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Conifers

Edited by Ana Cristina Gonçalves



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Preface

Conifer forests cover vast areas of the world and are present in a wide range of climates. Conifer stands and forests vary from simple systems, such as pure even-aged, to very complex systems, mixed uneven-aged. They also encompass a wide variety of products and services, from timber to non-timber products, protection of soil and water, conservation, recreation and aesthetics and other social and cultural services. Overall the evaluation, management and planning of the multiplicity of these systems requires effective and specific methods and tools for the maintenance of the sustainability of the systems as well as of their products and services.

This book reflects the current research on conifer stands and forests. The authors, specialists in different areas, addressed several issues in forest science, thus enabling the reader to have diverse and complementary perspectives of the silviculture, management, modelling and products and services of conifer stands and forests, in a frame of sustainability both of stands and of the several products and services they can offer. The book chapters focus on the species' characteristics, silviculture and climate change; growth analysis; reconstruction of stand dynamics of mixed stands; establishment, regeneration and succession; litter-fall, nutrient cycle and silviculture; distribution and zonation; and ecosystem services provided by monocultures and mixed stands.

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Lodgepole Pine (*Pinus contorta* Douglas ex Loudon) from the Perspective of Its Possible Utilization in Conditions of Changing Central European Climate

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Additional information is available at the end of the chapter

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Abstract

This chapter provides an overview regarding the lodgepole pine (*Pinus contorta* Douglas ex Loudon) from the perspective of its ecological demands and the possibilities of its silvicultural utilization in Central European conditions. Described are its natural habitat, variability, ecological properties, and the environmental demands (natural mixtures, geological needs, soil, temperature, humidity, etc.). Attention is given to characterizing the wood in terms of its production, properties, and possible uses. Furthermore, important aspects of this pine's cultivation are described as an aspect of forest management, as well as from the viewpoint of the species' utilization in reclamation of infertile anthropogenic substrates. Particular emphasis is given to current knowledge obtained through provenance research in relevant European countries. In connection with the changing climate in Central Europe, this pine tree can gradually gain in importance because it is a tree species with wide ecological adaptability. In spite of its lower production potential, the species is capable of creating stands on habitats that will be inappropriate in the future for many autochthonous Central European species.

Keywords: *Pinus contorta*, lodgepole pine, ecological characteristics, production, provenance research, silviculture, climatic changes

1. Introduction

In selecting tree species for introduction, attention is always focused on their productive abilities, quality characteristics, and resistance to local harmful agents. However, other ecological aspects,

such as suitability for stand mixtures, natural regeneration ability, and influence on stand environment, also are important. Assessing, whether a tree species or its specific subpopulation (provenance) is capable of being utilized in new conditions, is only possible on the basis of research results or practical experience—preferably local—or after a critical evaluation of foreign research and experience. An introduced species should only be planted into such habitats where it can demonstrate its positive influence and at the same time does not constitute a substantially negative element for the inanimate nature or autochthonous flora [1].

The stability of Central European forest ecosystems is diminishing with advancing climate change. In addition, the health state of certain stands of Scots pine (*Pinus sylvestris* L.) has deteriorated, having been attacked by fungal pathogens *Sphaeropsis sapinea* (Fr.) Dyko & B. Sutton 1980 and *Cenangium ferruginosum* Fr. 1818 [2] over several consecutive years. Even in the case of this autochthonous tree species that always has been relied upon for plantings in Central European locations with low soil moisture availability, it therefore seems rational preventively to consider other species that could prosper in extreme habitats. This would allow continuation of forests' nonproduction functions while retaining at least minimally acceptable production.

One possible alternative solution of this problem is lodgepole pine, *Pinus contorta* Douglas ex Loudon. Originally from western North America, it was first introduced into Europe in 1852 [3] and has since that time demonstrated a number of favorable properties.

The objective of this work is to provide comprehensive information about the character of the range, ecological properties, and growing requirements of lodgepole pine. In consideration of the latest findings from forestry and reclamation research, this allows for outlining the potential for possible use of this species in the transforming Central European conditions. The division into subsections reflects the various aspects important for judging its usefulness in regional forest management and application to reclamation.

2. Consideration of species characteristics from the perspective of possible use in Central Europe

2.1. Natural range

Forests with a predominance of *P. contorta* have an area of ca 6 million ha in the US and ca 20 million ha in Canada. In the north, the species' range is limited by 64° N (Yukon Territory) and in the South by ca 31° N (Baja California) [4]. The three currently distinguished subspecies have wide allopatric areas (**Figure 1**). The range of *Pinus contorta* subsp. *contorta* reaches from southern Alaska along the Pacific coast to northern California, including Queen Charlotte Islands and Vancouver Island. The western boundary of the subspecies *P. c.* subsp. *latifolia* traces across the Rocky Mountains from the north from Yukon and British Columbia across Washington State and Oregon to northern Utah, and the eastern from Alberta approximately to Colorado. In addition, disjunct populations of this subspecies are located in the Canadian Northwest Territories (Liard Mountains) and Saskatchewan (Cypress Hills Provincial Park),



Figure 1. Distribution area of three *Pinus contorta* subspecies according to the U.S. Geological Survey [6]; map background source: <https://www.seznam.cz/>.

and in the US in South Dakota (Black Hills). The range of *P. c. subsp. murrayana* reaches from the Cascades of southern Washington State and Oregon (Cascade Range) across the Sierra Nevada and Transverse Ranges in California to Baja California and Sierra de San Pedro Mártir in Mexico [5].

Vertically, this species grows from practically sea level altitudes on the coast up to 3400 m a.s.l. in the Sierra Nevada and in the southern Rocky Mountains [5], and according to other authors, it reaches up to 3900 m a.s.l. [4, 7]. Musil and Hamerník [8] state an altitude range of 0–3500 (–3660) m a.s.l. The *P. c. subsp. contorta* subspecies grows up to 600 m a.s.l., the *P. c. subsp. latifolia* subspecies up to 3500 m a.s.l., and *P. c. subsp. murrayana* from sea level also to 3500 m a.s.l. [9], and up to 3700 m a.s.l. in the Sierra Nevada [10].

The climate is considerably variable within the area, particularly in the N-S direction but also in the E-W direction. Minimum temperatures range from 7°C in the southern parts of the coast to –57°C in the Northern Rocky Mountains, while maximum temperatures extend from 27°C

along the coast and in the high altitudes to more than 38°C in low inland areas. Seedlings often survive in freezing conditions where other species could not, although the individual provenances must be distinguished in this regard [8, 11]. Mean annual temperatures fluctuate between –3 and 18°C. The absolute lowest temperature is –60°C [4]. Mean July minima at higher elevations are frequently below zero. Precipitation totals fluctuate from just 250 mm in the lower elevations of the cold continental inlands to more than 2500 mm in low elevations along the relatively mild, but cold and rainy (foggy) northern Pacific coastline [4, 8, 12].

Around 1950, lodgepole pine became the main species in afforestation of peat bogs in Britain, Ireland, Sweden, and Finland. Additional plantings can be found in the Netherlands, Denmark, Iceland, Norway, Germany, Poland, countries of the former USSR, and New Zealand. Probably the largest area outside of North America is in France [13, 14]. The species' use in Great Britain has decreased over time due to frequent occurrence of malformed trunks and a propensity for defoliation caused by insects, primarily pine beauty – *Panolis flammea* (Denis & Schiffermüller) [4].

2.2. Variability

Taxonomically, the species is divided into three varieties [9, 12, 15], or, according to other authors [10, 16] into three subspecies. Other studies [4, 17] distinguish an additional subspecies (sometimes just variety) *P. c.* subsp. *bolanderi*. This is not accepted in more recent monographs, however, and the variant is considered part of the *P. c.* subsp. *contorta* subspecies. Older literature had described two separate species: (1) lodgepole pine, which currently corresponds to the subspecies *P. c.* subsp. *contorta*, including the variety *P. c.* subsp. *contorta* var. *bolanderi* and (2) Murray pine, a currently invalid species including two subspecies of lodgepole pine (*P. c.* subsp. *murrayana* and *P. c.* subsp. *latifolia*) [18].

The individual subspecies differ in some of their botanical characteristics, as well as in their growth predispositions and dimensions achieved, although these are also partially affected by environment [12]. *P. c.* subsp. *contorta* usually takes a form ranging between a stunted bush and tree (rarely up to 30 m), often with a crooked or leaning trunk. The dark green needles are 2–5(7) cm long and 0.7–1.2 mm wide. The pine cones are asymmetrical, curved back against the axis of the branch, tenacious, sometimes serotinous (opening several years after maturing, e.g., after a forest fire). The umbo has a spike 6 mm long. Coastal stands of this subspecies in Mendocino County, California are considered by some authors to be *P. c.* var. *bolanderi*. *P. c.* subsp. *latifolia* are often tall trees (exceptionally up to 50 m). Needles are (4)5–8 cm long and 1–2(3) mm wide, yellowish green in color. Pine cones grow individually or in pairs, are asymmetrical, curved back against the axis of the branch, persistent, and variably serotinous. The umbo has a short dull spike. *P. c.* subsp. *murrayana* produces tall, often slim trees, up to 40 m tall. Needles are 5–8 cm long and 1–2 mm wide, yellowish green in color. Pine cones grow individually or in pairs, are relatively symmetrical, ascending, and nonserotinous (opening early and falling off quickly). The umbo has a small spike [9, 15, 17].

Morphological differentiation of the individual subspecies has a variance-statistical character, and therefore, determination is frequently problematic in the wild and unreliable in cultures

outside of provenance-defined plantings [10]. The species is difficult to distinguish from the closely related *P. banksiana* Lamb., with which it naturally interbreeds in the area at the foot of the Rocky Mountains in western Canada [15]. Hybrids between *P. contorta* and *P. banksiana* created in the US by controlled pollination for the purpose of plantation growing are named *P. ×murraybanksiana* [12, 15]. Successful interbreeding also has been achieved with Virginia pine *P. virginiana* Mill [4].

Auders and Spicer [9] characterize a total of 14 valid cultivars and 11 synonyms. Among the better known cultivars are 'Compacta', a shrub with dark to yellow-green needles; 'Tristan Gold', a shrub with long yellow to dark green needles later changing to tree growth; 'Span's Dwarf', a low irregular shrub [19]; and 'Pendula', with overhanging branches [20].

2.3. Ecological characteristics

Lodgepole pine grows well not only on shallow slopes and in basins, but also in rugged rocky terrains and on steep (humid) slopes and mountain ranges, including exposed gravel. It occurs more frequently in habitats with northern and eastern exposure [8]. Inland, partially also in the Rocky Mountains and in the northern part of the Yellowstone National Park in the US, it can create dense pioneering even-aged and pure stands on sterile soils despite its heliophilia, especially so in places burnt by forest fires, the periodical occurrence of which prevents the slower-growing spruces and firs from dominating. It usually is not dominant in the western mountain ranges, although it invades wildfire sites even there. In other cases, and especially in later seral succession stages, it is associated with a number of western conifers. In the coastal part of the northern Pacific region, it mixes with *Thuja plicata* D. Don, *Tsuga heterophylla* (Raf.) Sarg., *Pseudotsuga menziesii* subsp. *menziesii* (Mirbel) Franco, *Chamaecyparis lawsoniana* (A. Murray) Parl., and *Sequoia sempervirens* (D. Don) Endl. In the northern part of its area, it also frequently grows with *Picea glauca* (Moench) Voss, or alternatively with broadleaves (*Betula papyrifera* Marshall, *Populus tremula* L.), in higher elevations with *Tsuga mertensiana* (Bong.) Carr., *Picea engelmannii* Parry ex Engelm., *Abies lasiocarpa* (Hook.) Nutt., *A. magnifica* A. Murr., *Pinus jeffreyi* Grev. & Balf., *P. flexilis* James, and *P. aristata* Engelm., in the inland part of the range in middle elevations with e.g., *Pseudotsuga menziesii* subsp. *glauca* (Mayr) A.E. Murray, *Larix occidentalis* Nutt., *Abies grandis* (Douglas ex D. Don) Lindl., and *Picea pungens* Engelm., and in the lower elevations of the same part of the range with *Pinus ponderosa* P. & C. Lawson [5, 8, 12, 17, 21]. On drier slopes and on plateaus, it frequently grows with *Pinus monticola* Dougl. ex D. Don and the already mentioned *A. magnifica*. At the edges of forests, it is accompanied by *Pinus albicaulis* Engelm. and *P. balfouriana* Grev. & Balf. [22]. Diversity increases toward the south, so in California, it is a component of mixed coniferous forests and subalpine coniferous forests and meadows along with many other species. Because soils in these areas are much richer and fires are much less frequent, *P. contorta* is not dominant there [5, 12, 17, 21].

