	***
Coverage of grasses (*PK_T*) [%]	0.469	0.932	5.314	**
Coverage of mosses and lichens (*PK_M*) [%]	0.465	0.940	4.608	**
Aggregation index (*R*)	0.458	0.953	3.580	**
Coefficient of variation of tree diameter (*CV_D1.3*) [%]	0.442	0.988	0.862	

Table 14. Statistic characteristics of the discriminant model.

In order to explain the classification graphically, the canonical analysis was applied to the data set. Fig. 9. shows the position of the groups of the sample plots with the same forest naturalness class and their approximate borders. From this figure it is obvious that the marginal categories of naturalness class have the highest probability of correct classification because their overlap with the neighbouring class is the smallest.

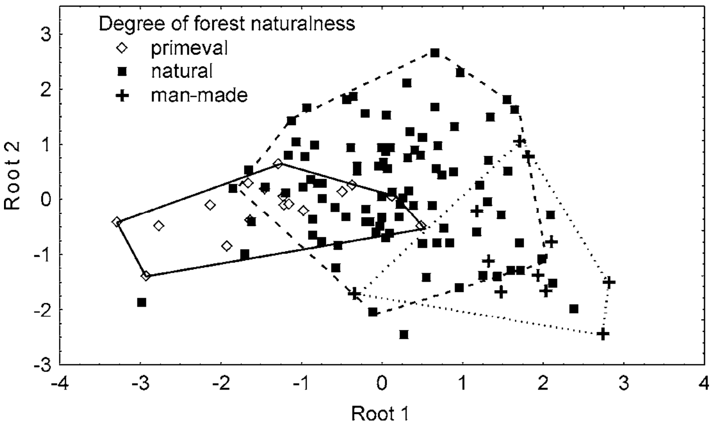


Fig. 9. Graphical interpretation of the classification of forest naturalness class with the discriminant model using canonical analysis.

Additive model

The partial indicators in the additive model are the same as in the discriminant model, i.e. the arithmetic mean of the ratio between crown length and tree height (AM_K), the deadwood volume (MOD), the coverage of grasses (PK_T), the coverage of mosses and lichens (PK_M), the aggregation index (R), and the coefficient of variation of tree diameters (CV_D1.3). The significance of the model was tested by singlefactor analysis of variance. The analysis revealed significant differences between the average values of IISP of the forest naturalness class (the whole model F(2, 150) = 21.849***, Tukey test). Figure 10. presents the graphical interpretation of the model. The range of IISP values was divided between the forest naturalness classes using the weighted approach, taking into account the error ranges of the average values of IISP and the percentiles of the values in every forest naturalness class. The objects, e.g. the stands, with the IISP values exceeding the value of 267 represent primeval forests; the IISP values in the range from 182 to 267 indicate that the forests are natural, while the values of IISP below 182 classify the objects as man-made forests.

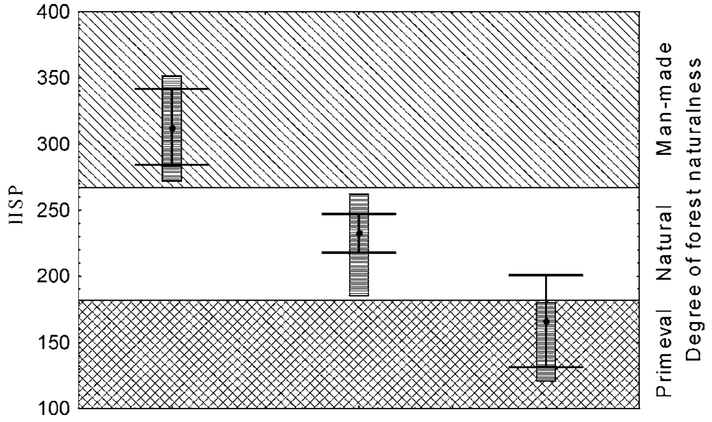


Fig. 10. Intervals of the integrated indicator of forest naturalness (IISP) specified for the three degrees of forest naturalness (primeval, natural, man-made forests); Legend: ▤ percentile 26–7 74% = 48% of values, ⌶ 95% confidence interval (1.96 × standard error).

The correctness of the model classification was determined on the base of the categorisation of individual plots into the forest naturalness class. The overall correctness of the classification using IISP is 63.4%. The individual forest naturalness classes 1, 2, and 3 were correctly classified in 74%, 56%, and 89% of cases, respectively.

Comparison of the models

The results of the classification of the forest naturalness degree indicate that both variants of the classification model have a similar probability of the correct classification of the assessed object into the forest naturalness class. The discriminant model behaves better, since its probability of correct classification is by approximately 11% higher than the probability of the additive model. Higher efficiency of the discriminant model is evident mainly in the proportion of correct classifications in 1st and 2nd forest naturalness classes. From the point of practical applicability, the additive model is simpler to use, but considering the current capacity of computers, it is also not difficult to apply the discriminant model in the form of a small computer program.

6. Conclusion

Because of enhancing requirements of public which are laid on forests the area of forests with prevailing social and ecological functions has been increasing in the last decades. Their important parts are forests in spruce vegetation zone. Therefore it is important to achieve status in which maximum fulfilment of mentioned functions through permanent existence of stable and healthy forest with corresponding stand structure is secured. Regeneration, improvement or maintenance of self-regulating ability of such forests should be essential. From these reasons forest management planning and subsequently also forestry operation should come out from appraisal and assessment of the class of natural structure conservation in carrying out of management measures. Naturalness class as indicator of natural structure conservation has to be a decisive criterion for determining need and urgency of the respective management measures.

For ensuring this approach there were chosen the most suitable indicators for quantification of stand structure status in primeval and natural forests which are characteristic with considerable degree of age, spatial, diameter and height diversity. Further there was collected and evaluated vast experimental material with objective of derivation of management targets – mainly target stand structure, target stocking and target tree species composition and criteria on identification of the basic naturalness classes – primeval forests, natural forests and man-made forests. The experimental material was collected in different natural, site and stand conditions from 122 permanent research plots in all significant groups of forest site types and altitudinal zones in the scope of spruce vegetation zone. Outcomes resulting from the evaluated experimental material confirmed statistically significant differences of forest status in various naturalness classes and actual development stages.

For needs of frameworking planning there were worked out: *differentiated tree species composition* by groups of forest site types and more detailed by altitudinal zones in the scope of spruce vegetation zone; *outlook target structure* derived following results of the primeval forests analysis and *available target structure* derived following results of the natural forest analysis and *target stocking* which was derived as optimum stocking on the basis of harmonising the requirements for fulfilment ecological functions, ensuring static stability and conditions for natural regeneration. The most suitable status of mentioned requirements was observed in stocking 0,7. There were derived differentiated rotation periods in dependence on the naturalness classes: 150 years for man-made forests, 200 years for natural forests and 250-300 years for primeval forests. However in primeval forests it is understood merely as a symbolic rotation period resulting from life-cycle of Norway spruce in respective natural preconditions. There were also identified the natural, site and stand preconditions of spruce vegetation zone in which forest stands could be utilised for more intensive commercial exploitation.

Likewise as the management targets and the basic decisions also management principles are differentiated in dependence on the naturalness classes. Basically it can be stated that only forests classified in the first naturalness class (primeval forests) can be left without any measures. In such stands concerning their structure, natural regeneration, health conditions self-regulating processes are usually in progress. Forest stands that do not meet these criteria – mostly man-made, even-aged, vertically and horizontally little-differentiated forests, but also natural forests with various development stages whose natural regeneration ability is insufficient – require concrete reconstruction measures. These stands can not be left for self-regulating because there is not possible to secure their required utility in acceptable temporal horizon.

Further there were proposed procedures for finding out and evaluating the forest status. They include the indicators and classification systems of evaluating the stand structure, status and conditions of natural regeneration, static stability, health conditions, determining the naturalness classes and evaluating ecological stability. Listed data are important for determining the need and urgency of respective measures.

Antoher very important outcome of this research is elaboration the methodology for the evaluation of forest naturalness on the base of the selected indicators of tree species and structural diversity. As we already stated, the knowledge about the naturalness of forest ecosystems is of great importance. Its objective assessment is essential in the decision-making process dealing with forest utilisation and subsequent forest management. Further more forest naturalness is the most significant and widely applied criterion for the forest evaluation from the viewpoint of nature conservation, and serves as a key tool in analyses and as a support in planning nature conservation measures. The currently proposed methodology, if applied within the practical forest management, can lead to the improvement of ecological stability of forests and landscape. Although the approach has already included several aspects of forest naturalness, it can be further enhanced by taking into account other components, e.g genetic diversity. The coupling of the model with statistical inventory and GIS tools can enable the creation of detailed maps of naturalness of forest ecosystems. Such information can further improve planning and practical application of nature conservation measures.

The developed classification model is easily applicable in practice and its application does not require intensive material and technical background. The applicability of the model for the classification of the forest naturalness classes has already been successfully tested on independent data (see Merganic and others 2009). **The method is applicable outside SVZ**

or even outside Slovakia. In any other conditions, appropriate indicators of forest naturalness need to be selected, data need to be gathered, and the model needs to be re-parameterised. The coupling of the model with statistical inventory and GIS tools can enable the creation of detailed maps of naturalness of forest ecosystems. Such information is important for planning as well as for practical application of nature conservation measures. The model is a powerful tool for objectifying the assessment and the evaluation of the development of forest ecosystems within monitoring schemes.

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18

Interactions of Forest Road, Forest Harvesting and Forest Ecosystems

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1. Introduction

Forestry developed with the goal, ultimately, of maximizing the long-term economic return from the forest, a goal that has remained virtually unchanged to the present day, despite the growth in understanding of ecosystem function (Farrell et al. 2000). Forest ecosystems supply a wide range of commodities sought by an expanding human population, including structural materials, fuels, and medicines, along with a wide range of critical ecosystem services including nutrient cycling, climate regulation, maintaining water balances and carbon sequestration (Klenner, 2009). The concept of sustainable forest management, which may be defined as the use and regulation of forests and forest areas, at local, national and global levels, in such manner and to such extent as to protect their biological diversification, their productivity, rejuvenation capacity and survival energy as well as their potential to fulfill their ecological, economic and social functions, both at present and in the future, while not causing any harm to other ecosystems, is well recognized by all countries in the world (Demir, 2007).

The use of the forests and other elements in the landscape is driven by our human needs in local, regional and global perspectives. The way we use the forest as a natural resource is determined by a number of factors. These factors, which in their character are social, economic, biological and ecological, can be seen as forces and constraints (Anderssona et al. 2000). Forests, which are renewable natural assets, are formed by gathering of a large number of living and non-living creatures. However, this formation is not a random mass, but whole, a system. When making use of the forest ecosystem for various purposes, care must be taken not to spoil the forest structure. As it is the case in every engineering activity, in carrying out the road planning and construction works, the requirements regarding compatibility with nature and safety and economy must be met. The compatibility with nature, that is, the requirement that the road to be constructed as a result of the works carried out should have the characteristics enabling it to perform its expected functions is thus recognized to be of primary concern. To meet this requirement, first the purpose of construction of planned facility must be precisely defined. Meeting the second requirement regarding safety involves the construction of planned facilities according to relevant standards within the prescribed period to enable them to serve in line with the contemplated purpose (Hasdemir and Demir, 2005).

Developing and maintaining the economic activity that is vital for the quality of modern life would be difficult without roads. Roads are critical component of civilization. Roads provide access for people to study, enjoy, or contemplate natural ecosystems. In fact, the development of human civilization has benefited from transportation systems that evolved from root trails to complex highway systems (Crisholm, 1990; Grübler, 1994). Building and maintaining roads have become controversial, however, because of public concerns about their short and long term effects on the environment and the value that society now places on road less wilderness (Cole and Landres, 1996). Oppositions to road building and pressure to decommission roads in rural landscapes will continue to increase as road less areas decrease in relation to roaded ones. Decisions about road alignment, building, maintenance, or decommissioning are complex because of the many trade off involved (Lugo and Gucinski, 2000).

Traditionally, the planning of rural road network is based on economic and social considerations. In the last years, traffic volumes showed a considerable growth, despite an extension of the road networks. Meanwhile, some harmful effects of these networks and their traffic flows appeared. Traffic unsafety, emissions and noise affect local people, flora and fauna (Jaarsma, 1994; Jaarsma and van Langevelde, 1996; Jaarsma, 1997). Evaluating the ecological effects of roads requires rigorous analysis and an understanding of the ecology of roads, that is, the interplay between all of the living components, the function of roads, and the environmental factors that regulate processes along the road corridor (Forman et.al. 1997).