In addition to its participation in primary succession in volcanic mountain ranges and in wildfire locations, it is represented also in dry and boggy sites in communities of early-medium-, and late-stage secondary succession. In succession, it can play the role of: (1) a component of even-aged stands, which is rapidly (over 50–200 years) replaced by shade-tolerant

communities, (2) a dominant species in even-aged stands with substantial undergrowth of shade-tolerating species and which is replaced over 100–200 years, (3) a dominant species of even-aged stands with only partial replacement by shade-tolerating species, and (4) in certain types of locations, the sole species capable of tree growth [4, 21].

It grows in the widest range of conditions of all North American tree species, from dry sands in the lower elevations to seasonally wet mountain meadows [17]. It creates pure stands in such meadows in California's Sierra Nevada at 2000–2700 m a.s.l. At high elevations reaching to the top of the forest boundary, however, it is considerably deformed and has the form of ground-hugging shrubs [22]. It is tolerant of flooding [4] and can be found not only in coastal, peat bog, wetland, and swampy communities, but also in coniferous and mixed and dry and mountainous forests, on poor sandy soils, rocks, and rubble [4, 21, 23]. It has modest requirements [23] that differ by individual ecotypes. The south-ranging *P. c.* subsp. *murrayana* and *P. c.* subsp. *contorta* var. *bolanderi* are undemanding of moisture and tolerate even soils that dry out in summer. The coastal subspecies *P. c.* subsp. *contorta* also requires higher air humidity [13]. The requirements of lodgepole pine are generally greater than those of *Pseudotsuga menziesii* and *Pinus ponderosa* but lower than those of *Picea engelmannii* and *Abies lasiocarpa* [8]. It is drought tolerant [4] and is intolerant only of drying sand soils [24]. It is most productive in deeper and richer soils with balanced moisture and porousness [8, 13, 23]. It fares well on granite, slate, and rough lava bedrocks. It avoids drier soils on limestone bedrock [8], although it does occur there, as well as on glacial moraine soils. It can grow on acidic, wetland, clay, gravel, mountain, peat, sandy, sandy-loamy, dusty and swampy soils, sandstone, cambisols, gley, luvisols, podzol-luvisols, podzols, and regosols [4, 13].

The root system is variable, usually shallow, but taproots or fibrous roots develop on well-permeable soil. It forms associations with ecto- and endomycorrhizal fungi [4, 8, 17].

The species does not tolerate shade and vegetation competition. It requires direct sunlight [4, 7, 8, 17] or can tolerate only slight lateral shading [13]. In lower lighting, it has a low potential for natural regeneration, which in such cases occurs only in a dry and cold climate within stand gaps [25]. Pokorný [23] characterizes it as an intermediately shade-tolerant species with slightly lower light requirements than Scots pine. Strong reproduction occurs in full sun, typically after wildfires or clear-cuts [17]. Depending upon origin, it is moderately to completely frost-resistant, being quite resilient even in St. Petersburg and Finland [23]. Corresponding provenances are resistant to winter cold, late spring frost, salty winds, and air pollution [26]. The subspecies *P. c.* subsp. *murrayana* is also relatively frost resistant [10]. The resistance of certain populations to air pollution results from the effects of long-term evolutionary adaptation in areas of the natural range with rich volcanic activity, e.g., [27, 28]. Tolerance to effects of SO₂ in Central European conditions was demonstrated in experiments established in the 1930s on the German side of the Ore Mountains [29].

Drought is the usual cause of mortality during the first years of the seedlings' lives. Losses fluctuate depending on soil type and numbers of individuals. The largest numbers of seedlings germinate and survive on disturbed mineral soil. Drought losses usually decline after the first growing season. Lodgepole pine seedlings are weak competitors, and competition with grasses is often unfavorable to them [4].

Pine cones mature more than 1 year after pollination—earlier at higher elevations and inland than on the coast or in lowlands [25]. Even though all subspecies are exposed to periodic fires, the serotinous of the pine cones is variable across the nature range and also locally [4]. Within California populations in the Sierra Nevada (*P. c.* subsp. *murrayana*) and in coastal populations (*P. c.* subsp. *contorta*), permanently closed cones are entirely absent or are very rare [8, 15]. Nonserotinous cones dominate in Oregon [4]. Serotinous closed cones are common in *P. c.* subsp. *latifolia* in the Rocky Mountains, although their proportion can decline below 50% [8]. This type of cones accumulates for decades [4], usually for 10–20 years [25]. They are opened by heat [17]. The heat necessary for their opening ranges between 45 and 60°C. Subsequently their opening is influenced hygroscopically. In open areas (e.g., after harvesting), cones near the surface of the soil (<30 cm) can open also due to increased insolation [4]. The bark of adult trees is relatively thin (under 2 cm). After fires, however, lodgepole pines regenerate well [7], which is due not only to the opening of serotinous cones but also due to the high viability of seeds, strong initial growth, and ability to cope with a wide range of soil and other microsite conditions [25].

Due to its limited root depth, it is susceptible to wind calamities, especially after stand walls have been opened by harvesting [11]. Strong wind and heavy snow may break or bend trees, especially in excessively dense stands with narrow canopies and strong competition in the root zone. In such stands, damage may further increase if the wind or snow exposure occurs shortly after thinning [25]. Lodgepole pine suffers crown breakage due to snow much less than does Scots pine [23].

Large, dense stands of *P. contorta* are susceptible also to insect damage, which usually is followed by a new fire several years later. Even though individual trees mostly do not live long and do not reach large dimensions, the species is, therefore, able to compete against other tree species [7]. The most common pest is the mountain pine beetle *Dendroctonus ponderosae* Hopkins, which attacks pines in July and August and spreads the blue-staining fungus *Grosmannia clavigera* (Rob.-Jeffer. & R.W. Davidson) Zipfel, Z.W. de Beer & M.J. Wingf. 2006. Pine beauty *Panolis flammea* (Denis & Schüffermiller, 1775) is another pest and is the main defoliator in northern Great Britain [4]. Serious damage in Britain is caused also by the European pine sawfly *Neodiprion sertifer* (Geoffroy in Fourcroy, 1785), the bordered white *Bupalus piniarius* (Linnaeus, 1758), and the common pine shoot beetle *Tomicus piniperda* (Linnaeus, 1758) [26]. In America, an important pest is the parasitic American dwarf mistletoe *Arceuthobium americanum* Nutt. ex Engelm., which infects up to 50% of stands in certain areas. In young stands, it spreads at a rate of 0.3–0.5 m per year (the highest in dense forests), increasing mortality, decreasing height and diameter increment, wood quality, seed production, and overall vitality [4, 8]. One of the most serious fungal diseases is stem canker caused by *Atropellis piniphila* (Weir) M.L. Lohman & E.K. Cash 1940. Stem cankers caused by rusts result in increased mortality and reduced growth. The most serious of these is Scots stem pine rust *Cronartium flaccidum* (Willd.) Jørst. 1925. *Endocronartium harknessii* (J.P. Moore) Y. Hirats. 1969 can kill seedlings and saplings. Other fungal pathogens include needle cast agents such as *Elytroderma deformans* (Weir) Darker 1932 and *Lophodermella concolor* (Dearn.) Darker 1967, root rot agents such as honey fungus *Armillaria mellea* (Vahl) P. Kumm. 1871 and *Heterobasidion annosum* (Fr.) Bref. 1888, and wood-decaying fungi such as *Phellinus pini* (Brot.) Murrill 1905

and *Peniophora pseudopini* Weresub & I.A.S. Gibson 1960 [11]. Serious damage is caused also by the fungus *Dothistroma septosporum* (Dorogin) M. Morelet 1968 and by deer [26].

2.4. Wood production and uses of the species

Generally, this is a medium-sized tree, exceptionally reaching heights of 35 m and diameter at breast height (DBH) of 60 cm [4]. Among other authors, Musil and Hamerník [8] have reported heights of (1–)10–25(–30) m and DBH of 18–33(–50) cm, Úradníček [13] height of 10–25(35) m and frequently only bush growth, and Farjon [12] bush or tree growth with height up to 50 m and DBH 100–200 cm. Auders and Spicer [9] indicate sizes ranging from shrubs and crooked trees on the coast of northern California to trees more than 50 m tall in the Sierra Nevada and the subalpine inlands of the northern Rocky Mountains. Eckenwalder [15] localizes miniature shrubs of 10–20 cm in height to coastal sites where soil is unformed.

The variability of growth indicators is related to the taxonomic division of the species at lower levels. *P. c.* subsp. *contorta* with substantially crooked limbs reaches heights of up to 10 m in its natural range [23]. According to Pilát [22], it is a tree or shrub 2–5 m in height, otherwise 6–10 m. *P. c.* subsp. *latifolia* reaches 20–27(40) m [23], or mostly under 25 m and rarely up to 50 m [22]. The greatest heights (40 m) are achieved by trees within river basins in Alberta, Canada [23]. According to Farjon [12], trees of the subspecies *P. c.* subsp. *murrayana* in Oregon and California reach the largest dimensions (height > 50 m and DBH 200 cm). The dimensions and growth achieved are strongly influenced, however, by stand density and environmental factors [25].

The lodgepole pine trunk is straight and cylindrical, i.e., fully woody and with little tapering, which applies especially in dense stands with small and narrow crowns. The trunks clear poorly in the stand, but the branches are thin and short, so they do not diminish wood quality very much [4, 8]. The stems are crooked in certain cases [12], and on exposed coastlines and ridgelines, the trees are sometimes multitemmed, often with irregular crowns [9]. The bark is relatively thin, under 2 cm [4]. The outer bark starts to form early in the subspecies *P. c.* subsp. *contorta*, whereas the individuals of *P. c.* subsp. *murrayana* and *P. c.* subsp. *latifolia* have smooth bark for the first 40–50 years, and thinner scaly outer bark is formed only later [30].

Generally, the species lives to less than 300 years [25]. Musil and Hamerník [8] provide ages of 200–500 years. According to Preston and Braham [17], it can exceptionally live for more than 600 years and reaches maturity at 200–300 years.

Especially, in western North America, it is an important, even main, production tree species, providing high-quality wood that has a greater volumetric production than a number of other species from the same area of comparable height and diameter due to its rapid growth, minimal tapering, and thin bark [4, 12, 25].

Initial growth (up to 5 years) is rapid, exceeding 50 cm per year in productive sites after the third growing season [4]. Acceleration of height increment starts earlier in natural conditions than in other tree species (with the exception of larches and other pines). At 20 years of age, average height is in the range of 2–8 m. During a single vegetation season, sprouts may undergo

dicyclic and polycyclic growth [8]. Nevertheless, lodgepole pine's overall growth is rather slow [17] and definitively starts to decline at ca 80–120 years [25].

Mean annual increment of old, unmanaged stands in the Rocky Mountains may be as little as $0.4\text{--}0.6\text{ m}^3\cdot\text{ha}^{-1}$ due to a large number of young trees and high infection by the parasitic shrub *Arceuthobium americanum*. On the other hand, total current increment after adjustment for stand density and reduction of parasitic plants may improve to $2.1\text{--}5.6\text{ m}^3\cdot\text{ha}^{-1}$ [4]. There can, therefore, be large differences in stand growing stocks. Maximum production in the Rocky Mountains in stands with density of $1980\text{ trees}\cdot\text{ha}^{-1}$ is stated as $280\text{ m}^3\cdot\text{ha}^{-1}$, but only $21\text{ m}^3\cdot\text{ha}^{-1}$ at $4450\text{ trees}\cdot\text{ha}^{-1}$. In an extreme case, in stands 70 years old with $247,000\text{ trees}\cdot\text{ha}^{-1}$, there are trees with average height of only 1.2 m and basal diameter of $<2.5\text{ cm}$. In typical cases, growing stocks reached $168\text{--}224\text{ m}^3\cdot\text{ha}^{-1}$ for adult stands in the Rocky Mountains, although there are also known stands with growing stocks exceeding $336\text{ m}^3\cdot\text{ha}^{-1}$. These were achieved by synergies with a suitable initial number of seedlings, good site quality, and absence of *A. americanum* and the mountain pine beetle *Dendroctonus ponderosae* [4, 11]. From the states of Idaho and Montana, there is data available on average indicators of stands aged 80 and 140 years. In the first case, at density of $1030\text{ trees}\cdot\text{ha}^{-1}$, height reached 18 m, DBH 20.6 cm, and growing stock $285.6\text{ m}^3\cdot\text{ha}^{-1}$; in the second case, at density $680\text{ trees}\cdot\text{ha}^{-1}$, average height was 25.3 m, DBH 26.7 cm, and growing stock $448.7\text{ m}^3\cdot\text{ha}^{-1}$.

In lodgepole pine plantations in Great Britain at a rotation period under the age of 80 years, the annual growth can reach $4\text{--}14\text{ m}^3\cdot\text{ha}^{-1}$ [4]. Average production is $6\text{--}10\text{ m}^3\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ (with a maximum of $14\text{ m}^3\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$), and in Ireland, it is commonly even $18\text{ m}^3\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ [26].

The species' wood is soft, light to medium weight, with density $380\text{--}465\text{ kg}\cdot\text{m}^{-3}$ [25] or $470\text{ kg}\cdot\text{m}^{-3}$ at 15% humidity [26]. It has a satisfying texture and a thin, almost white to yellowish sapwood, which is not sharply separated from the yellow-brown heartwood [4, 17], but is often overly knotty [22]. It has straight wood fibers, low warping during drying, and a relatively homogenous structure. Its wood is similar to that of Scots pine, although it has a higher proportion of heartwood. It is not resistant to rotting in contact with earth, and rotting occurs in as little as a year [26]. It is also susceptible to attacks by wood-boring insects [4].

Commercially, its wood is of intermediate importance [17]. Lodgepole pine is suitable for construction and carpentry purposes [22]. It is easy to plane, bend, color, drill, and carve [4]. Although the sapwood is highly permeable for preservatives, impregnation of the heartwood is more difficult [4, 26]. Unimpregnated wood, however, decays very rapidly [22]. It is used for producing sawmill logs and lower-quality lumber. It is used for the production of light building structures, frames, paneling, pillars, stakes, rods, poles, posts, timbering in mines, railway sleepers, floor coverings, fences, gates, crates, pallets, furniture, chipboard, plywood, etc. [11, 17]. There is an increasing trend for its modern use in the cellulose industry and composite materials [12], especially in production from plantation cultivation [4], which will apparently give priority to managing stands for rapid growth at early age [11].

In terms of nonproduction uses, this pioneering species is valued in North America for various purposes due to its quick growth and undemanding soil requirements. In volcanic mountain ranges, its vitality is used for its advantage in eliminating the influence of climatic extremes

and for protecting against soil erosion [21]. It is a highly regarded species for drying out bogs. Its planting in lowlands is not appealing, however, because other species outperform it for production and stem shape. In Britain, it is grown at higher elevations on the poorest and particularly swampy soils [26]. It grows well in Ukraine, Belarus, and the northern Caucasus, but it does not fare well on the southern coast of Crimea [22]. It is being tested in forest stands in several European countries [23]. It was frequently planted in Sweden in the 1960s. Its ability to grow on poor, recultivated locations and in a cold climate attracted attention. It was also experimentally used on pollution clearings. Sometimes, it fulfills the function of a protective tree species on infertile sterile soils [12]. Provenance experiments in Europe have demonstrated that it does not have such high production potential as Scots pine, but, depending on provenance, it can handle more severe exposure to frost and drought [31]. In western North America, it is also valued for its landscaping, water management, and ecological importance. Native Americans used to consume its juicy bark [4, 8].

From a gardening perspective, lodgepole pine has a lower decorative value (*P. c.* subsp. *murrayana* creates larger and prettier trees). Nevertheless, sometimes, it can give a nontraditional impression, and in smaller spaces, it serves well as a replacement for the more robust Austrian pine. It is planted as a solitary tree or in groups, as well as for contrast together with broadleaves. The species tolerates air pollution, and therefore, it is frequently used in urban areas, on embankments, etc. It is used in recreational forests, parks, castle gardens, along roads, and in reclamations [10, 13, 19, 22, 24, 30, 32].

2.5. Use in forest reclamation

The use of lodgepole pine in forest reclamation, which is substantially different from the common forest restoration, is a separate matter. Possibilities for use of forest species on extreme sites such as spoil banks or recultivated mining areas have been studied, e.g., [33–37].

The selection of tree species suitable for forest reclamation is based on evaluations of experimental plantings and pilot experiments. A number of factors are monitored, such as (1) natural occurrence of the species in the given area, (2) ecological characteristics of the species, (3) requirements for climatic and soil conditions (in particular, the occurrence of late or early frost or drought spells spanning several days), (4) pedological characteristics of the spoil bank soils (in particular, the range of pH at which the assessed woody species is vital) and the necessity for biological amelioration, (5) survival rate, growth and development of the species, or vitality of growth in monocultures and mixed stands, (6) function of the woody species on the spoil bank site (humus-forming, soil protection, amelioration, hygienic, esthetic, economic), (7) resistance of the woody species to industrial air pollution and to biotic and abiotic agents, and (8) health status. It is very difficult to compare the findings from these investigations with the results from typical forest stands. Important questions concern the creation of suitable mixtures, chronology of regeneration, tending, silviculture techniques, and spatial organization of stands [37–40].

Special particularities of forest reclamations concern the artificially created substrate from overburden overlying soil-lacking pedogenetic characteristics, and frequently also air contamination

by industrial pollution, undetermined founding and silviculture procedures, and generally poor knowledge of the trees' responses to spoil bank forest management [41]. The heterogeneity of spoil bank materials does not allow for a homogenous choice of afforestation work [38].

Considering the requirements for substrate modification, the most suitable introduced broadleaf has been found to be the northern red oak (*Quercus rubra* L.) and black locust (*Robinia pseudoacacia* L.), and among conifers Austrian pine (*Pinus nigra* J.F. Arnold) and lodgepole pine. In particular, the two conifers are, together with European larch (*Larix decidua* L.), highly tolerant to extreme soil reaction ($\text{pH} < 3$) of anthropogenic substrates where not even common forest weeds can grow. When other selection criteria are included (e.g., tolerance to climatic extremes, fast growth), however, relatively slowly growing lodgepole pine no longer belongs in that elite group [37].

Along with other woody species from higher latitudes, lodgepole pine demonstrates much richer foliage on anthropogenic substrates, as well as a longer vegetation period and lower transpiration. It is one of the species with the largest horizontally rooted profile [42]. It can be a truly promising conifer suitable for intentional forestation of anthropogenic substrates even where the air is rather highly polluted by SO_2 [33]. Together with some other species, if requirements for seedling quality and early, properly performed planting are fulfilled, it has an almost 100% survival rate even on such specific locations [42]. In soil substrates of the Czech Republic's Antonín reclamation arboretum, just as a number of other species, its development is not different from that on naturally developed soils [41].

Similarly to, for example, poplar cultivars, lodgepole pine requires a larger planting spacing. A shallow vertical rooting profile has been unequivocally demonstrated in this species. This means that in order to ensure lodgepole pine stands' stability against windthrow on clay anthropogenic soils, mixture with broadleaves is appropriate or even indispensable [39]. Ideal conditions for growing conifers (*Larix*, *Pinus*) are provided by the cover species European hornbeam (*Carpinus betulus* L.), which requires cyprus clays in the form of clay slate or flaky clays. Hornbeam has a high amelioration effect (heavy litterfall, good rooting), covers the soil surface well, and increases the infiltration capacity of surface layers in the soil profile. On biologically unaugmented soils, however, it only grows as a bush [38]. The selection of suitable mixtures of broadleaves and conifers is more difficult than in purely broadleaf mixtures. In selecting the conifers, one needs to consider primarily their resistance (plasticity) to industrial air pollution, in particular SO_2 . In anthropogenic sites, the maximum representation of conifers in stands (20–40%) is defined by soil-forming aspects. When the conifers are planted as individual component of mixture, it is desirable for the broadleaf species in these cases to have growth vitality the same as or lower than that of the conifer. In addition to European hornbeam, this criterion is fulfilled by, for example, small-leaved lime (*Tilia cordata* Mill.), common oak (*Quercus robur* L.), and sessile oak (*Q. petraea* /Matt./ Liebl.). In establishing broadleaf/conifer mixtures by group, almost all broadleaves suitable for anthropogenic substrates can be used [39].

The most recent findings from the forest reclamation area concern growing and tending interventions. Establishing and tending of mixed stands in clusters or groups is the most suitable. A major advantage is that it is not necessary to expend labor on freeing the conifers from shading by broadleaves during the first decade. The groups of broadleaves create very

good edge protection (improving moisture and microclimatic conditions), due to which the conifer groups have stable growth. To transform short-term and long-term preparatory stands, an underplanting of conifers (including *P. contorta*) can be used, in the form of circular, linear, wedge, striped, or combined removal methods [39]. Establishing mixed broadleaf-coniferous stands is realistic under the assumption that the predominance of broadleaves will be maintained [42].

Coniferous stands consisting of commonly deep-rooting species have the least stability among mixed-age stands on the clayey spoil banks because of absence of tap root formation in these conditions. This is the case especially for various species of pines, including lodgepole pine. Comparison tests have demonstrated that the thickness of heart roots and especially horizontal roots are positively influenced in this species by a selecting a wider spacing of 4×4 m. This is because in such case, stands are exposed to adverse weather conditions already from a young age, and especially to wind [42].

In 1973 at the Velký Riesel spoil bank in the Sokolov area in the Czech Republic, lodgepole pine was planted in alternating strips with common alder (*Alnus glutinosa* /L./ Gaertn.) and for comparison as underplanting of a 10-year-old chemically reduced (approximately to 50%) stand of gray alder (*A. incana* /L./ Moench.). In 1979, the height of lodgepole pine in the strips among common alder reached 298.6 cm, whereas in the underplanting into reduced gray alder, it was 272.2 cm [33]. Experimental combinations of lodgepole pine with common alder were demonstrated to be very suitable [42].

On tertiary substrates, higher mean annual increment in lodgepole pine can be assumed as compared to on quaternary substrates. In extreme conditions, packaged seedlings can be used [39].

As part of production research on a lodgepole pine monoculture at the recultivated Antonín spoil bank in the Sokolov area with average height of 15 m and diameter at breast height of 21 cm ($n > 100$), 10 sample trees were felled. In all 10 samples, growth increment reached its maximum in the first half of the tree's life (and in a majority already in the first third). Diameters at breast height of sample trees were in the range of 18.1–19.7 cm (mean 19.0 cm). Current diameter increment was 2.7–12.9 mm, and mean diameter increment was 6.3–9.5 mm [43]. Similar values had been determined by Bažant [44] on spoil bank sites of the Most basin in two samples of Scots pine with identical diameter at a breast height of 10.2 cm. Current diameter increments of the samples were 10.0 and 11.0 mm, and mean diameter increment was 5.0 and 5.5 mm.