2. Forest road ecosystems

Forest road can be defined as ecosystems because they occupy ecological space (Hall et.al.1992), have structure, support a specialized biota, exchange matter and energy with other ecosystems, and experience temporal change. Forest road ecosystem are built and maintained by people (Haber, 1990). Forest road ecosystem includes both the paved and unpaved rights of way and adjacent structure, including other infrastructure, ditches, drainage features, and other components that provide the means for vegetation to establish and provide habitat for associated plants and animals (Fig.1). Forest roads are crucial for effective forest management, regardless of its main objectives. Forest maintenance, wood harvesting, game control, recreational activities - all require the accessibility provided by a suitable road network. Forest roads, in former times planned and constructed for the needs of wood harvesting and transport, are the key factor for recreational access to and activities in forest environments. Leisure activities in urban forests include hiking, biking, horse-riding, jogging and inline-skating (Janowsky and Becker, 2003). The opening of forests to exploitation is usually realized by means of well-planned forest road networks. The parameters and location requirements of forest road networks vary depending on variations in landscape conditions and according to the technology used and administrative activities. These requirements and planning approaches may be related to economic, ecological and management characteristics (Potocnik, 1996). The road network is a form of land use, which planning strongly depends on for other land uses. These decide the desirable density of the network (mesh size) and the capacity of the road links (pavement width). Simultaneously, all human land uses are strongly dependent on this network. Economic developments, and efficient use of land resources and, as asocial aim, accessibility of rural areas, need a well-developed road network. Most regions in industrialized countries have, from a quantitative point of view, a sufficient rural road network (road density, mesh size) (Jaarsma, 1997). The model in Fig.1 highlights the six-way flow of materials, energy, and organisms along the road corridor; vegetation zone; the interaction with the human economy and human activity; external forces that converge on the road corridor. The structure and functioning of a road varies according to its design, use, type of surface, and location (Lugo and Gucinski, 2000). Forest roads are also corridors that can connect contrasting ecosystem types. Since forest roads provide a fairly homogeneous condition through the length of the corridor, they provide opportunity for organisms and materials to move along the corridor, thus increasing the connectivity among those ecosystems that interface with the forest road (Lugo and Gucinski, 2000; Merriam, 1984).

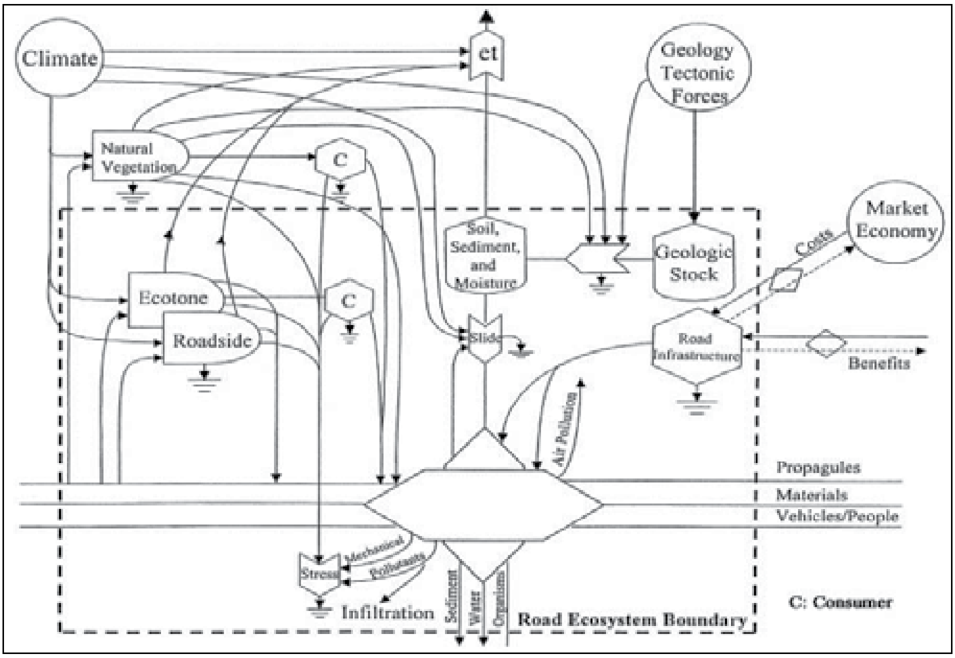

Fig. 1. Model of road ecosystem (Lugo and Gucinski, 2000).

3. Forest road impacts on forest ecosystems

Forest roads create many collateral problems adversely affecting the conservation of ecosystems and landscape integrity (Smith and Wass, 1980; Thompson, 1991). Like all ecosystems, roads are constantly changing as do the relations between the road ecosystem and adjacent ecosystems. The major phases of road development are building, operating, maintaining, and abandonment. Forest road building is often the most environmental traumatic to adjacent ecosystems because earth movement and other activities can disturb whole watersheds. Changes -mechanical, geochemical, hydrologic, biotic, and so on- to the immediate land area and any adjacent upstream and downstream ecosystem affected by building activities can be predicted. During this phase, the road is primarily a disturbance and agent of change (Lugo and Gucinski, 2000).

3.1 Wildlife

Forest roads segments can be part of forest road networks criss-crossing the landscape. A forest road network system has environmental effects and ecosystem properties that appear to transcend those of its individual segments. For example, some wildlife species, such as bear, wolf, or mountain lion, respond more to forest road density than to individual road segments (Forman et.al.1997). Similarly, forest road networks are more relevant to issues of forest fragmentation or to hydrological effects than are isolated forest road segments (Jones, 1998). Roads create barriers and additional that in turn causes fragmentation of the landscape and its populations (Jaarsma and Willems, 2002).

3.2 Vegetation

Maintaining forest roads, particularly if improperly done, act as periodic disturbances to both the road biota and landscape as a whole. Maintenance activities can approximate building activities in the amount and extent of disturbance, and they can prolong environmental effects to adjacent ecosystems. Not maintaining forest roads, however, can hinder the primary function of the road and also significantly affect the environment. For example, poorly maintained drainage systems in wet montane roads can induce mass-wasting events large enough to destroy the road and affect adjacent forest and aquatic systems. Such events sometimes exceed those observed during forest road building (Larsen and Parks, 1997).

Forest road use itself affects the landscape, for example through spills of toxic substances, pollution, dust, or effects on plants and animals by the presence of people. Forest roads as part of long-range transportation networks are likely to introduce alien species. The type and intensity of use are associated with particular environmental effects. For example, logging truck traffic is known to facilitate the transport of fungal root diseases and heavy vehicular traffic increases the risk of dispersing roadside weeds and different types and intensities of pollution (air, soil, or water) or chemical spills (Lugo and Gucinski, 2000). Furthermore, a dense forest road network for example, has a more likely effect on fragmentation than a low density network (Forman et.al.1997; Forman and Hersperger, 1996). High density road networks are more likely to affect hydrological parameters than low density ones. However, forest road density is less important to fragmentation of forest where topography dominates the structure and size of vegetation stands (Miller et al. 1996).

Road abandonment allows successional processes to recapture the road corridor. The speed and direction of succession after a road is abandoned depends on the type of road, landscape, and environment. Some road segments may be overgrown with vegetation quickly, but the pavement can arrest succession in others. Rehabilitation techniques are usually needed to accelerate succession to reach management goals after abandonment (Luce, 1997). With time, the road ecosystem ages and matures. As it does, and regardless of disturbances, segments of the road can adjust to conditions, blend with the landscape, and reach a new ecological and hydrological state (Olander et al.1998).

Finally, like other ecosystems, roads produce long term legacies on the landscape (Hutchinson, 1973). The environmental gradients believed to be most important in describing the ecological space in which roads function as ecosystem are shown in Fig 2.

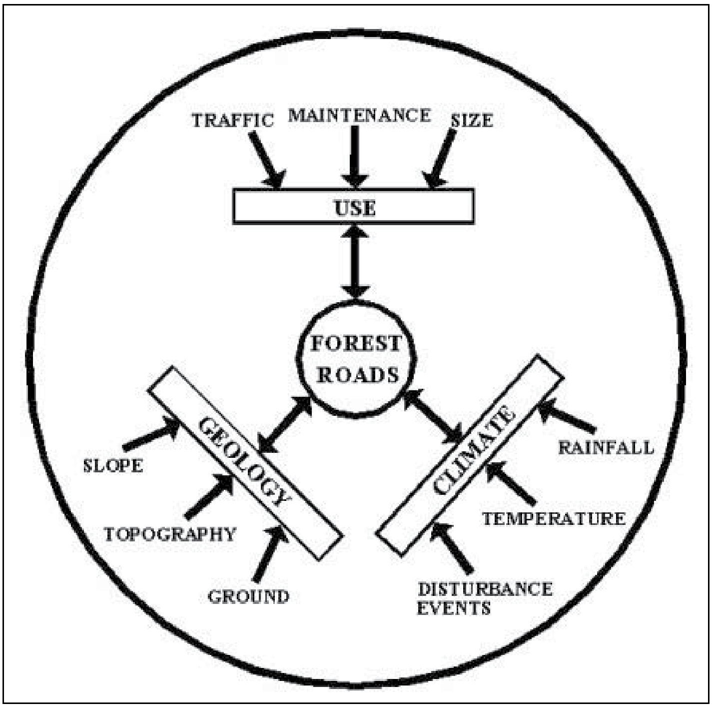

Fig. 2. Parameters of forest road ecosystems (Demir, 2007).

Forest road effects on surrounding environments and road function as ecosystem are mainly influenced by climate, geologic conditions, and uses or functions of the road. Climatic conditions are mainly the precipitation and temperature regime, and the frequency and intensity of climatic disturbance events. Geologic side is the type of substrate such as volcanic, limestone, or alluvial and the topography (Fig.3).

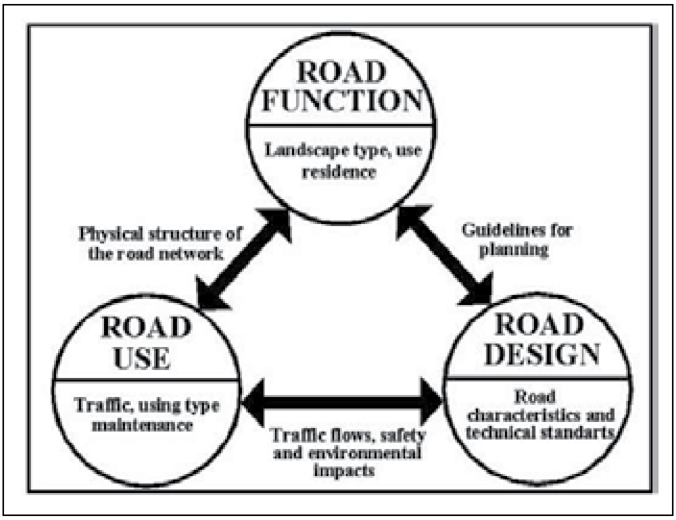

Fig. 3. Relationships between road function, design and use (Demir, 2007).

3.3 Soil

Forest roads produce the highest production of sediment yield to streams from forest lands (Binkley and Brown, 1993; McClelland at al. 1999; Reid and Dune 1984). Road construction removes the forest vegetation, disturbs forest floor, and damages soil structure, which dramatically increases the sediment yield (Grace, 2002; Megahan 1974). Sediment delivered to streams from road sections leads to number of dramatic effects on water quality (Megahan 1974). On unsealed roads, road surface erosion is generally the dominant source of sediment (Ramos Scharrón and MacDonald, 2007). Road surface and ditch areas still continue to deliver sediment to the streams as long as the road is used. The production of sediment produced from road surface highly depends on traffic density, road surface type, road dimensions, and road gradient. The ditches receive the sediment yield from the cut-slope areas, depending on road section length, ground slope, and vegetation and rock cover density. In slope roads with ditch keep the runoff water away from the fill-slope which may cause much smaller sediment yield than road surface and cut-slope areas (Akay et al. 2008). Sediment can be eroded from all road features. The factors affecting surface erosion from roads include rainfall intensity and duration, snowfall, the characteristics of surface materials, the hydraulic characteristics of the road surface, road slope, traffic, construction and maintenance, and the contributing road area (MacDonald and Coe, 2008). Previous studies indicated that sediment production rates from unpaved road surfaces were several orders of magnitude higher than undisturbed hill slopes (MacDonald et al. 1997; MacDonald 2001). Changes in vegetation cover also might have played a role in declining sediment production (Ramos Scharrón, 2010). Ditches are potentially important sediment sources particularly when erosion is caused by scour from road runoff. Ditches may deepen or widen, or be filled with deposited sediment during rainfall events (Croke et al. 2006; Lane and Sheridan 2002). Several studies found the sediment production between 0.01 and 105 kg m^{-2} yr^{-1} depending on the several observation time, different cut slopes characteristics, cover density and parent material (Table 1).

Sediment production from unpaved roads was significantly related to total rainfall, road segment slope and graded or no graded (Ramos Scharrón and MacDonald 2006). Ramos Scharrón and MacDonald (2006) obtained a different result measured sediment production rates for graded roads ranged from 5.7 to 580 Mg ha^{-1} yr^{-1} for roads with slopes of 2% and 21%, respectively. The sediment production rate for ungraded roads was about 40% lower than for comparable graded roads. Abandoned road segments had a mean erosion rate of 12 Mg ha^{-1} yr^{-1}. Reid and Dunne (1984) report that a heavily used road contributes 130 times as much sediment as an abandoned road and a paved road, along which cut slopes and ditches are the only sources of sediment, yields less than 1% as much sediment as a heavily used road with a gravel surface.

Kartaloğlu (2011) has been determined that through sediment traps established on unpaved (UPFR) and paved forest road (PFR) ditch and in an undisturbed (UA) area at Belgrad forest-Istanbul, Turkey between date of November 2009 to October 2010 (12 months) (Fig.4 and 5). In this research reported that significantly differences were found on sediment productions among experiment sites (UPFR, PFR and UA). Annual sediment production was 0.654 t ha^{-1} yr^{-1} on UPFR, 0.334 t ha^{-1} yr^{-1} on PFR and 0.056 t ha^{-1} yr^{-1} on UA. Total sediment production of UPFR was 1.96 times higher than to PFR and 11.68 times higher than UA. Kartaloğlu (2011) stated that monthly sediment production on UPFR significantly higher than the PFR an UA for each month and it clearly shows that stabilizing cover on forest road led to less sediment production and more soil protection. Significantly differences on monthly sediment production were determined among experiment sites in all observation period (12 months).