2.6. Growing aspects

The growth properties of lodgepole pine may differ not only depending on the conditions of the planted site, but also by the subspecies or provenance used. The differences in production among subspecies and provenances were confirmed in conditions of three Czech research trials [45–47], which were kept intentionally intervention free until the age of 34 years. The results, thus, obtained therefore allow us to make recommendation for certain habitats regarding potentially broader use of the provenance with the largest hectare growing stock, although if common forestry management had been carried out, their order in production achieved

could have been different to some degree. The literature does not specify tending interventions according to the individual subspecies of lodgepole pine, and this is why they are not differentiated in this subsection.

In the species' natural range, stands provide viable seeds from 5 to 10 years of age [11], even though male cones have been detected on seedlings in a nursery at just 2 years of age [8]. Mast years occur in intervals of 1 to 3 years, so production of reproductive material is sufficient [11]. The logging waste of branches with closed cones also can be used as a source of seeds. Serotinous cones produce 100,000–200,000 seeds·ha⁻¹·year⁻¹ (total growing stock may be up to 10× greater). Nonserotinous cones produce 35,000 to 1.2 million seeds·ha⁻¹·year⁻¹. One cone (Rocky Mountains) has approximately 10–24 developed seeds, and one adult tree may have several hundred to several thousand cones [8]. Cones mature in August to October, more than 1 year after pollination. Net seed proportion differs under various natural conditions (in various provenances), although even low values of this indicator are sufficient to ensure the necessary amount of seeds. The recorded difference in number of disbursed seeds per hectare in Oregon ranged between 35,000 and 1.2 million [11]. It can be assumed that parental stands of lodgepole pine in Central Europe would have similar rates. In Britain [26], production is 245,000 to 364,000 seeds per kilo, of which ca 270,000 are viable. For various provenances, however, it is necessary to account for diverse representation of serotinous cones, which open in outdoor conditions only after being subject to intense heat [4]. In order to obtain seeds for artificial regeneration purposes, this problem is technologically solvable in seed extraction facilities.

Germination proceeds best on a mineral soil without competition from weeds and in full sun [4]. Under advantageous conditions (temperature 8–26°C, corresponding humidity), it is fast and reaches almost 100%. The seeds are usually not preserved in the soil over the long term. The seedlings are relatively tolerant to extreme temperatures. Their survival, similarly to germination, is inhibited by shading, competition, and insufficient moisture. Preparation of seeds by stratification in nurseries is not necessary. Lodgepole pine can be reproduced vegetatively by grafting and cutting, including by micropropagation *in vitro*. Coppicing also has been observed in nature. A substantial increase of growth can be achieved by fertilization [8].

Mean regeneration ensuring full use of an area is 2470 trees·ha⁻¹ with subsequent reduction in order to achieve a suitable spacing. If the individual trees are equally spaced, their number at 5–20 years of age should not exceed 1200–2000 trees·ha⁻¹ [4]. For artificial regeneration, at least two-year container seedlings should be used, because most one-year seedlings do not have sufficiently developed root systems and that influences their vitality and stability. Detailed investigation has furthermore confirmed that root development depends also on seed origin [31].

A general problem in the early development stages of lodgepole pine stands is excessive density. This may lead to growth stagnation, especially on poor and dry sites. Adjusting the density of young stands is the best production-increasing option among all known measures, because the culmination of total volume increment occurs in seriously stagnating stands as early as 40 years of age and in overly dense but not too-stagnating stands at 50 to 80 years of age. In poor areas and in dense stands, intervention is necessary after a mere 10 years. Even though dense stands have a strong capability for self-thinning and low crown space

requirements, the difficulty of increasing their quality through tending increases with age. Thinning out of excessively dense and stagnating stands may renew growth potential and achieve production of good commercial assortments [4]. A comparison of the rate of commercial wood acquired from tended and untended stands after 25 years of development has shown that the tended stand exceeded the untended one by 460% in this parameter [48].

Especially in excessively dense stands with narrow crowns and strong root competition, there can occur damage due to strong winds and heavy snow that cause breakage and bending of stems [4, 25]. Calamity wood needs to be processed within 1 year due to its rapid decomposition in contact with soil [26]. It is, therefore, important to consider the degree of thinning, because substantial reduction in density may substantially increase the extent of this type of damage. Diameter increment usually accelerates the most after strong interventions, whereas the values for volume increment and basal area increment usually increase after lighter thinnings [4, 25].

Lodgepole pine can be grown in a monoculture as well as in mixed stands [25]. In order to achieve well-usable assortments, a spruce-pine-fir mixture is suitable [4]. Due to declining growth at 80–120 years, the rotation period may be theoretically established at 90 years. Due to light permeability, an understory is usually well formed under the canopies of mature stands in certain areas, which may create complications for their development for purposes of natural regeneration [25]. Shelterwood cutting is usually not sufficient [8]. Clear-cutting is considered the best regeneration method and in certain cases, depending on area and economic objectives, also group selection-cutting [25]. It is apparently optimal to create a cutting face in the parental stand and subsequently prepare the soil in a suitable manner. According to the literature [4], however, the response to reproduction cutting is very slow in terms of regeneration (more than 10 years). Therefore, if necessary, harvesting should be carried out early in the appropriate part of the cutting face in order to thin the canopy. Such prepared conditions should ensure rich natural regeneration in the next year.

In Britain, lodgepole pine was earlier used as a covering species, usually in a mixture with Sitka spruce. Rapid growth of the pines, however, frequently caused problems with the spruces being suppressed and even entirely eliminated. In some boggy areas, however, a previously unknown and still not entirely explained “caretaker” effect was attributed to this mix: in the cover of the pines (especially those of Alaskan provenance), the Sitka spruce achieved several classes greater production than when grown in a monoculture. This mechanism is probably related to intake of nitrogen and mycorrhizal ecological relationships [26].

2.7. Results of provenance experiments

In order to assess growth and adaptation characteristics of lodgepole pine in the Central European region, one can refer in particular to available findings acquired through past evaluations of long-term provenance experiments established in the Czech Republic and in Germany.

In the Czech Republic, the most recent results are from evaluations at three research trials, which were established in various site conditions by the Forestry and Game Management Research Institute in 1984 and 1985, e.g., [28, 49]. At 34 years of age, differences in the growth of subspecies and various provenances of pines were apparent. The site in an acidic oak forest

at the Sofronka location (Plzeňsko) at 330 m a.s.l. [45] is best suited to the provenances of the subspecies *P. c. subsp. contorta* from the coast of Washington, Oregon, and California, whereas the conditions of a poor pine forest at the Mláka location (Třeboňsko) at 435 m a.s.l. [46] are suitable for the Oregon provenances of the subspecies *P. c. subsp. contorta* and *P. c. subsp. latifolia*. Also, the site of acidic spruce forest at the Kovářská location (Ore Mountains) at 870 m a.s.l. [47] is most suitable for the Oregon provenance *P. c. subsp. latifolia*. Successful growing of lodgepole pine, therefore, requires analyzing natural conditions at the place of planting and subsequent selection of a corresponding provenance.

Two-factor analysis of variance was calculated for the stem volumes from three provenance trials of lodgepole pine for provenances represented in all three trials (**Table 1**). The factors were provenance and research trial locations.

There were significant differences among both research trials and provenances. The results are graphically represented in **Figure 2**, which clearly shows that the highest values are achieved by the provenance 2091 Mount Hood from the Oregon Cascades (*P. c. subsp. latifolia*) at the Kovářská location, reaching mean trunk volumes of 0.210 m³, followed by provenances 2130 Mineral from California (*P. c. subsp. murrayana*) and 2123 Enterprise from Oregon (*P. c. subsp. latifolia*) at the same location, reaching 0.169 and 0.161 m³, respectively. The provenance 2089 Chemult from Oregon (*P. c. subsp. contorta*) was also noteworthy, being the only one to achieve above-average production in all three trials. It, therefore, has the potential for universal use from lowlands to mountain areas. From the perspective of altitude range, the subspecies *P. c.*

Provenance	Origin	Subsp.*	Altitude (m a.s.l.)	Latitude N	Longitude W	
1901	Chetwynd	British Columbia (BC)	L	700–1000	55°37'	121°40'
1902	Mile 86	British Columbia (BC)	L	752–900	56°48'	121°35'
1903	Upper Liard	Yukon Territory (YT)	L	701–761	60°05'	129°18'
1904	Wonowon	British Columbia (BC)	L	825–950	56°46'	121°53'
2089	Manzanita	Oregon (OR)	C	30	45°43'	123°56'
2091	Mount Hood	Oregon (OR)	L	1280	45°18'	121°45'
2098	Chemult	Oregon (OR)	M	1675	43°19'	121°39'
2120	St. Regis	Montana (MT)	L	945	47°22'	115°24'
2123	Enterprise	Oregon (OR)	L	1310	45°38'	117°16'
2126	Prairie City	Oregon (OR)	L	1490	44°32'	118°34'
2130	Mineral	California (CA)	M	1490	40°21'	121°29'
2133	Truckee	California (CA)	M	1830	39°13'	120°12'
2138	Mineral King	California (CA)	M	2410	36°27'	118°36'
2234	Kananaskis	Alberta (AB)	L	1524	51°05'	114°45'
2235	Calling Lake	Alberta (AB)	L	1005	55°38'	113°27'

*L = *P. c. subsp. latifolia*, C = *P. c. subsp. contorta*, M = *P. c. subsp. murrayana*.

Table 1. Characteristics of provenances represented in all three trial sites.

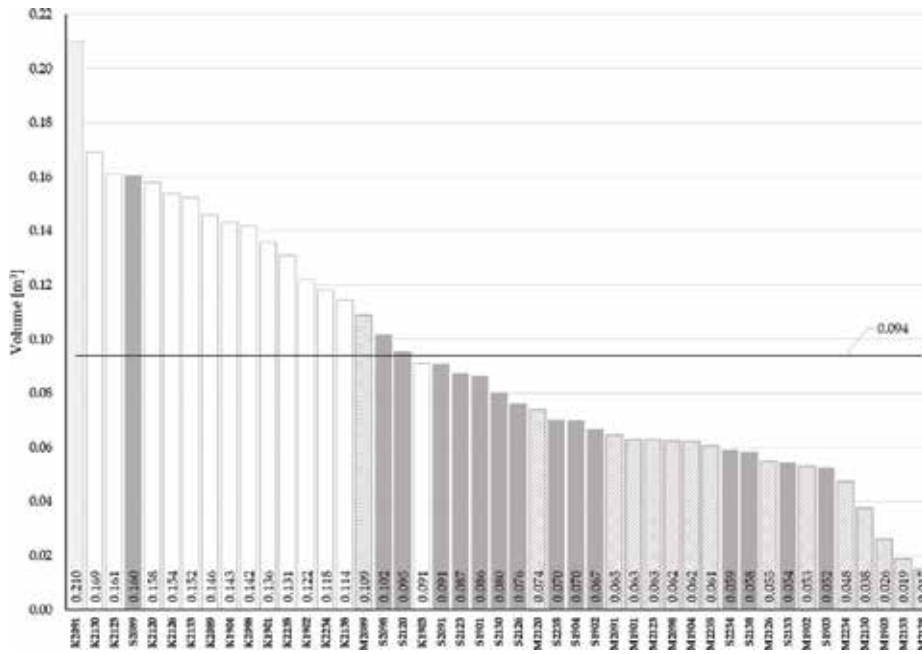


Figure 2. Trunk volume by provenances and locations (K = Kovářská, S = Sofronka, M = Mláka).

subsp. *contorta* appears to be universal, whereas *P. c.* subsp. *latifolia* and *P. c.* subsp. *murrayana* are more suited to middle to mountainous elevations. All provenances achieved their best values at the Kovářská location, followed by Sofronka, where trunk volume of most provenances was below average. The provenances grew slowest at the Mláka location. Generally, provenances from Oregon can be evaluated as the best without regard to subspecies or locations (2089, 2091, 2098).

In the acidophilic oak forest at the Sofronka location, the greatest heights were determined in *P. c.* subsp. *contorta* and the lowest in *P. c.* subsp. *murrayana*. In the subspecies *P. c.* subsp. *latifolia*, which has the largest natural range, it seems the heights of provenances decrease in the direction of gradient of the position of their parental locations from the ocean to the inland. Provenances from the coast of Washington, Oregon, and California demonstrated rapid growth. A similar result was determined on an extremely dry site with a minimum of nutrients at Mláka, where the best results were achieved by provenances 2089 Manzanita from the coast of Oregon (*P. c.* subsp. *contorta*) and 2091 Mount Hood from the Oregon Cascades (*P. c.* subsp. *latifolia*). On the other hand, in the Ore Mountains, especially the provenances of *P. c.* subsp. *latifolia* from middle elevations showed above-average growth. Among provenances of the subspecies of *P. c.* subsp. *contorta*, only the Oregon provenance 2099 Port Orford had positive results, and among those of *P. c.* subsp. *murrayana*, it was 2098 Chemult, also from Oregon.

Relative yield class was used to compare the growth of lodgepole pine provenances with the local type of Scots pine at the Mláka location. Relative yield class of neighboring Scots pine stands reaches 2–3. In the lodgepole pine provenance 2089 Manzanita *P. c.* subsp. *contorta*,

which has the largest growing stock of $175 \text{ m}^3 \cdot \text{ha}^{-1}$, the tabular relative yield class for Scots pine [50] corresponds to 4, which is an interesting result in the given location. Average relative yield class of lodgepole pine had a value of 6 whereas in the case of the poorest provenance 9. Results comparable with those of local pine were, therefore, provided only by the best provenances of the introduced species. Furthermore, a comparison of lodgepole pine's growth with that of Scots pine in the conditions of acidic spruce forests, poor sands [46], and oak-beech forest [29] demonstrated that the native species can be equaled only by the best provenances of the introduced tree. Different results, however, were provided by a comparison of Scots pine with Norway spruce on a series of experimental trials in Germany [51], where lodgepole pine unequivocally had outgrown both autochthonous species at 23 years of age.

Research on lodgepole pine is also being conducted in Germany [52]. Undoubtedly, the best height growth at 8 years of age has been demonstrated by provenances originating from the coast of Oregon, Washington, and southern British Columbia. In comparison with the earlier results from the Mláka and Sofronka trials at 7 years of age, the result was similar. A distinction in Czech trials is the positive evaluation of provenance 2120 from Montana.

At the Adorf, Hundhübel, and Steinbach research trials on the German side of the Ore Mountains, average heights of lodgepole pine at 32 years of age were determined to be 10.0, 11.3, and 13.0 m [53]. These values are also comparable to those from the Kovářská trial at 34 years (12.9 m). Replacement stands of lodgepole pine established in the past in polluted areas of the Ore Mountains in Saxony are still expected to perform productively [54].

On a series of six German experimental trials with 11 provenances of *P. contorta* [55] at 15 years of age, coastal provenances of *P. c.* subsp. *contorta* and several inland ones of *P. c.* subsp. *latifolia* fared the best. Provenances of *P. c.* subsp. *latifolia* from further inland grew at average rates, and inland provenances of *P. c.* subsp. *murrayana* grew unsatisfactorily. On another German series of eight IUFRO trials with 140 provenances of lodgepole pine [52] at 8 years of age, provenances of *P. c.* subsp. *contorta* from the coast of Oregon, Washington, and the south of British Columbia also grew the best, as did certain inland provenances of *P. c.* subsp. *latifolia* from southern and central British Columbia. Provenances from northern British Columbia, Alberta, Yukon, and Alaska grew unsatisfactorily, as did the mountain provenances of *P. c.* subsp. *murrayana*. Even though ecological conditions are different on German trials, the above-average growth of inland provenances of *P. c.* subsp. *latifolia* corresponds with the results from the Kovářská location.

The results of provenance experiments from the two countries are comparable and can serve as recommendations for the growing of *P. contorta* in Central Europe. A selection of suitable provenances in the current conditions of climate change ensures a certain stand quality, vitality, and productivity as well as other nonproduction functions.

2.8. General assessment

Lodgepole pine well tolerates the Central European climate and grows relatively well, especially when young. The subspecies *P. c.* subsp. *latifolia* and *P. c.* subsp. *murrayana* are grown most frequently there. The species is suitable for poorer sandy to sterile, dry to fresh sunny

locations. It is resistant especially at oak to beech vegetation levels, but is considered for forestry uses also in submountainous areas. The species does not suffer from snow damage here. In contrast to originally high-elevation mountainous locations (around 2800 m a.s.l.) of certain provenances, the species does not have sufficient air humidity in common Central European forests. That may have an effect on its vitality only after a certain time has passed after planting. Whether it can handle the new conditions depends on provenance and specific genotypes. Previous experimental applications of this species in forests (e.g., the Ore Mountains) can be considered successful. German experiments have demonstrated that it can be used, for example, to improve perennial spruce cultures. Its addition into mixtures is appropriate 4–6 years later, however, due to its rapid growth. Monocultures must be planted in a denser canopy, because in a more open spacing, it spreads its branches and suppresses neighboring trees [20, 22, 23, 30].

The species is reliably frost resistant in the conditions of Central European winters [13, 19]. Based on findings from research trials in the Czech Republic, the coastal *P. c.* subsp. *contorta* seems to be more suitable for poor locations at lower elevations, although it is only rarely grown in Central Europe [23, 24]. It is a resistant pioneering species suitable for polluted areas [13, 30]. In comparison with autochthonous and introduced pines, it tolerates, in particular, higher doses of SO₂ [24]. On the other hand, it is relatively sensitive to pollution by F₂ and HF [20]. Damage by game is not considered to be too substantial [13], although deer remain the main problem for experimental plantings in the Ore Mountains [8].

Based upon a critical assessment of information assembled in the previous sections, the potential for possibly broader forestry use of lodgepole pine in the Central European Region in future is summarized in **Table 2**. The principle is to consider the extent to which characteristics crucial for forestry usability are present or absent.

This subjective assessment can be supported by the following notes to the individual criteria. 1: lodgepole pine does not reach excellent production, although some of its provenances equal Scots pine. Therefore, an overall negative score is not justified. 2: the wood has larger heartwood and narrower sapwood; i.e., it has decorative qualities and can be used for paneling and staining. It is, therefore, well usable, although not for building and construction purposes. 3: the species' wide ecological valence enables the use of appropriate provenances in many location types. 4: as true of other pines, it acidifies the soil, and humification of its litterfall is

Species/criterion	1	2	3	4	5	6	7	8	9	10	11
<i>Pinus contorta</i>	0	+	++	–	+	+	0	++	?	+	+

Criterion: 1 production capacity, 2 wood usability, 3 suitability in various types of locations, 4 amelioration effects, 5 drought resistance, 6 resistance to other abiotic factors (frost, snow, wind, etc.), 7 resistance to biotic pests, 8 possibility of cross-breeding with local species, 9 invasiveness, 10 suitability for mixture, and 11 capability for natural regeneration. Species manifestation (at current level of knowledge): ++ very positive, + positive, 0 neutral, – negative, – – very negative, ? unknown.

Table 2. Assessment of important decision criteria for potential forestry use of lodgepole pine in Central European conditions.

Species/criterion	1	2	3	4	5	6	7	8
<i>P. c. subsp. latifolia</i>	No	Yes	Yes	Excellent	No	Tree	Yes	Rich

Criterion: 1 requirements for substrate modifications, 2 microclimate demandingness, 3 tolerance to pollution load, 4 growth vitality, 5 requirements for biological substrate preparation, 6 growth, 7 demandingness for protection from game damage, and 8 foliation.

Table 3. Assessment of important decision criteria for potential reclamation use of lodgepole pine [37, 38].

imperfect. 5: it is resistant to drought, which is especially true for certain provenances. This was confirmed in the Czech Republic e.g., in the extreme conditions of the Mláka research trial. 6: it has a stabilizing effect on stands. It is relatively resistant to frost in the Central European region. It grows well even in mountainous conditions (Ore Mountains), even though a certain proportion of crown breakage does occur. 7: insect pests are similar to those on Scots pine. Serious damage has not yet been observed. 8: it cross-breeds only with Jack pine, whereas hybridization with Central European pine species has not been documented. 9: applying the pioneering strategy of the species known from North America was not studied in Europe so far. 10: it is able to create excellent mixtures with European hornbeam, and northern red oak, among other broadleaves. In mixtures, however, it requires a larger insulated growth space. 11: natural regeneration does occur, although more-detailed findings are not yet available.

Regarding lodgepole pine's importance in terms of forest reclamations, it is one of the most suitable species, e.g., [33, 34, 39, 42]. In the Czech Republic, it has been proven successful in afforestation of barren clay soils, such as brown coal dumps in the Under Ore Mountain Basin and in the upper Ohře/Eger River area, and in reclamation of exploited peat bogs in the Třeboň Basin. In general, the findings suggest that it is possible not only to survive on substrates with insufficient nutrients but that it even can create a continuous-canopy stand there. Štrudl [43] has pointed out, for example, that in addition to being capable to create a canopy, it is tolerant of inhospitable environments, adapts speedily to substrate, and has a favorable initial growth. Despite later slowing growth, based upon a growth analysis that determined satisfactory dimensions, he regards the species as having potential for wider use.

A collective assessment of selected species characteristics based upon results of the so-called "Czech" reclamation school that began taking shape after World War II is presented in **Table 3**.

The positive verification of lodgepole pine's species characteristics on extreme locations of forest reclamation can be, to a certain degree, an indicator for its selection into the species range of plantings in suburban vegetation areas within industrial urban areas, protective forest bands, etc. [39].

3. Conclusion

Lodgepole pine is interesting for forestry use in Central Europe especially due to its resistance to biotic and abiotic factors (e.g., drought) and due to its outstanding pioneering properties,

including the ability to colonize areas disturbed by human activities. In forestry reclamations, it has already been proven to be one of the best introduced species and that, in addition to meeting basic requirements, it can satisfactorily fulfill also the production function. In future, it will undoubtedly gain in importance for the ability of certain provenances to grow in locations that are already today unfavorable for growing native forest species, including Scots pine. These are in particular extremely dry, poor, and warming locations on sandy soils. Other provenances can be utilized in mountainous areas, on locations with anthropogenically polluted air, and in urban green areas. In addition, if the scenarios assuming substantial changes of basic climatic characteristics in Central Europe are fulfilled, then its currently low evaluation for production capacity can be viewed differently.

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A New Method to Reconstruct Recent Tree and Stand Attributes of Temporary Research Plots: New Opportunity to Analyse Mixed Forest Stands

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Abstract

In the last decades, studying effects of mixing tree species is increasingly important. In particular, under changing growing conditions and social requirements, investigations on mixed forest compared to mono-specific stands are of special interest, for example, stability, resilience or ecosystem services. Permanent forest research plots are a unique data source, providing the required information but being time-consuming and costly to establish. Moreover, large data sets of such plots are missing but needed for generalising any findings. Temporary research plots provide ad hoc information of its status quo and require less effort than permanent plots. Usually, such plots provide no information of the recent tree and stand characteristics. We demonstrate a new method developed under the scope of COST action FP 1206 EuMIXFOR (European Network on Mixed Forests) to estimate retrospective tree dynamics and stand characteristics. The results of validation reveal its usefulness for reconstructing 5–10 years. Thus, the method provides new potential in establishing larger networks across several countries, in particular, for studying underlying processes when comparing mono-specific with mixed forest stands.