Location	Cutslope description	Reported sediment production rate	Normalized sediment production (kg m^{-2} yr^{-1})	Reference
Georgia, USA	Unvegetated	102–230 Mg ha^{-1} yr^{-1}	5,1-11	Diseker and Richardson (1962)
Oregon, USA	6–7 yr old cutslopes	153 Mg ha^{-1} yr^{-1}	15	Wilson (1963)
	New cutslopes	370 Mg ha^{-1} yr^{-1}	37	Wilson (1963)
Oregon, USA	5 yr old cutslopes	0.5 cm yr^{-1}	7,5	Dyrness (1970 and 1975)
	1 yr old cutslopes	0.7 cm yr^{-1}	10	Dyrness (1970 and 1975)
Idaho, USA	45 yr old cutslopes, soil	0.01 m^{3} m^{-2} yr^{-1}	15	Megahan (1980)
	45 yr old cutslopes, granite	0.011 m^{3} m^{-2} yr^{-1}	16	Megahan (1980)
Washington, USA	55-70 degrees	16.5 mm yr^{-1}	25	Reid (1981)
Papua New Guinea	NA	70 mm yr^{-1}	105	Blong and Humphyreys (1982)
Idaho, USA	NA	11 mm yr^{-1}	16	Megahan et al. (1983)
New South Wales, Australia	NA	2.4–3.9 mm yr^{-1}	3,6-5,8	Riley (1988)
New Zeland	Unvegetated, granite	NA	5,2-15	Fahey and Coker (1989 ve 1992) Smith and Fenton (1993)
Idaho, USA	Cover density 0.1–89%, 55–104% gradient	0.1–248 Mg ha^{-1} yr^{-1}	0,01-25	Megahan et al. (2001)
St. John, USA	Unvegetated, 2–5 m high	NA	2-17	Ramos-Scharrón and MacDonald (2007)

Table 1. Estimated cutslope contribution to sediment yields at the road segment (Ramos-Scharrón ve MacDonald, 2007).

Fig. 4. Sediment traps on forest road and collected sediments on sediment traps at Belgrad Forest-Istanbul, Turkey (Kartaloğlu, 2011).

Fig. 5. Collected sediments on sediment traps at Belgrad Forest-Istanbul, Turkey (Kartaloğlu, 2011).

4. Forest harvesting impacts on forest ecosystems

4.1 Vegetation

Production work being carried out in the forest have many negative impact on the forest ecosystem is well known. Skidding or yarding on terrain requires the construction of relatively dense network of forest roads including skid roads, haul roads and landings (Demir et al. 2007a; Demir et al. 2008; Ketcheson et al., 1999; Makineci et al. 2007a; Makineci et al. 2007b; Swift, 1988). It has also been determined that the forest harvesting, timber production and timber skidding negatively affect the amount and variety of forest floor and herbaceous understory as well as youth development and living conditions of the soil organisms (Arocena, 2000; Bengtsson et al., 1998; Gilliam, 2002; Godefroid and Koedam, 2004; Johnston and Johnston, 2004; Marshall, 2000; Messina et al., 1997; Wang, 1997; Williamson and Neilsen, 2003).

Several studies have documented varying degrees of reduced tree growth on non-rehabilitated skid roads, ranging from 15% to 59% averaged over the trail, when compared to trees grown on undisturbed soil in the same cut block (Smith and Wass, 1980; Thompson, 1991). The wide variation in previous findings may be due to species and site-specific responses to soil disturbance, variations in the severity of disturbance, or other growth limiting factors that may magnify or alleviate the impacts of soil disturbance (Lewis, 1991; Dykstra and Curran, 2000). Sat Gungor et al. (2008) stated that ground based skidding destroyed the soil and ecosystem and the timber skidding limits recovery and growth of plant cover on skid roads. However, some herbaceous plant species show healthy habitat, and they can revegetate and survive after the extreme degradation in study area. Earlier results clearly show that skidding has particularly negative impacts on herbaceous cover, forest floor and soil. These effects of skidding on skid road have been demonstrated to have detrimental impacts on native flora and herbaceous plant establishing and maintaining were limited. Similarly, Mariani et al. (2006) reported that organic layer removal reduced abundance of herbs and shrubs.

Soil compaction can also severely reduce plant growth by restricting root growth may be due to oxygen stress and lower the percentage of water and air space in the soil (Berzegar et al. 2006). Also, Kozlowski (1999) mentioned a reduced total photosynthesis when soils become increasingly compacted, as a result of smaller leaf areas.

Yilmaz et al. (2010) reported that significant differences on widths of annual rings, dbh growth and increment values are found same tree species when in an undisturbed area and adjacent to a road under the same microclimate and site conditions, supporting the notion that long term timber skidding reduces the annual ring width, dbh growth and increment of nearby trees. The trees growing there commonly display better growth and diameter increment than the trees growing on the skid road. Tree growth and increment on the undisturbed area was found to be about 60% greater than the skid road.

4.2 Soil

Logging operations can cause significant and wide spread soil disturbance, including removal, mixing and compaction of the various soil layers (Demir et al. 2007b ; Demir et al. 2010; ; Makineci et al. 2007c; Makineci et al. 2007d; Makineci et al. 2008) . Ground based skidding, timber harvesting and logging operations in forest ecosystems cause the reduction and redistribution of organic matter, changes in plant cover, organic layer and soil properties, and modification of microclimate (Buckley et al., 2003). Timber harvesting can adversely affect both soil physical properties and soil nutrient levels. Logging can cause diminished growth of subsequent tree rotations, significant increase in runoff and sediment loads (Laffan et al., 2001). Erosion of organic and nutrient rich surface soil and compaction decrease forest productivity (Pritchett and Fisher, 1987) and the transport of sediment to streams and subsequent sedimentation lead to loss of stream habitat and altered stream hydrology. The soil micro flora and fauna complement each other in the commination of litter, mineralization of essential plant nutrients and conservation of these nutrients within the soil system. Harvesting directly affects these processes through the reduction and redistribution of organic matter, compaction, changes in plant cover, and modification of microclimate (Marshall, 2000).

The extent of severe disturbance from ground based timber harvesting systems varies due to slope and terrain, timber harvesting machines, methods of designating skid roads and harvesting season. Forest harvesting and ground based skidding may result in soil compaction and other soil structural changes, influencing soil water retention, and reducing soil aeration, drainage and root penetration (Froehlich et al., 1986). Soil damage on forest roads, skid roads and landings includes the removal of the organic layer and topsoil, soil compaction and erosion of the exposed soil. The soil damage affects hill slope infiltration and surface and subsurface flows (Binkley, 1986).

5. Conclusion

Sustainable forest management requires an adequate understanding not only of the forest ecosystem but also of the interaction between different disciplines. The planning process and finding the appropriate balance of different interests for the use of our forest and landscape resources will be vital to the achievement of the goal of sustainable forest management. The main purpose in the planning of forest roads is that, when then unfavorable effects of planned and constructed forest roads on the forest ecosystem are compared with the benefit to be derived from the roads constructed as a result of planning within the concept of sustainable forest management, such benefit must be within the acceptable limits. In this context, it has become evident that the density and road space criteria presently employed to provide each piece of a forest area with a systematic forest road network in order to enable it to fulfill its planned functions shall not be equally applicable to every area. In summary, it is recommended that the purposes of management of forests should be put forth in detail, and the road density and road space values to enable the realization of these purposes should be determined separately (Demir, 2007).

Roads affect both the biotic and the abiotic components of landscapes by changing the dynamics of populations of plants and animals, altering flows of materials in the landscape, introducing exotic elements, and changing levels of available resources, such as water, light and nutrients (Coffin, 2007).

In the recent years, an ever-increasing trend has been observed in public consciousness regarding environment. This has led to the creation of a medium of constant controversy between the foresters and environmentalists. The main issue of controversy is centered on the argument that the construction of forest roads destroys the natural environment to a great extent, causes soil erosion, completely destroys the habitat and impairs the integrity of landscape. As stated also in the declaration issued by UNCED (United Nations Conference on Environment and Development), the utilization of nature's renewable resources is a key component of development based on environment. It is, however, an essential requirement that access to relevant areas be provided for utilization of resources concerned. Therefore the construction of forest roads can in no case be abandoned. It follows, however, that relevant forestry organizations are obliged to figure out new ways that could be approved by the public and would cause no harm to the environment (Heinimann, 1996).

Coffin (2007) stated that roads have many direct ecological effects on adjacent aquatic and terrestrial systems, as network structures, they also have far reaching, cumulative effects on landscapes (Riitters and Wickham, 2003). Some major effects to landscapes that directly relate to roads include the loss of habitat through the transformation of existing land covers to roads and road-induced land use and land cover change (Angelsen and Kaimowitz, 1999) and reduced habitat quality by fragmentation and the loss of connectivity (Theobald et al., 1997; Carr et al., 2002). Together they point to the larger issue of the synergistic effects of roads and road networks on ecosystems at broader scales (Forman et al., 2003).

In tropical forested areas, econometric models of land use and land cover change have revealed important relationships between biophysical and economic variables relative to roads. In rural areas, particularly in developing countries, the presence of roads has been most strongly correlated with processes of land cover change by facilitating deforestation (Chomitz and Gray, 1996; Angelsen and Kaimowitz, 1999; Lambin et al., 2001; Mertens and Lambin, 1997). There are a variety of different effects of roads in boreal, temperate, Mediterranean, tropical and sub-tropical or alpine forest ecosystems.

In this study, tried to give interactions of forest roads, forest harvesting and forest ecosystems. Furthermore, the study results were tried to give related to the subject in the world and Turkey. Despite the negative impacts of forest roads, forest harvesting and wood transports the realization of sustainable forestry on these structures, and studies are needed. Forest roads construction, forest harvesting and wood transports eliminating the negative effects to the realization of appropriate technique.

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19

Forest Transportation Systems as a Key Factor in Quality Management of Forest Ecosystems

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1. Introduction

Forests and forested land cover 24,018 km^2 in the Republic of Croatia, which accounts for 42% of its land surface. Its greatest part consists of state-owned forests (2,018,987 ha or 75.10%), which are, just as other forests owned by state institutions (87,930 ha or 3.30%), managed by the company »Hrvatske Šume« Ltd. Zagreb, through its 16 Forest Administration Units, distributed throughout the territory of the Republic of Croatia. A significantly smaller forest surface is in private ownership (581,770 ha or 21.60%).

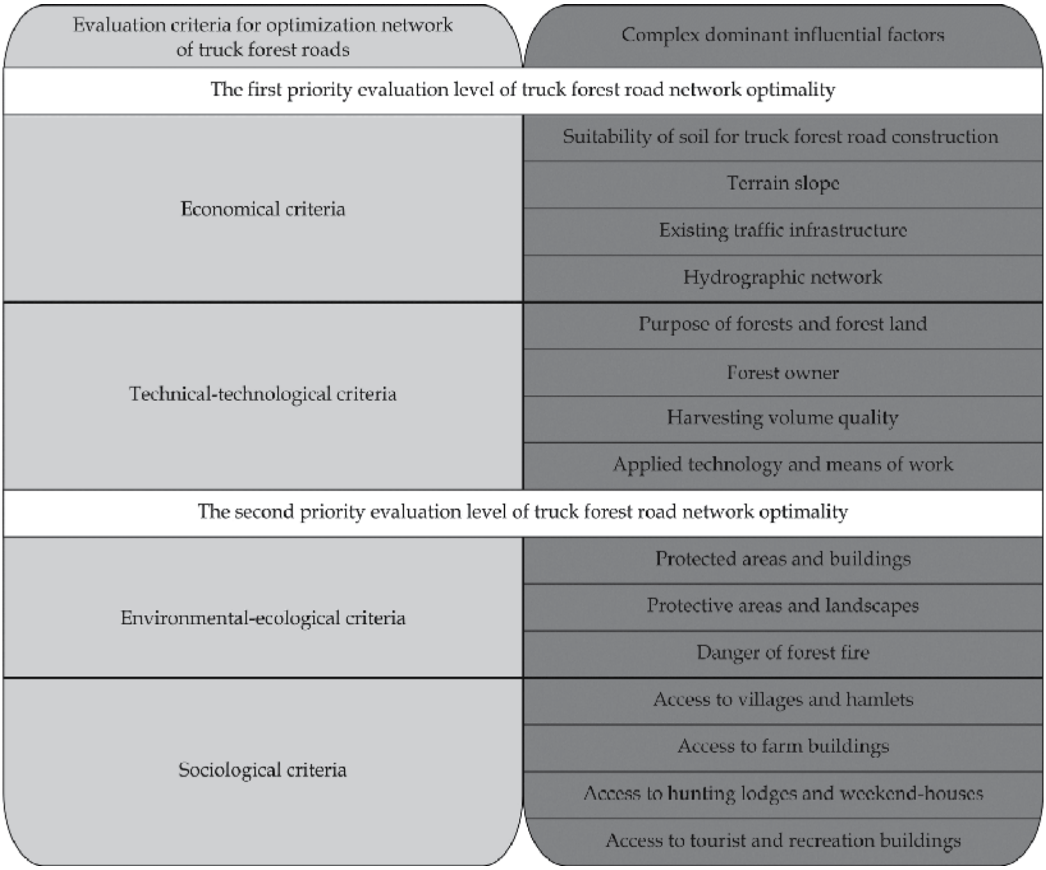
It is indisputable that the forest transportation system is a required and above all necessary precondition in today's modern, technologically advanced, rational, economical, ecologically orientated, environmentally-friendly management of forest ecosystems, based on biodiversity, natural forests and income sustainability.