Keywords: temporary research plots, mixed stands, retrospective growth analysis, increment cores, reconstruction of stand dynamics, mixing effects

1. Introduction

In the last decades, researches of forest growth and yield have increasingly focussed on comparing mono-specific forest stands with mixed forest stands [1–3]. Often, the main focus covers mono-specific and mixed forest stands involving coniferous species. In particular, the effects when mixing coniferous species with broadleaved species either with similar or contrasting functional traits are of special interest. From a historical perspective, mono-specific stands, in particular, those composed by coniferous species, have been silviculturally favoured due to their lower management costs and their seemingly higher productivity compared to broadleaved or mixed stands. Driven by the first empirical observation of yield growth, recommendations have been made of converting mixed forest stands towards mono-specific coniferous stands, when the former is composed by both coniferous and broadleaved species. For example, concerned about serious production losses in mixed stands, one of the founding fathers of forest science—Hartig [4]—recommended that ‘All mixed stands with coniferous and deciduous species should be converted into pure stands of the coniferous species, as soon as circumstances permit’. In addition, the increasing need for wood during the early and middle nineteenth century required high production forests with low rotation periods [5, 6]. Consequently, the first systematic long-term yield observations plots have been established in mono-specific stands [7, 8]. Those plots served as the data base to analyse stand growth dynamics and in developing yield tables, summarising age- and site-dependent stand productivity. The results of converting the forest into mono-specific stands composed by coniferous tree species are visible until today. San-Miguel-Ayanz et al. [9] characterised Europe’s forests and illustrate a predominance of mono-specific stands with superiority of approximately 50% coniferous, 27% broadleaved while only the remaining refer to mixed forest stands.

In the last decades, however, growth and yield research increasingly focus on productivity dynamics in mixed stands. Mixed stands are assumed to better resist biotic and abiotic damages and provide a broader range of ecosystem services [10–12]. Thus, the early investigations of comparing effects on yield growth when mixing tree species have been extended, for example, by Wiedemann [13], Assmann [14] or Schober [15]. For example, the results reveal the early findings and even show that mono-specific stands of Norway spruce or Douglas fir show by a far greater productivity than in any mixture on many sites in temperate and boreal zones [8, 13–15]. In addition, in the last decades, many mono-specific forest stands collapsed due to several biotic and abiotic reasons, for example, calamities, storm or socio-economic changes. Recent studies reveal that interspecific interactions in many cases can lead to higher rates of productivity in mixed stands compared to the mono-specific stands comprised by respective tree species [2, 3, 16–20]. Although many theories exist about the superiority of mixtures, the effects of mixing tree species and underlying processes are still poorly understood. Therefore, in the last decades, investigations on mixed forest stands compared to mono-specific stands widen their focus, for example, considering structural differences [3], stability [21–23] and resilience [22] for ecosystems services [3, 11, 24, 25]. Usually, permanent research plots provide a sufficient data source while covering attributes at tree and stand level. However, in order to generalise any finding, varying growing conditions and a sufficient number of plots similar in their stand characteristics, for example, growing condition, density, age and species composition, are crucial. Unfortunately, establishing networks

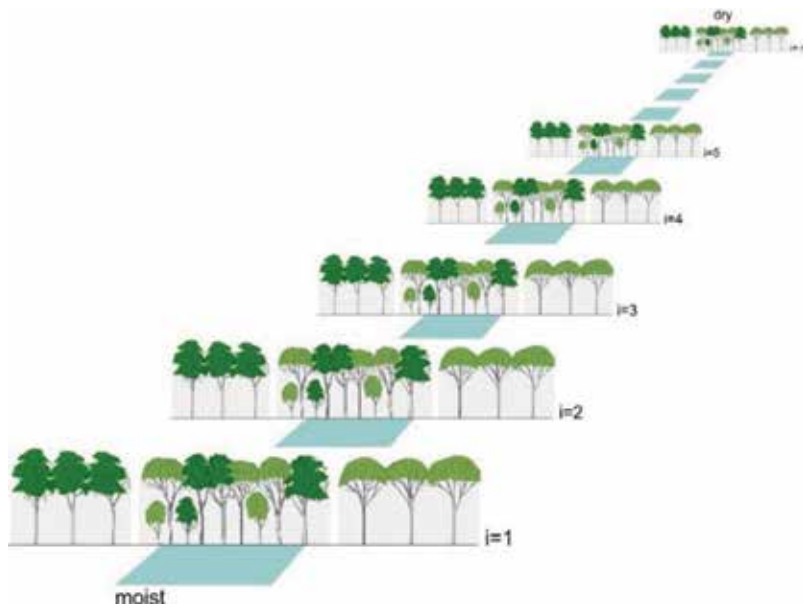


Figure 1. Principle of the transect study: an ecological gradient from moist to dry sites including 32 triplets (temporal plots), consisting of pure Scots pine stands, pure European beech stands, and mixed stands of Scots pine and European beech, which were established in 2014 within COST Action FP1206 EuMIXFOR (after Pretzsch et al. 2015).

are time-consuming, expensive and difficult to realise, in particular, if multiple countries are involved. In addition, it requires decades of continuous survey to get the first results. Alternatively, temporal research plots have been used to overcome these limitations but having the disadvantage of missing information of any historical stand situation. Researches with respect to yield growth are therefore based on increment cores and limited at tree level, unless all trees are sampled. To this extent, standardised valid methods to reconstruct the recent tree and stand development for a specific plot are missing.

Therefore, we demonstrate a new method to reconstruct recent tree and stand development for mono-specific and mixed forest stands, developed based on triplets study design established under the scope of COST action FP 1206 EuMIXFOR (European Network on Mixed Forests) [19, 26] (**Figure 1**). Thus, this topic is up to date and of particular interest when developing strategies of converting mono-specific stands into mixed forest stands. The introduced method aims to (1) predict recent retrospective diameter and height development at tree level, (2) predict recent stand characteristics, (3) develop standardised routines and (4) being extendible and applicable for multiple tree species.

2. Method and validation

2.1. Requirements of plot selection

The reconstruction of stand characteristics based on temporary plots requires a set of minimum sample trees, plot data and increment cores. For living trees and snags, the attributes

like calendar and physiological (before, during or after a growing season) year of survey, tree number (nr), tree species, diameter at breast height (dbh), tree height (h) and age per tree species must be available. The diameter at breast height is required for all living trees and standing dead wood exceeding a defined threshold value, for example, 7 cm. In addition, for occurring stumps tree species, the estimated year of removal and the corresponding dbh are needed. Measurements of tree heights can either cover a full survey or being representative per species. While the former represents all height variation, the sample must strictly cover the complete range of heights per tree species. Missing individual heights will be derived by applying parameterised height curve functions. Usually, such functions are based on the height to diameter relationships, for example, Petterson, Prodan, Freese, Michailov or Korsun [27]. Here, the measured h-dbh pairs are used for parameterisation and should be species-specific. Species-specific age is required for each tree species and stand layer. For plot characteristic, only the size is required. Increment cores must cover a sufficient number of trees, for example, 20–40% of the living trees per plot and tree species. However, this depends on the stand structure and species composition. Nevertheless, the selected trees must represent the diameter range at plot and species level. Increment cores should be taken at a 1.30-m height, at least two cores per tree, for example, north and east direction.

2.2. Stand reconstruction based on tree and increment core data

The reconstruction aims to provide a tree list covering the diameter at breast height, tree height, basal area and volume per tree for pre-defined years. Here, the tree list per year represents artificial surveys and will be evaluated following DESER Norm [28]. The proposed method follows a three-step approach and implemented as standardised routines. In a first step, all increment cores are measured and the year ring widths synchronised, for example, following standardised methods [29–31]. The recent diameter at breast height will be derived for all cored trees and reconstructed for non-cored trees applying regression analysis. Second, standardised height curve functions, for example, Kennel [32] and Franz et al. [33], can be applied to derive retrospective tree heights. Finally, the individual tree's diameter, tree's height and species-specific form factors (f), for example, those provided by Franz [34], are used to calculate tree's volume per year with $v = dbh^2 \cdot \pi / 4 \cdot h \cdot f$.

2.2.1. Diameter reconstruction

For all cored trees, the retrospective diameter is derived from the measured and analysed increment cores and measured dbh in the years of survey. In case of non-cored living trees and standing dead wood, regression models are used to calculate the previous diameter. So far, an exponential (Eq. (1)) and quadratic model (Eq. (2)) are used. Here, the models predict the retrospective cumulative diameter increment based on a given dbh, assuming a constant bark width over time. The increment refers to a specific period covering a pre-defined number of years (growing season), while dbh characterises the diameter at the end of the corresponding period. For parameterisation, only cores that cover the full requested time range should be considered. Moreover, a minimum threshold number of cored trees, for example, five trees, can be considered prior to model parameterisation. The two implemented models are

$$id_i = a * d_{i_end}^b \quad (1)$$

$$id_i = a + b * d_{i_end} + d_{i_end}^2 \quad (2)$$

with id_i as cumulative diameter increment (mm) of period i . The diameter at breast height at the end of period i is expressed by d_{i_end} (mm). The models are species-specific; however, tree species can also be linked to a particular species group, while a and b are function parameters to be estimated. The number of years (growing seasons) covered by each period i can vary. Thus, the overall time range is defined by the number of periods and their corresponding amount of years covered. Considering multiple years per period will smooth the diameter increment, for example, similar to repeated measurements of permanent research plots. By contrast, the parameterisation at annual level may better characterise its variability (**Figure 2a–c**). For the latter, it is particularly important to cover the overall diameter range per species and plot. In order to support the selection of one of the two models, we implemented a decision support routine. Here, from all trees, where cores are available, a user-defined number can be eliminated prior to model parameterisation. The parameterisation is based on the remaining trees, is species-specific, comprises both models and applied for a pre-defined time range. The number of years per period vary from 1 to 10 and cover the overall time range. For the eliminated trees, the retrospective diameter is calculated based on the model outputs. The results are compared with the derived diameter, considering the year ring widths. Here, the validation process covers all possible combinations of eliminating one or multiple trees. Graphical and numerical output summarise the validation. After selecting a model and defining a time range, the diameter reconstruction for all non-cored trees is realised by subtracting the functional values of period i from the diameter at the end of the corresponding period. Consequently, the result refers to the start diameter of period $i-1$. In addition, the cumulative diameter increment will be distributed linearly across the years of period i . Thus, we ensure to reconstruct any time range covered by the data, for example, when period i exceeds the last year considered. **Figure 2** illustrates an example of parameterising Eq. (1) for a mono-specific forest stand of Scots pine. **Figure 2** shows an example of different model outputs covering 1-year (**Figure 2a**), 3-years (**Figure 2b**) and 5-years (**Figure 2c**) per period. The black data points represent single trees. When considering multiple years, the variability of diameter increment slightly decreases (from **Figure 2a** to **c**). The diameter for all non-cored trees is based on the parameterised models (red lines). In case of negative functional values, the increment is set to zero. By default, both models have a flexible intercept; however, in particular cases, it may be useful to force the model through a zero intercept. Moreover, a constant bark width is considered during the reconstruction by default. If required, it is possible to utilise algorithms for calculating bark widths. Here, after the reconstruction, the bark width is initially calculated for the year of survey and subtracted for all diameters (a constant bark width over time), resulting in the diameter without a bark. Thereafter, the bark width is calculated and added to the corresponding diameter, resulting in the diameter over a bark. For final plausibility, the standardised graphical output supports the calculated recent diameter reconstruction (**Figure 3**). **Figure 3** exemplarily demonstrates the result of the diameter reconstruction for a mono-specific stand of Scots pine including a few oak trees which have been reconstructed