Type, amount and layout of all forest transportation system components have to be carefully planned in order to establish a truly optimal forest transportation system within a forest. The optimal quality of a primary forest transportation system is estimated from economic, technical-technological, environmental (ecological-esthetical) and sociological point of view, and it is necessary to achieve harmony among all the mentioned evaluation criteria, as well as reach the level of overall optimization (all evaluation criteria have to be brought within the limits of acceptability).

Each evaluation criterion of the optimal quality of the existing transportation system is composed of complex dominant influential factors (which combine close and mutually dependent simple dominant influential factors).

1.1 Environmental component of establishing the forest transportation system

As it was mentioned previously, the forest transportation system is an indispensable and obligatory component in quality management of forest ecosystems. Forest roads, both primary and secondary, are still a foreign body in a forest, therefore, in their planning, design, construction and maintenance (repairs) and possible reconstruction, we should take into account the minimal disruption of the laws, relations and balance existing in a forest ecosystem. When individual primary forest roads or secondary forest roads of permanent character (skid roads) are no longer necessary for forest ecosystem management, or in time they have lost most of its function because of which they had been built, they should be closed down, disbanded, and the surface on which they had been built should be restored to its previous purpose (productive forest land) by technical and biological methods. The procedure of removing the unnecessary (redundant) forest roads and restoring the habitat is neither cheap nor short, but it is necessary and, in the end, cost-effective in the long run.



Evaluation criteria for optimization network of truck forest roads	Complex dominant influential factors
The first priority evaluation level of truck forest road network optimality	
Economical criteria	Suitability of soil for truck forest road construction
	Terrain slope
	Existing traffic infrastructure
	Hydrographic network
Technical-technological criteria	Purpose of forests and forest land
	Forest owner
	Harvesting volume quality
	Applied technology and means of work
The second priority evaluation level of truck forest road network optimality	
Environmental-ecological criteria	Protected areas and buildings
	Protective areas and landscapes
	Danger of forest fire
Sociological criteria	Access to villages and hamlets
	Access to farm buildings
	Access to hunting lodges and weekend-houses
	Access to tourist and recreation buildings

Fig. 1. Structure of evaluation criteria for the optimal quality of the primary forest transport system estimation.

In the overall procedure of establishing each of the components of an optimal forest transportation system, the forest experts-designers should be guided with the idea of achieving an undivided whole consisting of constituents-habitat-forest road. In order to make that possible, the most important rules for the establishment of environmentally-ecologically-esthetically suitable truck forest roads in the planning and designing stage will be stated below:

While planning the environmentally-ecologically-esthetically suitable truck forest roads, the following remarks should be adhered to.

- Forest opening should be based on the *Studies of Primary and Secondary Forest Opening* of certain forest areas made according to a scientific-expert principle, because this is the only way to produce comprehensive, generally acceptable solutions.

- The production of a *Study of Primary and Secondary Forest Opening* should include all physical and legal entities (private forest owners, local government and self-government units, relevant ministries and institutions, etc.) which find it in their interest to participate in forestry planning (in this case, in planning truck forest roads).
- Bounded areas (protective zones) should be laid around the waterway network at a distance of at least 50 m.
- Truck forest road routes should not be laid in the immediate vicinity of accumulations and water-protective areas, unless it is absolutely necessary or contrary to the laws and sub-acts. Furthermore, lakes, surface waterways of permanent and periodic character, as well as the areas around water surfaces should be avoided.
- Low-land truck forest roads in the immediate vicinity of waterways may influence on the disruption of the underground water system, which would alter the microclimatic conditions of the site, resulting in a physiological decline of trees, lower quality of harvesting volume, and in the end, dieback and degradation of forests. The communication among underground water (even by means of artificially constructed technical objects) should be ensured.
- Because of rough ground conditions and required communication, it is necessary to set a truck forest road crossing over the waterway, subject to prior water management use approval, waterways should be crossed in their upper flow, and the road should not in any way influence on the change of the waterway direction and course. From the ecological and technical point of view, bridges would be preferred over roads, but they are expensive and non-profitable when it comes to low flow waterways.
- It is good to prefer soft construction material categories (soil with smaller or greater share of rock and softer rock), because on the one hand, earthwork expenses are low, and on the other, these categories have qualities sufficient for forming a quality truck forest road structure. The key factor in categorizing construction land favorability is its internal strength and hardness, or the share of rocky material of certain hardness in the overall amount of soil.
- Non-bearing base substratum, or soils having poor bearing capacity or none at all, should be avoided, because the construction procedure requires the use of one of the stabilization methods (soil improvement) or delivery of significant quantity of rock material in forming the truck forest road structure. Furthermore, such soils are quite often erosive, which increases the subsequent costs of truck forest road maintenance, as well as repair of possible damage and disturbing the forest ecosystem balance.
- Various categories of average terrain inclination are not equally favorable for truck forest road construction; therefore, it might be concluded that it is more favorable to construct truck forest roads on terrains with gentler average inclination than those with greater average inclination. Average terrain inclination has a direct influence on the transversal terrain inclination (terrain inclination perpendicular to the truck forest road axis), which dictates the terrain configuration at the truck forest road cross-section and has an influence on the amount of excavation and material filling during construction.
- In average terrain inclination of over 70%, it is very difficult to make stable excavation and embankment slopes in truck forest road construction of a normal cross section profile of fill slopes, so the danger of erosive processes is quite serious. In addition, in the process of construction, the level line elevation must be lowered deep below the terrain elevation at least for the roadway width, in order to make a normal cross-section

profile of the fill slope (or the technology of embankment construction is used on inclined terrains with the use of excavators). Therefore, forest road construction on inclined terrains, particularly on slopes with an inclination of over 70%, is very expensive and demanding, it significantly encroaches upon the forest ecosystem and causes possible significant damage on the same, so truck forest road construction is not recommended on the slopes with an inclination of over 70%.

The following recommendations are stated for the design of environmentally-ecologically-esthetically suitable truck forest roads:

- The main truck forest road projects should be produced by authorized independent designers – foresters, who will gain the mentioned title by taking a professional examination at the *Chamber of Forestry*, and later on design the proscribed number of truck forest road kilometers, first with the guidance of a senior authorized designer, and only then independently.
- It is necessary to have good *Technical Requirements for Truck Forest Roads* in the framework of which the basic components of truck forest road main design content should be defined, with a detailed analysis of each sub-appendix in order to achieve uniformity and standardized quality of produced projects.
- A professional, qualified committee for the revision of produced projects should be constituted within the Chamber of Forestry, which would ensure the credibility and quality of technical documentation prior to starting a construction business.
- Integrating the truck forest road level line into the existing longitudinal profile of the terrain is one of the more sensitive and more responsible jobs of a designer in the very procedure of project production. The positionally (horizontally) fixed route (in the direction of x and y coordinates) should be defined in the direction of the z-axis as well. Balance should be found between the efforts to integrate the route as well as possible into its surroundings and satisfying minimal proscribed technical requirements of a certain truck forest road category.
- From the point of view of minimal costs of subsequent upper structure maintenance, the most favorable solution would be to design the truck forest route level line on an inclination of 4 to 6%. This is also a favorable longitudinal inclination for traffic operation. On level line inclinations greater than 8%, besides other drainage structures, it is necessary to make soakaways (transversal drainage ditches over the truck forest road structure at an angle of 30^o on the longitudinal road axis).
- Maximal values of longitudinal inclinations of truck forest road level line should remain within permitted limits, while the same should be applied only on the most difficult parts of the route and on as short a distance as possible. The consequence of the use of great road inclinations in longitudinal direction is a significant problem which leads to harmful erosive effects of water on the upper structure and its washing away. This automatically requires high maintenance costs and investment into the construction of drainage elements.
- The maximal permitted longitudinal level line slopes are connected with the truck forest road category and the terrain configuration opened by a road. Before, between and after the maximal longitudinal slopes, smaller level line slopes are integrated, in order to provide a relief to the vehicle engine, as well as to reduce the strength of erosive influence of water.

- The distance between oppositely directed vertical curve apex should be at least 60 m (the exact value depends on the value of level line grade change points) in order to ensure a straight level line stroke of minimally 35 m between the end of the previous and the beginning of the following vertical curve arc (it would be better if we could achieve greater distances). We are often torn between the wish to follow the ground conditions as well as gaining minimal costs (greater distance between vertical curve apex are proportional to the earthwork volume and its value), and simultaneously respect the rules described in this passage.
- Considering the level line slopes, the grade change points become round in concave or convex vertical curve arches. The following factors must be decisive in the choice of vertical curve radius: safety against grinding of the bottom part of the vehicle against the truck forest road surface, safety against lifting the wheels off the road under the influence of the centrifugal force, and sufficient visibility of the road in case two vehicles meet at the vertical grade change point. The minimal radius of concave vertical curves amounts to 200 m, while the least radius of convex vertical curves amounts to 400 m.
- The reduction of the level line longitudinal slope at steep and step-like terrains is often possible only by increasing the earthwork volume. This is more expensive at the beginning, but in the end, it is a much better solution because the overall costs in the truck forest road depreciation period are definitely reduced when compared with maintaining greater level line slopes with fewer initial construction costs.
- The truck forest road route level line should be laid in a way as to avoid the deep cuttings and high embankments (over 3 m) because, besides representing an aggression to the environment, they also have little esthetic value. The so-called „dead sections" of truck forest roads render it more difficult to perform works of forest harvesting, and other primary or secondary forest roads cannot be connected to them. The same are justified in the case of the necessary crossing of truck forest road route over prominent ridges and larger lowlands when the terrain configuration simply does not enable a different, better solution.
- In designing level line, account should be taken of the land mass distribution diagram. A quality distribution of land masses presupposes equal amounts of excavation and embankment at a distance of up to 50 m, with at least oscillations of the cube profile ordinate curve as possible around the x-axis. This puts the cheaper side material transport into the limelight, thus avoiding the longitudinal material transport at longer sections.
- Often not even the use of the greatest allowed level line slopes can negotiate a certain altitude difference, which is why truck forest road constructive elements are made, characteristic, above all, for mountainous and hilly areas – switchback. When they are unavoidable, switchbacks should be laid on locations of milder transversal terrain slopes (up to 40%), in order to avoid greater works on the terrain and the necessity of constructing retaining walls, but also for reducing danger of stimulating erosion processes.
- In lowland areas, special attention should be paid to raising the truck forest road route level line, owing to drainage above the surrounding terrain, that is, above the level of the highest water. The level line slope must amount to a minimum of 0.5%, because in smaller level line slopes there is more damage on the upper structure due to the interaction between vehicles and water retaining on the roadway.

- Minimal diameters of horizontal circular arches amount to 20 m and they should be avoided, because they have an indirect influence on the truck forest road width by widening the road in the curves, reducing the safety of operation speed and having a negative influence on the safety of traffic. However, the fact is that we often follow the terrain owing to the road construction cost-effectiveness in the hilly and mountainous area, which of course, has an influence on laying the route with smaller diameters. Therefore, it is necessary to find an optimal compromise in such terrains between the well-integrated truck forest roads into the terrain contours on the one hand, and the safety of traffic, minimal diameters of horizontal curves, cost-effectiveness of construction and other relevant environmental, technical, financial, ecological and social factors, on the other.
- Passing areas (full or partial) are built on straight lines, outside vertical curves, on smaller longitudinal level line slopes and points with good visibility, often on the excavation side of fill slopes (due to stability), at a distance of 200 to 500 m. Their task is to ensure the possibility of evasion of two vehicles moving in opposite directions, as truck forest roads are made with one lane.
- Taking into consideration everything that was said before, a passing area should be located, according to the designer's evaluation and perhaps according to the collected samples, where there is material, which by using certain contemporary, environmentally friendly work technologies and technical means, might be used for the building into the upper structure. That is a soft and averagely tough rocky material, in which excavations can be done by means of a hydraulic hammer excavator (without the use of explosives). In this way, we avoid the opening of stone material borrow pits (quarry) in a forest, thus completely reducing or decreasing the need for the supply and delivery of stone material of a certain granulation from often very distant quarries (the overall costs of procurement and remote transport of the stone material do not incur the total expenses of truck forest road construction).
- Drainage ditches of trapeze or triangle shape (grader ditches) are always at the internal (excavating) fill slope side. Water from the drainage ditches can be drained into the surrounding terrain, and in order for the ditches to preserve their function, they need to be regularly maintained.
- Pipe culverts should be built on the crossing of truck forest road routes over small capacity surface waterways, which, considering their cross-section might be round or square, and they are most often made of reinforced concrete. The diameter dimension is determined with regard to the calculated water flow. Each culvert, regardless of its dimension, must be set in an appropriate way at sufficient depth under the level line elevation (so that during traffic operation they would not break).
- The junction of truck forest and asphalt public roads (crossroads) should be made in accordance with the proscribed Technical Requirements. The approach from a truck forest road into an asphalt public road should be elevated between 2% and 4%, so that during precipitations the stone material would not be washed away from the truck forest road into the public road, thus endangering traffic. If it is not possible to follow the proscribed inclinations, then the end of the truck forest road superstructure (20 m in length) should be made with concrete or asphalt carpet.
- The retaining walls are used for the stabilization of embankment slope, shortening the length of embankment and reducing the volume of material that should be fitted into

the embankment on steep terrains. There are several forms of retaining walls, but regarding all of them, attention should be paid to regular dimensioning and fitting into the environment (which will best be achieved by using autochthonous stone material, which besides their functionality will provide the retaining walls with a more prominent esthetic function). Similarly, lining walls built on the excavation side of the fill slope and serving for the repair of excavation slopes (they do not carry the traffic burden).