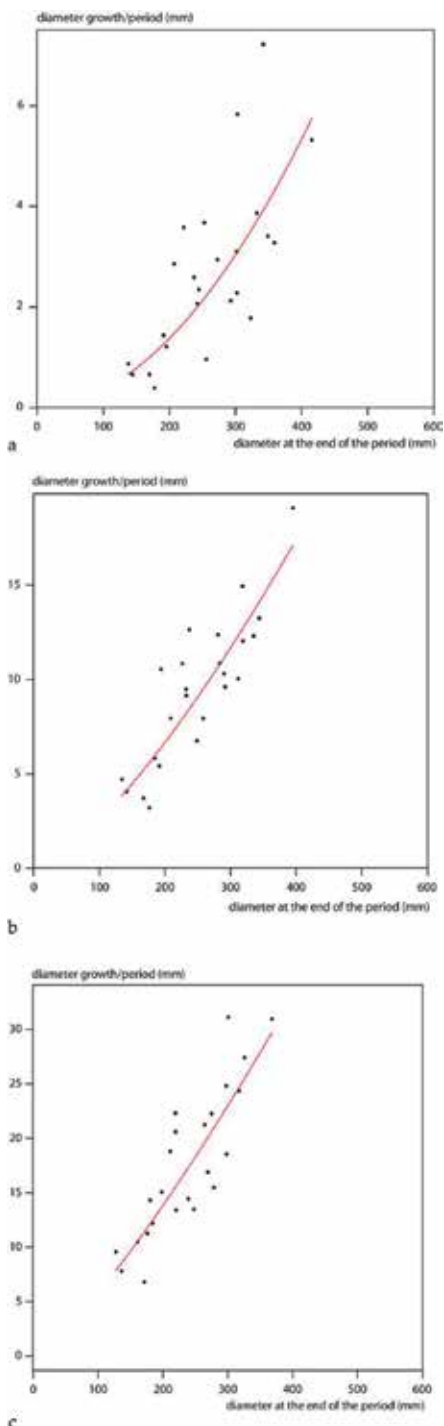


Figure 2. An example of output for Eq. (1) for 1 period covering 1-year (a), 3-year (b) and 5-year (c) resolution. Illustrated are cored trees with their dbh at the end of the period (x-axis, mm) and cumulative diameter increment (y-axis, mm) for the given period. Solid red lines represent the predicted models.

using the model of Scots pine. Thus, the specific behaviour of diameter development of the non-cored trees (triangles) is directly compared with that of the cored trees (circles). All diameter values are given in mm over bark. The reconstruction ends if a diameter falls below the user-defined minimum value, for example, 7 cm. For stumps, the diameter reconstruction follows a similar procedure (grey lines). In a first step, the stump is treated as a living tree with a given diameter (estimated for the year of removal). However, the initial diameter refers to the year of removal and thus may differ from the year of survey. Therefore, we firstly estimated the time between the survey and the year of removal. Secondly, the overall diameter increment for this period is estimated and added to the diameter at the year of survey. Finally, we repeat the diameter reconstruction as described earlier and drop all years between the survey and the year of removal. As a result, the diameter is reconstructed from the year of removal until the reconstruction time range, for example, grey lines shown in **Figure 3**.

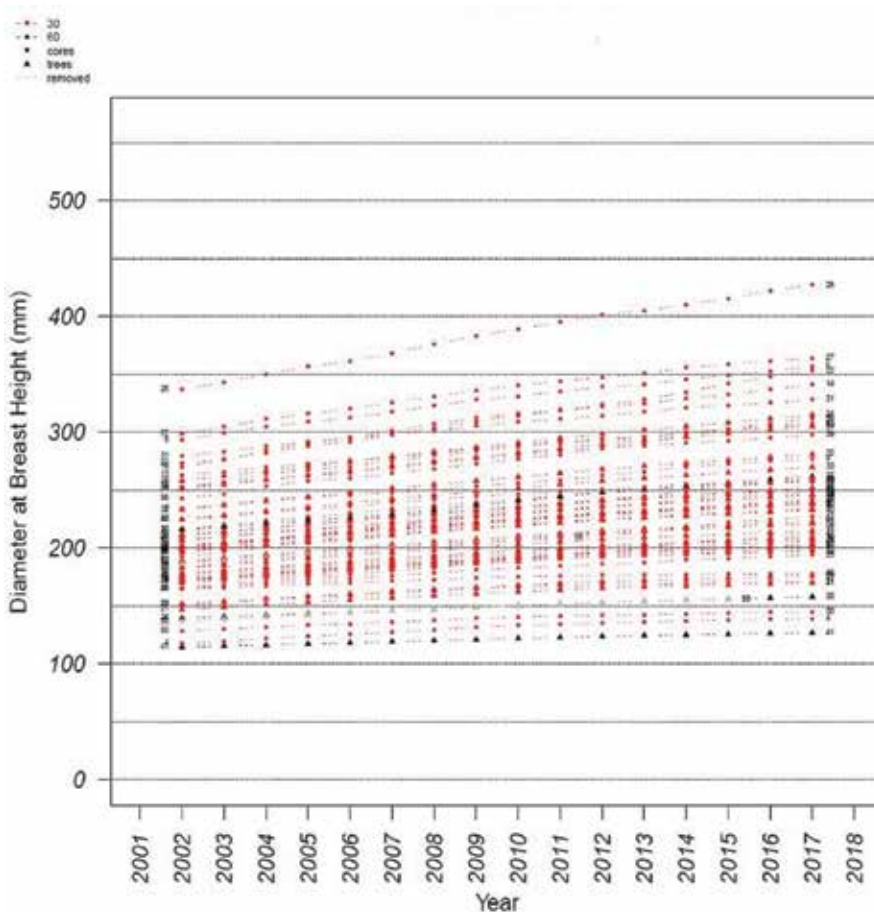


Figure 3. Reconstructed diameter at breast height (y-axis, mm) from year 2017 to 2002 (x-axis) is illustrated. Cored trees are characterised by circles and non-cored trees by triangles. The numbers indicate the specific tree number. Grey lines represent trees which have been removed (stumps). Red and black colour indicate Scots pine and sessile oak, respectively.

2.2.2. Height reconstruction

Uniform height curve systems provide a potential to predict retrospective heights. We implemented a system developed by Kennel [32] and transferred and parameterised for other species by Franz et al. [33]. Individual tree heights will be estimated for each pre-defined year as a function of their diameter [35].

$$h_i = 1.3 + \left(\frac{d_i}{b_0 * d_i + b_1} \right)^3 \quad (3)$$

where h_i and d_i refer to the individual tree height and diameter at the breast height of year i , respectively. The parameter values b_0 and b_1 are species-specific and depends on age, quadratic mean diameter (dq) and its corresponding height (hq). The parameters are required to be calculated at species level for each year. In a first step, the reversal point (drp) of the diameter-height relationship is calculated for each species, year and age (Eq. (4)). Second, b_0 is derived per year, considering drp , dq and hq (Eq. (5)). Third, b_1 is calculated by considering drp and b_0 (Eq. (6))

$$drp = 0.4 + \exp^{A+B*\ln(age)+C*age} \quad (4)$$

$$b_0 = \frac{1}{\exp^{(\frac{1}{3}*\ln(hq-1.3))}} * \frac{1}{1 + \frac{drp}{dq_i}} \quad (5)$$

$$b_1 = b_0 * drp \quad (6)$$

with age as species-specific age for year i , hq and dq as species-specific quadratic mean diameter and its corresponding height for year i . Parameters A , B and C are species-specific and depends on age [33]. Based on the given species-specific age at the time of survey, the retrospective age can be derived for each pre-defined years. Likewise, the quadratic mean diameter is calculated based on the tree list, including the reconstructed diameter. By contrast, the height of the quadratic mean diameter cannot be directly derived. Thus, we using height-age curves provided by yield tables in order to calculate hq for each pre-defined year. The species-specific height curves are selected using the corresponding age and mean height taken from the survey, respectively. Individual tree heights are then calculated for each pre-defined year by applying Eqs. (3)–(6). Following this approach, the method cannot be applied for tree species not covered by a yield table. Instead, heights will be estimated during the stand level evaluation using the available heights to parameterise a Petterson height curve function [35]. Here, Eq. (3) is parameterised based on the reconstructed heights. **Figure 4** exemplarily represents the result of height reconstruction for a mono-specific stand of Scots pine, including few oak trees. The reconstruction covers a 15-year time range with a 1-year resolution (15 periods with 1 year). Based on the visualisation and corresponding tree list, implausible height reconstruction can be detect and deleted. Missing tree heights will be calculated during the stand level evaluation.

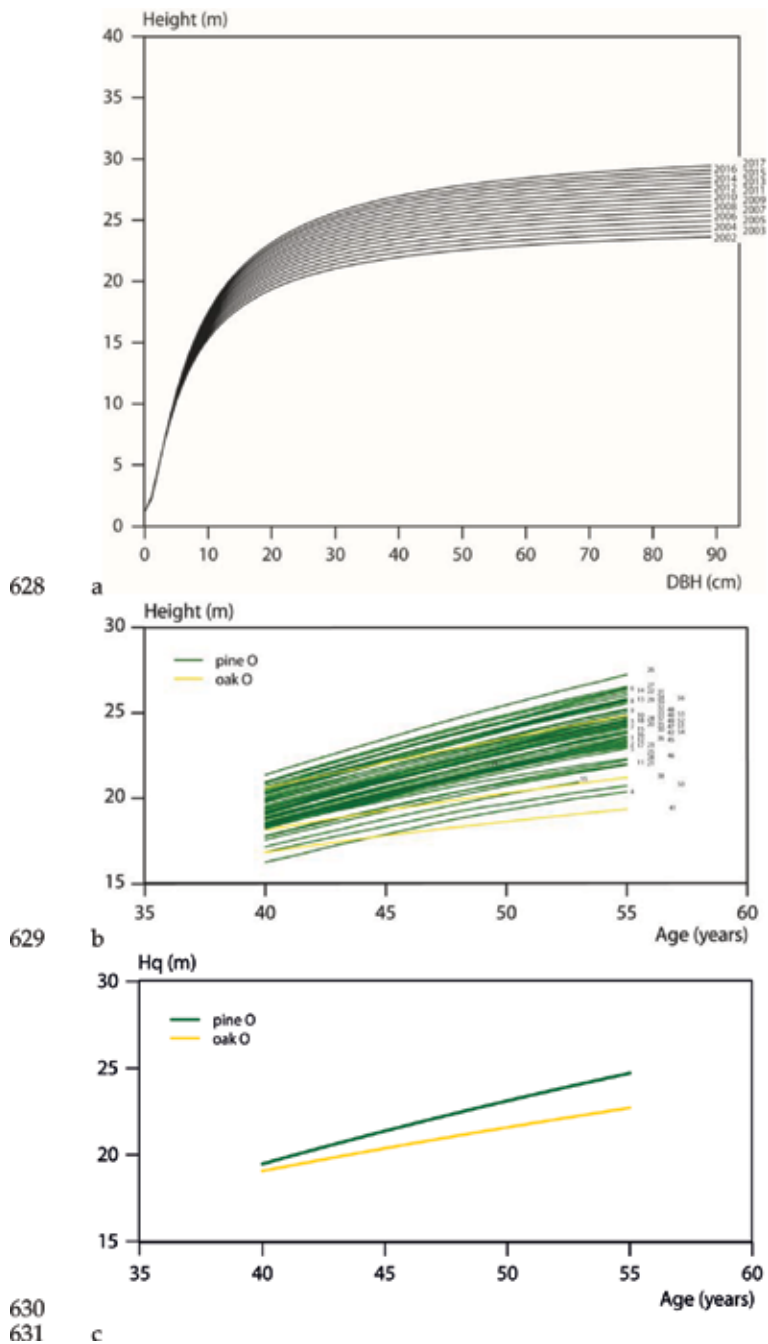


Figure 4. An illustration of height reconstruction for Scots pine and oak in a mono-specific stand of Scots pine. The standardised height curves used (a) are shown in a 1-year resolution from 2017 to 2002 (number right at each curve), exemplarily for Scots pine. Reconstructed tree heights for Scots pine and oak (b) show individual heights (y-axis) for 1-year resolution. Tree numbers are assigned right to individual curves. The relationship of quadratic mean height and species-specific age is illustrated for both species in 1-year resolution for the same time range (c). Green colour is used for Scots pine green yellow colour for oak.