- Owing to the evaluated construction material category, while forming cross-sections, it is necessary to make the excavation slopes and the embankment slopes at a certain inclination. Besides reducing the possibility of material sliding down to the surface of the roadway and endangering traffic (at the excavation side), as well as material sliding down the embankment, damaging trees at the lower side of the truck forest road and stimulating erosion processes, it also achieves an esthetic effect and a more pleasant surroundings for the drivers. Besides the mentioned ones, there are other technical recovery methods of excavation and embankment inclinations, which should definitely be combined with biological methods of recovery, because that is the only way to achieve the ultimate effect.

2. Research area

2.1 Classification of forest transportation systems

Forest transportation systems may be classified into primary, secondary and special-purpose forest transportation systems. Public roads are a generally common good owned by the Republic of Croatia, and according to the Public Roads Act (Official Gazette no. 180/04, 82/06, 138/06, 146/08, 152/08, 38/09, 124/09, 153/09, 73/10 and 91/10), depending on social, traffic and economic significance, they may be: motorways, state roads, county roads and local roads.

Primary forest transportation system consists of all categories of truck forest roads, as well as public roads which may be used for forestry operations (these are often lower level public roads – county roads and local roads). Forest roads are permanent construction facilities, enabling constant motorcar traffic for the completion of tasks anticipated by the Management Plan. With their construction, the amount of productive land in a forest is permanently reduced (except in the case of their closing down and revitalizing sites). They consist of a lower structure and an upper structure with all technical characteristics of a road. They may be divided on the basis of several criteria.

The components of secondary forest transportation system are secondary forest roads: skid roads, skid trails and cable yarder corridors. Their main purpose is timber extraction from the bunching point to roadside landing (primary timber transport) and, occasionally, completing assignments anticipated by the Management Plan. From the roadside landing to the ultimate user, timber may be transported by constructed transportation systems (forest and public roads, as well as railroads) or waterways (rivers, lakes, seas, oceans).

Skid roads are construction facilities of permanent character (except in the case of their closing down and revitalizing sites), built only with a lower structure. They are associated with sloping terrains, heavier material construction categories and the presence of surface obstacles.

Skid trails are secondary forest roads of temporary character, made by cutting a route through a forest, possible extraction of stumps and a repeated passing of a timber extraction machine (skidder, forwarder) on the same route. They are characteristic of flat terrains, lighter material construction categories and the absence of surface obstacles (easily passable terrains).

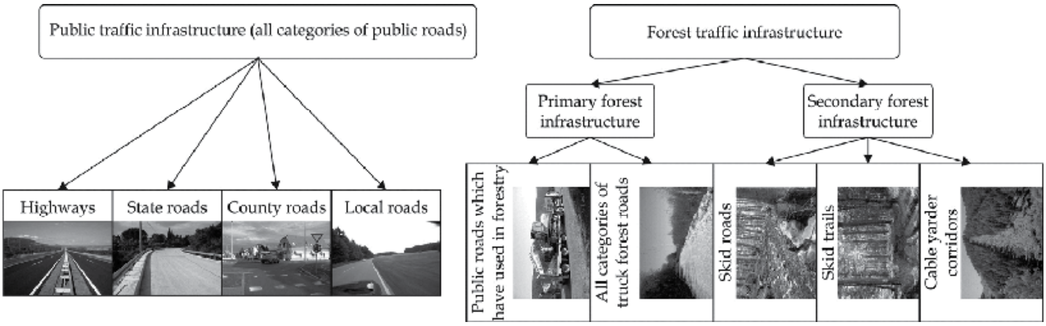


Fig. 2. Classification of forest transportation system.

2.2 Stages of establishing an optimal forest transportation system network

Establishing an optimal network of forest roads in the field has to unfold through the following operational stages: planning, designing, construction with supervision and maintenance/repairing (*Pentek et al. 2004*). These stages are mutually related and dependent, they should be performed in the order as they are stated, taking into account the unfeasibility of each of the operational stages in case the previous one has not been completed in a satisfying manner.

Besides the mentioned, always present stages of forest transportation system optimization, there are occasionally two additional operational stages: stage of forest roads reconstruction (in order to increase their standards when it comes to forest roads, or turning skid roads into forest roads) and the stage of forest road removing/restoring (besides the revitalization/restoration of sites, or restoring the function and form of a site as close as possible to what it had been before the road was built).

2.3 Planning of forest roads

A comprehensive planning of forest roads is the first, initial and unavoidable stage of establishing an optimal forest transportation system network in the field. In the last 20 years, GIS (Geographical Information System) is applied in primary and secondary forest opening, in combination with other contemporary technologies (*Pentek, 2007a*). The data required for making a quality GIS of a research area are collected from the following sources (*Pentek, 2002*): thematic maps, computer databases, written databases, Management Plans, field measurements, field observations and notes, other sources, arithmetic and logical operations with the data from previously mentioned sources.

The result of a contemporary approach to forest opening are the Studies of Forest Opening (primary and secondary), made for the period of 10 (20) years, after which they are renewed or revised. These documents are considered as a part of tactical planning in forestry. Tactical plans provide answers to the question of what to do in order to achieve the set goals of strategic planning and what decisions are necessary for that (*Kangas and Kangas, 2002*), and they are made for a shorter period of time (depending on the circumstances, they cover a period of 5 to 20 years); they result in a list of measures (operations or interventions) planned to be done within the following time period.

2.3.1 A study of primary forest opening

Every good Study of Primary Forest Opening should contain the following data:

- for the existing forest transportation system:
    - a complete (updated) cadastre of the existing primary forest transportation system,
    - a complete (updated) cadastre of the existing secondary forest transportation system,
    - the existing primary and secondary road density (m/ha),
    - the existing mean distance of timber extraction for each particular compartment (m),
    - the target primary road density and the target (planned) mean distance of timber extraction calculated from it,
    - numerical, graphical and pictorial (map) results of the analysis of the existing relative primary openness;
- for the improved primary forest transportation system:
    - numerical, graphical and pictorial (map) results of the analysis of the existing relative primary openness for the improved primary forest transportation system,
    - primary road density of the improved primary forest transportation system (m/ha),
    - mean distance of timber extraction for each particular compartment (m),
    - conceptual route of planned truck forest roads (defined by the coordinates of route break-points),
    - category of each conceptual truck forest road route,
    - cost component (anticipated expenses) and economic justification for the construction of each conceptual truck forest road route,
    - dynamics of the construction of the overall (optimal) future primary forest transportation system network, aligned with the proscribed works in the Management Plan,
    - dynamics of the maintenance of the overall (optimal) future primary forest transportation system network,
    - other data significant for any of the stages of establishing the optimal primary forest transportation system network.

2.3.2 Primary road density

Primary road density represents the sum of lengths of all components of primary forest transportation system (which influence on the openness of the respective area) divided with the surface on which the respective roads are located. It is expressed in m/ha or km/1000 ha. *Šikić et al.* (1989) defined the fundamental criteria on the basis of which a certain road, or a particular part of it, is taken into consideration when calculating primary road density.

Pentek (2002) distinguishes five basic variants of primary road density:

- The existing primary road density – calculated for the existing (real) primary forest transportation network of a certain forest area, often a Management Unit,
- Minimum required primary road density – set for a greater forest area, in most cases related to a relief area, used in the strategic planning of forest-management area as a minimum goal which should be reached within a given time period for a more rational forest management,
- Planned primary road density – it is also set for a greater forest area (relief area), and serves as a marker within a defined time period in the strategic planning of forest-management area and in making long-range plans of primary forest transportation system construction,
- Target primary road density – most often defined for a management unit area and represents the final goal of primary road density of a certain forest area; it is closely connected with the methods and procedures of timber harvesting, as well as morphological relief characteristics in a specific Management Unit; it is used in the context of tactical planning and making Studies of Primary Forest Opening,
- Optimal primary road density – calculated by applying a known method of primary forest transportation system optimization; it is related to the management unit surface area and is most often based on the model of minimum overall cost of timber harvesting.

Relief area of the Republic Croatia	**Minimum required road density**	**Planned road density 2010th**	**Planned road density 2020th**
	km/1000 ha		
Low-land area (Flat terrain)	7.00	15.00	It is not the subject of research
Hilly area	12.00	20.00	25.00
Mountainous area	15.00	25.00	30.00
Karst area	No data	10.00	15.00

Table 1. Minimum required (*Šikić et al. 1989*)., planned 2010th(*Anon., 1997*) and planned 2020th (*Pentek et al. 2007a, Pentek et al. 2011)* primary road density for different relief areas in Croatia.

2.4 Truck forest roads designing

To design a certain truck forest road (*Pentek, 2010b*) means to conceptualize it, describe it and present it arithmetically and graphically. Only a completely finished main truck forest road design may be analyzed, and construction may ensue after its approval.

Designing truck forest roads consists of collecting general and technical data, as well as route layout and design creation. The first stage of designing includes collecting general and technical data, which present a basis for making a feasibility study. Route layout (field measurement) and design creation (office data processing and print-out of results) represents a designing components which combines all field and office route layout work, making of investment program, as well as conceptual, general and main forest road design.

Truck forest road layout is performed by way of a direct layout. The result of the planning stage, observed from the level of a single truck forest road, is a larger number of projected zero line variants (at least three) on forest-management contour maps with the scale 1:10000 or even better 1:5000 in digital form. These are the so called conceptual layouts of the future truck forest road.

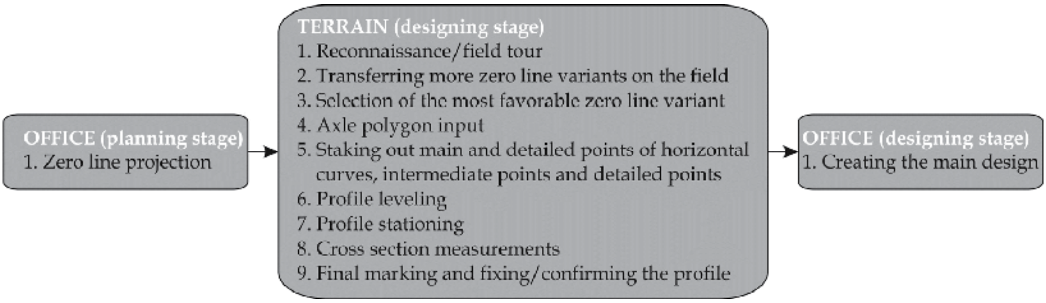


Fig. 3. Direct layout – basic operation stages.

Two procedures may be applied in truck forest road designing (*Pentek, 2010*), according to the valid regulations – short procedure: implies the making of the conceptual and main truck forest road design; and full or complete procedure: encompasses the making of conceptual, general and main truck forest road design.

Conceptual design – this design deals with the conceptual layouts of truck forest roads, along with the making of technical and economic study. It is made on contour maps with the scale 1:5000, 1:10000, 1:25000 and 1:50000. Maps need to have a marked management division – borders Management Units, compartments and sub-compartments as well as a complete cadastre of primary forest transportation system (if possible, also the cadastre of secondary forest roads). Important components of the maps are permanent and occasional waterways. It is necessary to be acquainted with the Management Plan, as well as study the information about growing stock, harvesting volume (allowable cut) and timber assortment structure of an individual compartment and a harvesting plan. The contour map has to contain more zero line variants for each truck forest road. At the same time, attention should be paid to key points, which have to be connected by the future route, as well as to the position and capacity of landings, branching of skid roads, etc. All zero line variants are transferred to the field, the most favourable one is chosen, and then follows the making of a rough cost estimate and a technical and economic study for it.

General design – made on the basis of previously made and approved conceptual design. Tachometry measurement is made around the operative polygon of conceptual route (in order to make a contour plan). Then, a contour plan is made in the office, the axle polygon is integrated into the zero line, horizontal curves of the selected radius are determined and drawn in. A longitudinal section is drawn on the basis of a situation plan, and cross sections are made based on a round level line in order to make a report of land work cubage. General design provides more realistic technical and economic indicators on the future truck forest road than the conceptual design.

Main design – made on the basis of the conceptual and general design, or just on the conceptual design. This is the most comprehensive design, which represents the basis for commencing the construction procedure.

• Court Register Certificate	• Declaration of conformity of project documentation	• Drawn longitudinal section
• Certificate on the Appointment of an Architect	• Calculation of mechanical resistance and stability	• Normal cross sections
• Certificate on Architect Authorization	• Technical description of forest road layout	• Drawn cross sections
• Ownership Certificate and a copy of cadastre plan	• Position plan	• Land mass cubage and a quantity statement
• Certificate of Title and a land register transcript	• Detailed position plan	• Mass-haul diagram
• Record of zero line handover	• Print-out of longitudinal section	• Bill of quantities
• Record of staked-out route handover	• Data on horizontal and vertical curves	• Estimate – priced bill of quantities
• Fire protection document		

Table 2. Basic components of the main truck forest road design.

2.5 Truck forest road construction with supervision

Following the designing stage, there is the construction stage with supervision, representing the greatest expense in the overall process of making a new truck forest road. In the Republic of Croatia (*Pentek, 2010*), the construction procedure, in the widest sense of the word, is performed through the following operational stages:

- carrying out the public tender procedure and the selection of the most favorable tenderer,
- signing the Implementation of Works Contract and reporting the work-site to relevant institutions,
- record on possession of site,
- renewal of construction stake-out of truck forest road axle layout,
- execution of works of truck forest road construction,
- permanent and occasional work supervision,
- taking-over certificate.

The works during truck forest road construction (*Pentek, 2010*) are divided into several main groups: preparatory works, works on lower structure, improvement of the soil with various stabilization methods, works on facilities of underground and surface drainage, works on incline/slope stabilization, works on upper structure and other works.

Until the middle of the 1990s, the construction of truck forest roads in all relief conditions was performed by means of dozers, while explosives and pneumatic hammers were used on rocky soils. Nowadays, in general, dozers are used in lowlands and for lighter material construction categories, while excavators fitted with hydraulic hammers are used on sloping terrains and rocky media. Explosives are applied only for the toughest rocks where the use of a hydraulic hammer would not yield satisfying results.

The choice of technology to be used in the construction of a certain truck forest road depends on the following: relief characteristics of the terrain where the works are performed, material construction categories on the truck forest road route, economic indicators, availability of construction machinery and equipment, valid regulations in the area of forestry, civil engineering, protection of nature and the environment, as well as other influential factors.

Lowland area (flat terrain)	**Hilly and mountainous area (inclined terrain)**
• non-bearing and poor capacity soil (necessary soil stabilization)	• heavy material construction categories (sometimes the use of explosives required)
• lack of rocky material on the forest road route	• large transversal inclinations of grounds
• distance of a quarry from the site (high cost of stone material transport)	• deep cuttings and high embankments (construction of retaining and revetment walls)
• developed hydrographic network – constant large flow waterways (necessary construction of bridges)	• danger of stimulating erosion processes
• high level of underground water (construction of embankment in order to raise the forest road level line, construction of drainage ditches)	• necessity of using larger longitudinal level line slopes
• significant oscillations of water levels in a forest stand (construction of overflow channels),	• necessity of using minimum horizontal curves radius
• avoiding the compartmentalization of forest areas (necessary construction of culverts)	• danger of sudden rush of water on the forest road route (construction of drainage ditches, culverts and soakaways)

Table 3. Most important problems encountered during truck forest road construction.

The construction of truck forest roads should be approached in a very responsible and professional manner, at the same time trying to the utmost to minimize their harmful (negative) influence on the forest ecosystem. Soil compaction and reduction of airiness, interruption of waterways, reduced biological activity in the soil, erosion, floods, landslide sites, etc., represent just some of the consequences of the construction and use of truck forest roads. A good way of achieving a balance between the forest ecosystem and truck forest roads is through high expertise and constant professional improvement of forest road designers, developed awareness of maintaining the forest ecosystem and knowledge of its functioning as a whole, good Technical Requirements for Forest Roads, valid and consistently respected regulations, good and thoroughly respected procedures of establishing optimal primary forest transportation system network (according to defined operational stages), and a selection of ecologically suitable construction technologies and construction supervision on more levels.

Expert supervision of truck forest roads construction on more levels is necessary in order to ensure the adherence to project documentation (main design of truck forest road), or transferring the vision and conception of forest roads designers from paper into the forest ecosystem. It is recommended to have designer's supervision because, besides guaranteeing expertise and a good knowledge of project documentation of a certain forest road, this kind of supervision provides good and fast elimination of possible vagueness or disputable situations.

Constant and occasional work supervision is performed on more levels:

- the construction site superintendent controls the machinist and keeps the Engineering Log and Engineering Record on a daily basis,
- the supervising engineer controls the contractors (machinist and construction site superintendent) and signs the Engineering Log and Engineering Record on a daily basis,
- occasionally and if necessary, the main supervising engineer controls the works,
- the final works control is performed by the Committee for Handover of Works.

2.6 Truck forest roads maintenance

Maintenance of truck forest roads represents a series of construction-technical procedures, which should be performed regularly in order to keep the roads in their original condition, in which they may complete all the tasks proscribed by the Management Plan. Construction cost and costs of truck forest road maintenance in the period of its depreciation (25 – 40 years, depending on the authors and calculation method) constitute the overall costs of truck forest road management.

As a rule (in normal weather conditions, the usual regime of usage and similar site and stand conditions), well-built truck forest roads require lower maintenance costs during the depreciation period than those truck forest roads in the construction of which the costs were cut down at the expense of quality or the works were in a hurry (each work needs to be realized within a certain time factor). In the end, the overall costs of well-built and well-kept truck forest roads are considerably lower than those of badly and quickly built roads (which often in certain periods of the year, during rough weather, cannot complete their tasks).

2.6.1 Forest road maintenance types

According to the frequency and regularity of performing maintenance works, there are several types of maintenance:

- Regular maintenance – consists of constant visiting and inspections of truck forest roads, as well as establishing possible defects and damages. Besides recording damages, we should also determine the measures for their elimination, define the time for the performance of works, necessary material, machinery and the number of workers, as well as calculate the costs of repair. The following works form a part of regular maintenance: cleaning of drainage ditches, culverts and other drainage facilities, cleaning of road upper structure, maintenance of incline/slope and road shoulders, mowing grass, maintenance of plants, etc.
- **Investment maintenance** – implies larger works on the earth road structure, replacement of damaged and worn-out culverts and drainages, repair of retaining and revetment walls, etc.
- **Periodic maintenance** – related to a certain period, season or particular circumstances (e.g. snow cleaning, works after sudden floods, etc.).

According to the component of a truck forest road being maintained, road maintenance may be divided into:

- lower structure maintenance:
  - maintenance of the earth road structure,
  - maintenance of the surface and underground drainage system,
  - maintenance of retaining and revetment walls,
  - maintenance of cuttings and embankment slopes,
  - vegetation maintenance (also includes road shoulder maintenance),
  - bridge maintenance;
- upper structure maintenance.

3. Research goals and methods

3.1 Research goal

Research Goals are defined by these encompassed and logical units:

- classification of Management Units (MU) and Forest Administration Units (FAU) into relief categories,
- establish the existing primary road density (Management Units, FAUs and relief categories),
- calculate the length of the planned truck forest road network (in FAUs and in relief areas, with the purpose of achieving the planned primary road density until 2010 and 2020),
- calculate the construction cost of the planned truck forest road network (in FAUs and in relief areas, with the purpose of achieving the planned primary road density until 2010 and 2020),
- suggest guidelines for further primary opening of the forests of the Republic of Croatia.

3.2 Research methods

3.2.1 Classification of MUs and FAUs into relief categories

There are four categories of relief areas: lowland area, hilly area, mountainous area and karst area. According to Management Plans, each Management Unit is located within its relief category. The surfaces of each relief category on the level of FAUs were summed up in order to calculate first the absolute, and then the percentage share of each relief category in the overall FAU surface.

3.2.2 Establish the existing primary road density

The existing primary road density by Management Units will be determined on the basis of the cadastre of primary forest transportation system, constituted on the level of the company »Hrvatske Šume« Ltd. Zagreb, as it was on 31st December 2009. This is followed by the collection of all data from all Management Units of the same relief category on the level of FAUs and the overall research area.

3.2.3 Calculate the length of the planned truck forest road network

The difference between the existing and the planned primary road density (year 2010 and 2020) of an individual FAU and its surface gives the overall length of planned truck forest roads which ought to be built. It is assumed that all future truck forest roads will be a part of the calculation of openness with their entire length. Planned primary road density in 2020 for lowland relief area has not been calculated; lowland area has not been the subject of research neither the length nor the cost of planned truck forest road network in 2020.

3.2.4 Calculate the construction cost of the planned truck forest road network

Cost analysis of the new planned truck forest road network will be constructed according to technical characteristics of forest roads proscribed by the valid Technical Requirements for Industrial Roads (*Šikić et al., 1989*) and planned costs of truck forest road construction in various relief categories by the company »Hrvatske Šume« Ltd. Zagreb.

3.2.5 Suggest guidelines for further primary opening of the forests in the republic of Croatia

The dynamics and the priorities of the development of the existing primary forest transportation system network will be defined through a detailed analysis of the need for the construction of primary forest transportation system for the following 20 years, upon examination of the past dynamics of truck forest road construction, taking into consideration the financial, productional, organizational, expert and technical-technological capacities of the company »Hrvatske Šume« Ltd. Zagreb.

4. Research area

Research was conducted on the area of 15 Forest Administration Units which are a part of the company »Hrvatske Šume« Ltd. Zagreb. Owing to the lack of data, FAU Split was not included in the research.

Fig. 4. Location and area of each Forest Administration Unit.

5. Research results

5.1 Classification of FAUs into relief categories and determining the existing primary road density

On the basis of the conducted relief area classification (Fig. 5.), FAUs have been grouped into relief categories for the purpose of easy reference and result comparability.

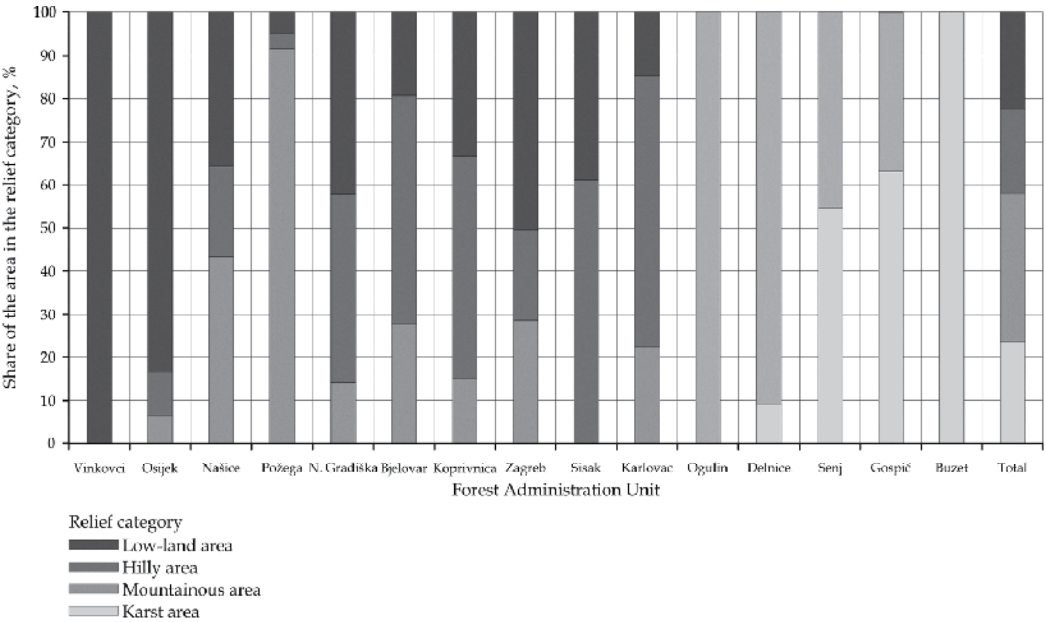


Fig. 5. The share of relief area in each of the FAU.

In the overall forest surface under research (1,442,140 ha), the lowland area accounts for 322,320 ha (22.35%), the hilly area for 282,560 ha (19.59%), the mountainous area for 497,830 ha (34.52%) and the karst area for 339,430 ha (23.54%). Only three FAUs are located with their entire surface in one relief category (FAU Vinkovci in lowland area, FAU Ogulin in the mountainous area and FAU Buzet in the karst area). The areas under management by the other FAUs stretch throughout two (four FAUs) or three (eight FAUs) relief categories.

In the lowland area, the average existing primary road density amounts to 8.85 m/ha, in the hilly area 11.26 m/ha, in the mountainous area 15.64 m/ha and in the karst area 7.63 m/ha.

By comparing the existing density of the primary forest transportation system by a particular relief area category, we may conclude the following: in the lowland area, the greatest primary road density exists in the FAU Karlovac (16.08 m/ha), and the least in FAU Osijek (4.37 m/ha); in the hilly area, FAU Koprivnica (17.02 m/ha) has the best primary road density, while FAU Sisak (6.88 m/ha) has the lowest classical primary openness; in the mountainous area, the highest degree of classical primary openness is in the FAU Našice (23.27 m/ha), and the lowest in FAU Gospić (10.32 m/ha); in the karst area the greatest priary road density is present in FAU Delnice (12.47 /ha), and the lowest in FAU Gospić (5.76 ha).

5.2 Calculate the length of planned truck forest road network in 2010 and 2020

The primary road density in 2010 and 2020 was calculated according to relief categories and the overall surface of each FAU. The length of truck forest roads to be built until the expiration of the planned period was set for both variants of primary road density. The results are shown in the Tables 5 and 6.

The data from the Tables 4 and 5 show that, although we stepped out of 2010, primary road density defined as planned for that year (Table 1) has not been achieved in any FAU in the whole area. In FAU Karlovac (lowland) and in FAU Delnice and Senj (karst) the planned primary road density for 2010 was exceeded (FAU Karlovac built 13.13 km, FAU Delnice 21.97 km, and FAU Senj 82.36 km of truck forest roads which influence on primary road density more than was planned).

Forest Administration Unit	Total area of FAU	Low-land area		Hilly area		Mountainous area		Karst area	
		Area	RD	Area	RD	Area	RD	Area	RD
	1000 ha	1000 ha	km/1000 ha	1000 ha	km/1000 ha	1000 ha	km/1000ha	1000 ha	km/1000 ha
VINKOVCI	72.37	72.37	6.84	-	-	-	-	-	-
OSIJEK	62.83	52.41	4.37	6.35	6.99	4.07	11.06	-	-
NAŠICE	82.95	29.73	12.70	17.26	16.84	35.96	23.27	-	-
POŽEGA	51.23	2.60	5.14	1.70	12.76	46.93	15.59	-	-
NOVA GRADIŠKA	73.57	31.07	8.73	32.21	8.52	10.29	11.70	-	-
BJELOVAR	131.83	25.42	11.92	69.84	11.68	36.57	11.84	-	-
KOPRIVNICA	62.37	20.79	13.74	32.29	17.02	9.29	17.50	-	-
ZAGREB	81.52	41.13	10.88	17.21	13.26	23.18	15.90	-	-
SISAK	87.99	34.28	6.68	53.71	6.88	-	-	-	-
KARLOVAC	82.45	12.11	16.08	51.99	11.32	18.35	12.02	-	-
OGULIN	59.58	-	-	-	-	59.58	14.11	-	-
DELNICE	96.31	-	-	-	-	87.41	22.55	8.90	12.47
SENJ	112.19	-	-	-	-	51.01	17.03	61.18	11.35
GOSPIĆ	312.67	0.41	12.10	-	-	115.19	10.32	197.07	5.76
BUZET	72.28	-	-	-	-	-	-	72.28	9.01
Total/Average	**1,442.14**	**322.32**	**8.85**	**282.56**	**11.26**	**497.83**	**15.64**	**339.43**	**7.63**

Table 4. Existing primary road density (RD) by relief areas in each FAU.

The greatest volume of new truck forest road construction should be carried out in FAU Gospić (2,529.04 km). According to relief areas, truck forest roads should be constructed mostly in FAU Vinkovci (590.36 km) in the lowland area, in FAU Sisak (704.66 km) in the hilly area in the mountainous area (1,691.35 km) and in the karst area (836.50 km) in FAU Gospić.

Planned primary road density for 2010 in the lowland area, in comparison with the existing primary road density in the same relief area, implicates the need of very intensive interventions of truck forest road construction (especially in the area of FAU Vinkovci and Osijek).

The obtained results should be observed in the context of historic guidelines in lowland forest management in FAU Vinkovci and Osijek (compartments of a symmetrical quadrangular shape with dimensions 750x750 m with a regular pattern of secondary forest roads, so called *»šljukarica«*, with the mutual distance among the middle of the passages (axle) from 37.5 m (*Posarić, 2007*)), but also in the sense of new (today accepted) technologies of timber harvesting in Croatian low-land forests.

Forest Administration Unit	**Length of TFR**									
	Low-land area		**Hilly area**		**Mountainous area**		**Karst area**		**Total**	
	km	**km/1000 ha**	**km**	**km/1000 ha**	**km**	**km/1000 ha**	**km**	**km/1000 ha**	**km**	**km/1000 ha**
VINKOVCI	590.36	8.16	-	-	-	-	-	-	590.36	8.16
OSIJEK	557.21	10.63	82.64	13.01	56.75	13.94	-	-	696.60	11.09
NAŠICE	68.41	2.30	54.47	3.16	62.21	1.73	-	-	185.09	2.23
POŽEGA	25.64	9.86	12.31	7.24	441.60	9.41	-	-	479.55	9.36
NOVA GRADIŠKA	194.70	6.27	369.93	11.48	136.81	13.30	-	-	701.44	9.53
BJELOVAR	78.39	3.08	581.08	8.32	481.14	13.16	-	-	1,140.61	8.65
KOPRIVNICA	26.19	1.26	96.12	2.98	69.64	7.50	-	-	191.95	3.08
ZAGREB	169.36	4.12	116.04	6.74	211.03	9.10	-	-	496.43	6.09
SISAK	285.38	8.32	704.66	13.12	-	-	-	-	990.04	11.25
KARLOVAC	0.00 (+13.13)*	-	451.44	8.68	238.12	12.98	-	-	689.56	8.36
OGULIN	-	-	-	-	648.54	10.89	-	-	648.54	10.89
DELNICE	-	-	-	-	213.99	2.45	0.00 (+21.97)*	-	213.99	2.22
SENJ	-	-	-	-	406.62	7.97	0.00 (+82.36)*	-	406.62	3.62
GOSPIĆ	1.19	-	-	-	1,691.35	14.68	836.50	4.24	2,529.04	8.09
BUZET	-		-	-	-	-	71.52	0.99	71.52	0.99
Total	**1,996.83**	**6.20**	**2,468.69**	**8.74**	**4,657.80**	**9.36**	**908.02**	**2.68**	**10,031.34**	**6.96**

** FAU Karlovac (low-land area), Delnice and Senj (karst area) built more roads than planned so the need to build by 2010. in these FAU is 0.00 km.*

Table 5. Required length of truck forest roads that need to be built to achieve the planned primary road density for 2010 by the FAU and relief categories.

Forest Administration Unit	**Length of TFR**							
	Hilly area		**Mountainous area**		**Karst area**		**Total**	
	km	**km/1000 ha**	**km**	**km/1000 ha**	**km**	**km/1000 ha**	**km**	**km/1000 ha**
OSIJEK	114.39	18.01	77.10	18.94	-	-	191.49	3.05
NAŠICE	140.77	8.16	242.01	6.73	-	-	382.78	4.61
POŽEGA	20.81	12.24	676.25	14.41	-	-	697.06	13.61
NOVA GRADIŠKA	530.98	16.48	188.26	18.30	-	-	719.24	9.78
BJELOVAR	930.28	13.32	663.99	18.16	-	-	1,594.27	12.09
KOPRIVNICA	257.57	7.98	116.09	12.50	-	-	373.66	5.99
ZAGREB	202.09	11.74	326.93	14.10	-	-	529.02	6.49
SISAK	973.21	18.12	-	-	-	-	973.21	11.06
KARLOVAC	711.39	13.68	329.87	17.98	-	-	1,041.26	12.63
OGULIN	-	-	946.44	15.89	-	-	946.44	15.89
DELNICE	-	-	651.04	7.45	0.56*	0.06	651.60	6.77
SENJ	-	-	661.67	12.97	141.18*	2.31	802.85	7.16
GOSPIĆ	-	-	2,267.30	19.68	1,821.85	9.24	4,089.15	13.08
BUZET	-	-	-	-	432.92	5.99	432.92	5.99
Total	**3,881.49**	**13.74**	**7,146.95**	**14.36**	**2,396.51**	**7.06**	**13,424.95**	**9.31**

** Values are reduced by the length of more constructed forest roads in the FAU Delnice and Senj by 2010 shown in Table 5.*

Table 6. Required length of truck forest roads that need to be built to achieve the planned primary road density for 2020 by the FAU and relief categories.

According to the openness plan for 2020, the greatest volume of new truck forest road construction should be carried out in FAU Gospić (4,089.15 km). Analyzing the relief areas, the construction of most truck forest roads will be required: in the hilly area in FAU Sisak (973.21 km), in the mountainous area (2,267.30 km) and in the karst area (1,821.85 km) in FAU Gospić.

Forest Administration Unit	Current (existing):		Planned 2010th:		Planned 2020th: (without low-land area)	
	RD	Length of TFR	RD	Length of new TFR	RD	Length of new TFR
	km/1000 ha	km	km/1000 ha	km	km/1000 ha	km
VINKOVCI	6.84	495.19	15.00	590.36		
OSIJEK	5.07	318.30	16.15	696.60	26.95	191.49
NAŠICE	18.14	1,505.06	20.38	185.09	28.38	382.78
POŽEGA	14.97	766.70	24.33	479.55	29.83	697.06
NOVA GRADIŠKA	9.05	666.06	18.59	701.44	26.21	719.24
BJELOVAR	11.77	1,551.74	20.42	1,140.61	26.72	1,594.27
KOPRIVNICA	16.00	997.95	19.08	191.95	26.12	373.66
ZAGREB	12.81	1,044.22	18.90	496.43	27.87	529.02
SISAK	6.80	598.36	18.05	990.04	25.00	973.21
KARLOVAC	12.17	1,003.77	20.38	689.56	26.30	1,041.26
OGULIN	14.11	840.96	25.00	648.54	30.00	946.44
DELNICE	21.62	2,082.23	23.61	213.99	28.61	651.60
SENJ	13.93	1,562.79	16.82	406.62	21.82	802.85
GOSPIĆ	7.44	2,327.56	15.53	2,529.04	20.53	4,089.15
BUZET	9.01	651,28	10.00	71.52	15.00	432.92
Total/Average	**11.38**	**16,412.17**	**18.25**	**10,031.34**	**24.19**	**13,424.95**

Table 7. Existing and planned primary road density for 2010 and 2020 by the FAU and the length of truck forest roads that need to be built.

Relief category	Length of TFR	Existing TFR density	Planned length of TFR 2010th	Planned TFR density (until 2010)	Planned length of TFR 2020th	Planned TFR density (until 2020)
	km	km/1000 ha	km	km/1000 ha	km	km/1000 ha
Low-land area	2,851.10	8.85	1,983.70	15.00		
Hilly area	3,182.51	11.26	2,468.69	20.00	3,881.49 (1,412.80)	25.00
Mountainous area	7,787.95	15.64	4,657.80	25.00	7,146.95 (2,489.15)	30.00
Karst area	2,590.61	7.63	803.69	10.00	2,500.84 (1,697.15)	15.00
Total/Average	**16,412.17**	**11.38**	**10,031.34**	**18.25**	**13,424.95** **(3,393.61)**	**24.19**

() Length of forest roads that need to be constructed in 2010-2020 to achieve the planned openness 2020th.

Table 8. Existing and planned primary road density for 2010 and 2020 in different relief areas and length of truck forest roads that need to be built.

5.3 Calculation of the cost of planned truck forest road construction in 2010 and 2020

On the basis of planned costs of truck forest road construction for each relief area (*Anon., 2010*): lowland area (500,000.00 HRK/km), hilly area (350,000.00 HRK/km), mountainous area (250,000.00 HRK/km) and karst area (225,000.00 HRK/km) and the applicable Technical Requirements for Economic Roads (*Šikić et al. 1989*), the total price was calculated for all truck forest roads which need to be built for achieving the planned primary road density in 2010 and 2020.

Forest Administration Unit	The construction costs of a new truck forest roads network, €			
	Planned by 2010		Planned by 2020 (without low-land area)	
	kn	**€***	**kn**	**€***
VINKOVCI	295,180,000.00	40,056,234.51		
OSIJEK	321,716,500.00	43,657,265.30	59,311,500.00	8,048,632.54
NAŠICE	68,822,000.00	9,339,217.33	109,772,000.00	14,896,175.13
POŽEGA	127,528,500.00	17,305,750.74	176,346,000.00	23,930,336.51
NOVA	261,028,000.00	35,421,772.42	232,908,000.00	31,605,859.03
BJELOVAR	362,858,000.00	49,240,209.85	491,595,500.00	66,710,023.15
KOPRIVNICA	64,147,000.00	8,704,814.94	119,172,000.00	16,171,764.95
ZAGREB	178,051,500.00	24,161,774.64	152,464,000.00	20,689,524.15
SISAK	389,321,000.00	52,831,266.61	340,623,500.00	46,222,964.96
KARLOVAC	217,534,000.00	29,519,591.16	331,454,000.00	44,978,654.23
OGULIN	162,135,000.00	22,001,888.96	236,610,000.00	32,108,224.30
DELNICE	53,497,500.00	7,259,666.66	162,886,000.00	22,103,800.44
SENJ	101,655,000.00	13,794,689.75	197,183,000.00	26,757,939.19
GOSPIĆ	611,645,000.00	83,000,865.77	976,741,250.00	132,544,808.49
BUZET	16,092,000.00	2,183,701.22	97,407,000.00	13,218,231.71
Total	**3,231,211,000.00**	**438,478,709.86**	**3,684,473,750.00**	**499,986,938.77**

* Middle exchange rate of euro in the Croatian National Bank on day 13.11.2010 (1 € = 7.36914 kn).

Table 9. Construction costs of the planned network of truck forest roads in 2010 and 2020 according to the current Technical Requirements.

In order to achieve the planned primary road density in 2010, at the level of »Hrvatske Šume« Ltd. Zagreb, according to the applicable Technical Requirements, it is necessary to invest HRK 3,231,211,000, and for achieving the planned primary classical openness in 2020 it is necessary to invest HRK 3,684,473,750 (without the lowland relief area).

Fig. 7. shows the dynamics of the construction of lower and upper truck forest road structure for the period from 2004 - 2009 by Forest Administration Units. During the six

observed years, a total of 1,295.86 km of lower structure and 1,438.64 km of upper structure were built, or on average 215.98 km of lower structure and 239.77 km of upper structure of truck forest roads per year. The greatest amount of lower and upper structure were built in 2006 (246.69 km and 307.49 km), and the least in 2009. The difference between the constructed lengths of lower and upper structures indicate that truck forest roads are not always constructed all at once, but the construction procedure extends over two or more years. Most often the reasons are the following: lack of financial means, unfavourable weather conditions at the end of the year, construction technology or simply, because that is how it was conceived by the construction plan.

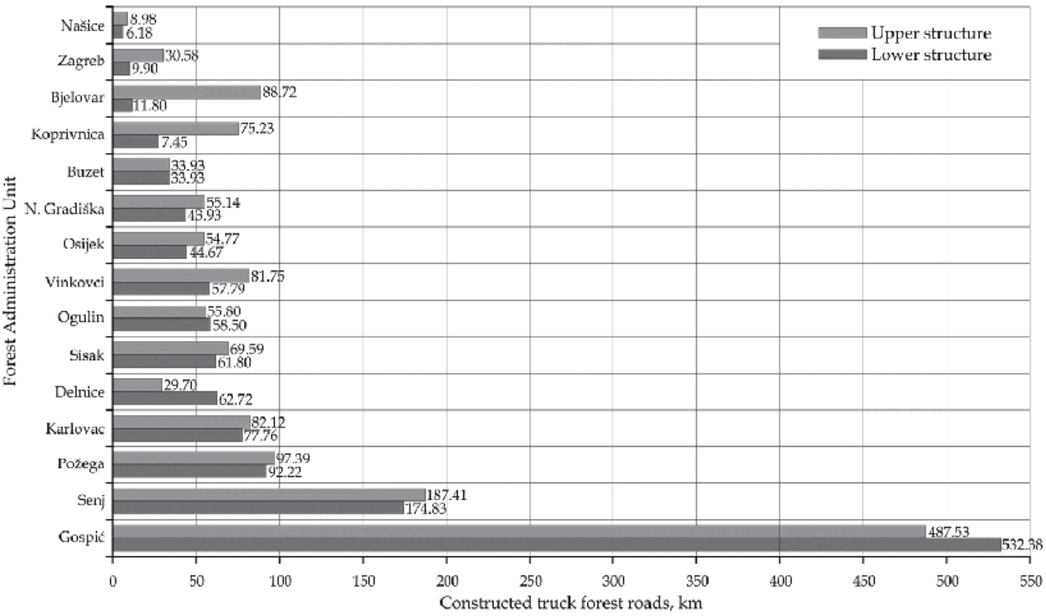


Fig. 6. Construction of the lower and upper structure of the TFR for the period from 2004 to 2009 by the FAU-s.

6. Discussion

A significant diversity of Croatian forestry from the point of view of terrain orthography (lowland, hilly, mountainous and karst), site and stand characteristics, as well as the way of forest management (regular, selection), but also the ways of forest opening in certain orthographic areas, or the degree of forest road density, indicates the need of good planning in the entire forestry department, as well as in timber harvesting works, or forest opening. Quality and reliable planning, in this case of forest roads, guarantees rationalization (a collection of procedures for achieving savings in business) in a part of forestry production.

Planning forest roads is a starting, unavoidable and very important stage of establishing an optimal forest road network in the field. Planning may be strategic, tactical and operative. On the level of strategic planning, we use the so called descriptive (primary) classification of terrains, which describes a terrain according to measurable characteristics and divides it into categories, independently of the applied timber harvesting systems.

Planned values of primary road density in 2010 and 2020 on the level of relief categories represent only guidelines which should be followed, but should not (and must not) be strictly adhered to in the final design of primary forest transportation system network. It is recommended to re-examine and, if necessary, redefine the values of planned primary road density by relief areas (Table 1), at the same time recognizing all the factors which have an influence on the calculation of planned primary forest transportation system density.

At the lower, also more accurate, planning stage (tactical planning), it is possible to deviate from the values defined at the strategic level, both in positive and negative, but acceptable intervals. Target (optimal/best possible) primary road density is defined on the level of a Management Unit; Studies of Primary Forest Opening are made at this level.

The accuracy of planning is the greatest and suits the best to the actual condition at the lowest planning level, but it also requires the most precise and the most complete data and information. In operative planning, sometimes even the division into Management Units is not accurate enough, because within the same Management Unit there may be two or more (very rarely) relief categories. This planning level presupposes a purposeful (functional or secondary) terrain classification, which associates the possibility of application of potential and suitable harvesting systems with classes of terrain factors. The harvesting system is determined by procedures, method of timber processing (cut-to-length, half-tree, full-tree, tree-length), as well as machines and tools used in the harvesting of a cut-block. The selection (use) of a timber extraction device (skidder, forwarder, adapted farm tractor – AFT, AFT with semitrailer, cable yarder) in the light of the influence of terrain (relief categories) and stand factors, as well as the level of primary and secondary forest openness is the most important determinant of the entire harvesting system.

By analyzing the existing primary road density by FAUs and by relief categories conclusively with 31st December 2009 at the researched area, it is concluded that the planned primary road density has not been achieved on the greatest part of state-owned forests. Moreover, in the better part of the forests, not even the minimal necessary primary road density has been reached, specifically, in the lowland area in 4 out of 11 FAUs, in the hilly area in 5 out of 9 FAUs, in the mountainous area in 6 out of 12 FAUs, which has a significant negative influence on the quality, efficiency and rationality of management in these insufficiently opened forests.

With the average annual intensity of truck forest road construction, based on the data from 2004 – 2009 (taking into consideration the average constructed length of the lower truck forest road structure of about 216 km/y), it would take 47 years to achieve the planned openness in 2010, and 63 years to achieve the same for 2020 (without the construction of truck forest roads in lowland area).

It should be considered to extend the time period for the attempt to achieve the planned values of primary forest transportation system density. At the same time, the construction of truck forest roads should be intensified, and raised from the present 216 km/y to at least 600-800 km/y. Thus, the planned values of primary road density for 2010 (counting with the construction of 700 km/y of truck forest roads) might be achieved in about 15 years, and for

2020 in about 20 years (without the construction of truck forest roads in the lowland area). Because of that, the objective financial, expert and infrastructural capacities of the company »Hrvatske Šume« Ltd. should be acknowledged. Besides the existing sources of financing, the means from current business operations and the means from the fund for generally beneficial forest functions, it is necessary to search for other sources of financing of all the stages for establishing an optimal primary forest transportation system network, e.g. EU funds, etc.

There is a significant gap among the primary road density of forest areas which belong to the same relief category. In the future, while planning investments into the rebuilding and development of primary forest transportation system, the priority orientation of financial means into the less opened forest areas should be taken into consideration, all until there is a balance of primary road density on the level of the overall relief area.

The values of primary road density (existing, as well as planned for 2010 and 2020) will be compared with the average values of the existing primary road density in the forests of the Republic of Austria (*Stampfer 2011* according to *Austrian Forest Inventory 1992/96*). In order to make the comparison complete, the basic characteristics of Austrian forests and harvesting works are provided:

- forest ownership (48.3% are private forests with the surface of less than 200 ha, 22.4% are private forests with the surface of more than 200 ha, 15.7% are state-owned forests, and 15,6% are forests owned by other forest owners – community forests, communal forests and provincial forests),
- inclination of the terrain where forests grow (more than 22% of the forests grow on inclined terrains with an inclination of more than 60%, and 39% of forests on terrains inclined 30-60%; other forests are situated on inclinations up to 30%),
- particularities (way) of forest management,
- generally useful forest functions,
- harvesting systems (procedures, method of timber processing, machines and tools used):
    - applied device for timber cutting and processing (82.41% of harvesting volume is cut and processed with a chainsaw, and 17.59% with a harvester),
    - means used for timber extraction (skidder extracts 53.1%, forwarder 26.8, cable yarder 14.2%, manually 4.6%, horse-power 0.4% and other ways – e.g. helicopter 0.9% of the overall annual allowable cut).

Forest ovners	**Road density km/1000 ha**
Smale scale forest owners (< 200 ha)	49.1
Private Companies (> 200 ha)	41.8
Federal Austrian Forests	33.7
Average	**45.0**

Table 10. The existing primary road density in the Republic of Austria (*Stampfer 2011* according to *Austrian Forest Inventory 1992/96*).

In smaller forest properties, where less modern machinery is used for timber extraction (mostly AFTs and AFTs with semitrailers); there is a denser primary forest transportation system network owing to the rationalization of overall timber harvesting costs.

The existing primary road density in the Republic of Austria (in Austrian state forests) is far greater than the planned openness in the hilly area of the Republic of Croatia for 2020; of course, there is an even greater difference when comparing with the planned openness for 2010, while the greatest differences exist when comparing with the existing primary road density. There are Management Units in Croatian state forests whose primary road density is on the level of those in Austrian state forests, but these are rare. As an example, there are three Management Units situated in selection forests of Gorski Kotar, owned by the state but managed by the University of Zagreb Faculty of Forestry. The primary road density in those units amounts to between 32 and 36 km/1000 ha, with the average values of mean timber extraction distance of 150 m.

Habsburg (1970), *Sanktjohanser* (1971) and *Piest* (1974) agree that the optimal primary road density for the needs of forest exploitation varies between 17 and 30 m/ha, depending on the terrain and site characteristics, while the optimal primary road density for rational overall forest management is a bit greater. The suggested values correspond very well to the planned primary road density in Croatia for 2010 and 2020, while there are slight deviations in lowland forests and karst area forests. Considering the time distance and the development of the entire timber harvesting system, as well as the total forest ecosystem management that has been established in the meantime, the recommended primary forest transportation system density by the three above mentioned authors should be taken with a grain of salt.

7. Concluding remarks

The planned values of primary road density in 2010 and 2020 on the level of various relief categories of the Republic of Croatia, besides being the guidelines for strategic planning in the Republic of Croatia, may also be used as landmarks in primary forest road planning on a strategic level in countries of similar orographic, site and stand conditions, as well as the ways of forest management. The existing primary road density should certainly be taken into consideration, and in accordance with the financial, professional and infrastructural resources of a certain country and its forestry, the deadlines for achieving the planned values of primary road density, annual intensity and construction priorities should be defined.

The more developed countries and countries with a long forestry tradition, which could have invested significant financial means permanently and systematically into the primary openness of their forests during the last few decades, are expected to have a better primary road density than the Republic of Croatia (which could have started with a more systematic and more intensive forest opening only after being proclaimed independent in the 1990s), and therefore, less need for primary classical openness in the future (with the purpose of achieving planned primary road density) and probably less differences in the existing primary road density of equal or similar (comparable) forest areas, that is, they have a uniform existing primary road density of the same relief categories. A multiple use of truck forest roads, by first of all users outside forestry (e.g. tourism), contributes to greater density and better quality of truck forest roads.

Operative planning, as the lowest and the most accurate level of forest road planning, requires a purposeful analysis of the terrain, connecting the possibility of applying potential and suitable timber harvesting systems with terrain factor analysis. At this planning level, timber harvesting systems have a significant influence on the shape and density of the truck forest roads, but even more on the on the shape and density (and existence, in general) of the secondary forest road network. The application of certain timber harvesting systems is, besides the terrain factors, conditioned by the degree of technological growth (technological awareness), resulting in utilization (the possibility of using) the most up-to-date means of timber extraction, and connected with that, the procedures and methods of timber processing. The selection of a timber extraction system is often under the influence of traditional forestry values of a certain country.

This paper describes and applies the methodology, but it can serve as a starting point for making a case study in any European and non-European country. Individual differences (specific qualities) of a certain country should be recognized and integrated into the modified methodology in a proper way to make the research results achieve an expected high level.

The data about the primary road density does not say much about the quality of spatial distribution of primary forest transportation system components. For better understanding of the real value of primary road density, it is always necessary to present primary classical openness coupled with the average timber extraction distance, or the mean distance of access to the endangered forest area, in the case of forest fire-prevention roads in the karst area. A clear insight into the real, quantitative (amount of primary forest roads) and qualitative (spatial coverage with primary forest roads) parameters of primary forest transportation system may only be achieved by a parallel consideration of primary road density and mean timber extraction distance.

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The common idea for many people is that forests are just a collection of trees. However, they are much more than that. They are a complex, functional system of interacting and often interdependent biological, physical, and chemical components, the biological part of which has evolved to perpetuate itself. This complexity produces combinations of climate, soils, trees and plant species unique to each site, resulting in hundreds of different forest types around the world. Logically, trees are an important component for the research in forest ecosystems, but the wide variety of other life forms and abiotic components in most forests means that other elements, such as wildlife or soil nutrients, should also be the focal point in ecological studies and management plans to be carried out in forest ecosystems. In this book, the readers can find the latest research related to forest ecosystems but with a different twist. The research described here is not just on trees and is focused on the other components, structures and functions that are usually overshadowed by the focus on trees, but are equally important to maintain the diversity, function and services provided by forests. The first section of this book explores the structure and biodiversity of forest ecosystems, whereas the second section reviews the research done on ecosystem structure and functioning. The third and last section explores the issues related to forest management as an ecosystem-level activity, all of them from the perspective of the "other" parts of a forest.

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