2.2.3. Stand level evaluation

The diameter and height reconstruction results in a tree list for each pre-defined year. Stand characteristics (**Figure 5**), for example, the mean tree dimension, basal area (BA $\text{m}^2 \text{ha}^{-1}$) and volume stock ($V \text{ m}^3 \text{ha}^{-1}$) per hectare, will be derived according to the guidelines of DESER-Norm 1993 [28, 29]. Here, we apply a software which is available at the Chair of Forest Growth and Yield Science, TU München [37]. For each pre-defined year, missing tree heights are calculated by parameterising a species-specific height curve [35] based on the reconstructed heights. Here, species can be grouped. Individual trees' diameter (d_i), height (h_i) and species-specific form factor (f_i) [34] are applied to $v_i = d_i^2/4 * h_i * f_i$ with i being a pre-defined year. Tree-specific volume (v_i) and basal area increment (ba_i) are derived by $v_i = (v_i - v_{i-n})/n$ and $ba_i = (ba_i - ba_{i-n})/n$, respectively, where i refers to the i^{th} year and n to the number of years to the previous year. **Figure 5** exemplarily provides the result of stand level evaluation for the mono-specific pure stand used earlier. **Figure 5** summarises the result stand level evaluation based on the tree list for the years 2017, 2012 and 2007. The stand characteristics of the remaining and removed stand per year at species and stand level, respectively, are shown. For the latter, only aggregated information is described. Individual tree volume was calculated, using form factors for Scots pine and oak provided by Franz et al. [34].

		Remaining Stand										Removal Stand					Total Stand			
YEAR	A	SP	NV	HO	DO	HO/DO	HGV	DGV	HG/DG	GV	VV	NA	HGA	DGA	h/d	GA	VA	IG	IV	PER
			m	cm	cm	m	cm	m	cm	m^2	m^3	m	cm	cm	m^2	m^3	m^2	m^3	m^2	m^3
2007	45	Scots pine	850	23.0	31.6	73	21.4	22.3	96	33.28	321	0			0.00	0				
2007	45	Oak	50	22.1	22.6	98	20.4	16.9	121	1.12	11	0			0.00	0				
2007		Total	900							34.40	332	0			0.00	0				
2012	50	Scots pine	833	24.8	34.2	73	23.1	24.0	96	37.85	396	17	22.2	20.7	107	0.56	5	1.0	16.0	5
2012	50	Oak	50	23.5	24.7	95	21.6	18.2	119	1.30	14	0			0.00	0		0.0	0.6	5
2012		Total	883							39.15	409	17			0.56	5		1.1	16.5	5
2017	55	Scots pine	817	26.6	36.5	73	24.7	25.6	97	41.98	469	17	21.3	15.5	137	0.32	3	0.9	15.3	5
2017	55	Oak	50	24.8	26.2	95	22.7	19.1	119	1.44	16	0			0.00	0		0.0	0.5	5
2017		Total	867							43.42	486	17			0.32	3		0.9	15.8	5

Figure 5. An example of stand characteristics after a reconstruction time of 10 years, with 2 periods with 5 years. The following are shown: calendar year (Year), species-specific age (A), tree species (SP) remaining stand characteristic with trees per hectare (NV [ha^{-1}]), top diameter (DO [cm]) and height (HO [m]) including their relationship (HO/DO), quadratic mean diameter (DGV [cm]) and height (HGV [m]) including their relationship (HGV/DGV), basal area (GV [$\text{m}^2 \text{ha}^{-1}$]) and volume stock over bark (VV [$\text{m}^3 \text{ha}^{-1}$]) per hectare; removed stand characteristics with trees per hectare (NA [ha^{-1}]), quadratic mean diameter (DGA [cm]) and height (HGA [m]) including its relationship (DGA/HGA), basal area (GA [$\text{m}^2 \text{ha}^{-1}$]) and volume over bark (VA [$\text{m}^3 \text{ha}^{-1}$]) per hectare; increment of basal area (IG [$\text{m}^2 \text{ha}^{-1}$]) and volume increment (IV [$\text{m}^3 \text{ha}^{-1}$]) per hectare and year and period length (PER [number of years]).

The diameter and height reconstruction are standardised procedures implemented in the statistical software R [38].

2.3. Validation of results

For validation, we used three different data sources. First, we reconstructed individual tree's diameter for eight research plots covering mono-specific stands of Douglas fir ($n = 401$). The primary goal of the experimental plots is to analyse reaction pattern on growth at stand level under varying spacing treatments. For each plot, complete stand surveys are available in 2009,

2004, 1999 and 1994. In addition, 6–10 dominant/subdominant trees have been felled in March 2010 and stem discs were taken at 1.30 m. Thus, the retrospective diameter increments for those trees are available. The diameter reconstruction was applied as described above and the results compared with the empirical observations. Second, to validate tree height reconstruction, we used a data set covering five mono-specific plots of Scots pine and Norway spruce. In addition, five plots with both species in mixture are tested. For Scots pine and Norway spruce, six trees per plot have been felled and the shoot length measured from top to down. Thus, the height reconstruction for those trees is validated based on the empirical measured values. Third, we used long-term research plots to validate the reconstruction at stand level.

2.3.1. Diameter reconstruction

Stem discs of the felled trees have been measured and analysed with the digital positometer after Johann (Biritz + Hatzl GmbH, Austria). The results have been used for model parameterisation comprising three periods with a 5-year resolution, respectively (2009–2005, 2004–2000 and 1999–1995). Based on the fitted models, the diameter for all non-felled trees was calculated. We applied both models (Eqs. (1) and (2)) with and without considering bark width, respectively. The reconstructed diameter is compared with the observations available from stand survey for the years 2004, 1999 and 1994, using only remaining trees (non-felled). **Table 1** provides the overview of the results. We show the average arithmetic difference between reconstructed and observed dbh for the year 2004, 1999 and 1994. Besides the average difference, the corresponding standard deviation per plot and year are shown for Eqs. (1) and (2), respectively. In addition, we include the effect when bark width is not considered (no) and considered (yes). On average (total), the results indicate an increasing difference from 2004 until 1994 with a lower effect when bark width is considered. For both models, the difference exceeds 1 cm only in 1994 when bark width is considered. By contrast, this can be confirmed only for the year 2004 in the other case. The standard deviations vary only slightly between Eqs. (1) and (2). **Figure 6** illustrates, exemplarily, the results for Eq. (2) and plot 2. Here, we demonstrate the effect of considering bark width. The results for plot 2 show the effect when bark width is considered (**Table 1** and **Figure 6**). While marginal difference occurs for the year 2004, it significantly increased for 1999 and 1994. As opposed to the results of considering bark width (**Figure 6b**), a slightly systematic deviation can be observed when bark width is not considered (**Figure 6a**). In particular, this tendency increases from 2004 to 1994. The highest deviation occurs for trees with dbh below 15 cm.

PlotID	bark width	n	2004		1999		1994	
			Eq. 1	Eq. 2	Eq. 1	Eq. 2	Eq. 1	Eq. 2
			avg ± sd	avg ± sd	avg ± sd	avg ± sd	avg ± sd	avg ± sd
2	no	50	2.1 ± 8.6	1.7 ± 8.6	8.1 ± 13.4	7.2 ± 13.1	17.1 ± 17.8	15.8 ± 17.5
	yes	50	-1.8 ± 7.9	-2.2 ± 7.9	1.8 ± 12.3	0.8 ± 12.1	8.1 ± 16.3	6.6 ± 16.1
3	no	53	10.1 ± 8.2	9.4 ± 8.1	17.5 ± 10.9	15.4 ± 10.9	26.9 ± 10.7	25 ± 10.7
	yes	53	6.3 ± 8.8	5.6 ± 8.4	10.8 ± 11.7	8.5 ± 11.6	16.7 ± 11.7	14.6 ± 12.1

PlotID	bark width	n	2004		1999		1994	
			Eq. 1	Eq. 2	Eq. 1	Eq. 2	Eq. 1	Eq. 2
			avg \pm sd	avg \pm sd	avg \pm sd	avg \pm sd	avg \pm sd	avg \pm sd
4	no	47	11.8 \pm 13.1	11.7 \pm 13.7	18 \pm 25.3	18 \pm 26.2	24.2 \pm 32.4	22.1 \pm 31
	yes	47	8.7 \pm 12.4	8.6 \pm 13.1	12.8 \pm 24.7	12.9 \pm 25.6	16.1 \pm 30.8	13.9 \pm 29.1
5	no	47	10.2 \pm 9.7	9.9 \pm 11.1	18.7 \pm 16.3	18.1 \pm 18.1	29.5 \pm 21.3	28.3 \pm 22.9
	yes	47	7.1 \pm 9.2	6.8 \pm 10.5	13.4 \pm 15.4	12.7 \pm 17.1	20.7 \pm 19.4	19.3 \pm 20.9
7	no	53	6 \pm 12.9	6.9 \pm 12.6	10.4 \pm 26.4	12.5 \pm 27.1	16 \pm 26.6	17.8 \pm 27.1
	yes	53	2.5 \pm 12.6	3.4 \pm 12.2	4 \pm 26.4	6.6 \pm 27.2	6.2 \pm 25.4	8.4 \pm 25.7
9	no	49	9.2 \pm 10.2	7.8 \pm 9.1	13.3 \pm 17.8	11.1 \pm 15.9	20.4 \pm 21.8	17.2 \pm 20.4
	yes	49	6.7 \pm 9.6	5 \pm 8.6	8.5 \pm 16.6	6.1 \pm 14.8	12.9 \pm 19.7	9.3 \pm 18.3
11	no	53	8 \pm 10.8	7.4 \pm 10.6	12.8 \pm 16.4	11.9 \pm 15.8	18.1 \pm 18.5	16.5 \pm 18.4
	yes	53	4.9 \pm 11.1	4.2 \pm 10.6	7.4 \pm 17.2	6.3 \pm 16.1	9.4 \pm 19.2	7.6 \pm 18.8
12	no	49	7.3 \pm 11.4	6 \pm 11.3	13.5 \pm 19.1	11.2 \pm 18.9	21.5 \pm 29.4	17.8 \pm 29.2
	yes	49	4.5 \pm 10.9	3.1 \pm 10.9	8.6 \pm 18.3	6 \pm 18	13.7 \pm 28	9.6 \pm 27.7
total	no	401	8 \pm 11	7.6 \pm 11	14 \pm 19	13.1 \pm 19.2	21.6 \pm 23.3	20 \pm 23.1
	yes	401	4.8 \pm 10.8	4.3 \pm 10.8	8.3 \pm 18.7	7.4 \pm 18.9	12.8 \pm 22.3	11.1 \pm 21.9

With individual plot, PlotID; considering bark, bark width (no = no bark width was considered, yes = bark was considered); number of trees, n; average difference (reconstructed-observed diameter), avg. and its standard deviation, sd.

Table 1. Average differences are shown between reconstructed and observed diameter (in mm) for the years 2004, 1999 and 1994 for each plot and total.

2.3.2. Height reconstruction

In order to validate tree height reconstruction, we used 161 felled trees in autumn 2013 with measured shoot lengths of the last 40 years. In total, individuals of 32 Scots pine and 40 Norway spruce are available from mono-specific stands of each species. In addition, stands with both species in mixture cover 37 trees of Scots pine and 52 trees of Norway spruce [39]. For each felled tree, shoot lengths have been measured from stem top downwards the trunk. Thus, by stepwise subtracting from the total tree height, we derived tree heights per year from 2013 to 1973. Moreover, stem discs are taken at a 1.30-m height for each felled tree. In a first step, the stem discs were measured and analysed. Tree age was estimated based on the stem discs at plot and species level. Applying Eq. (1), the individual tree's diameter at breast height was calculated for all non-felled trees, using four periods with 5 years (2013–2009, 2008–2004, 2003–1999 and 1998–1994). Likewise, the retrospective tree height was calculated, applying the method described earlier by plot and species-specific age estimated from the stem discs. For all felled trees, we then compared the reconstructed heights with the measurements for the years

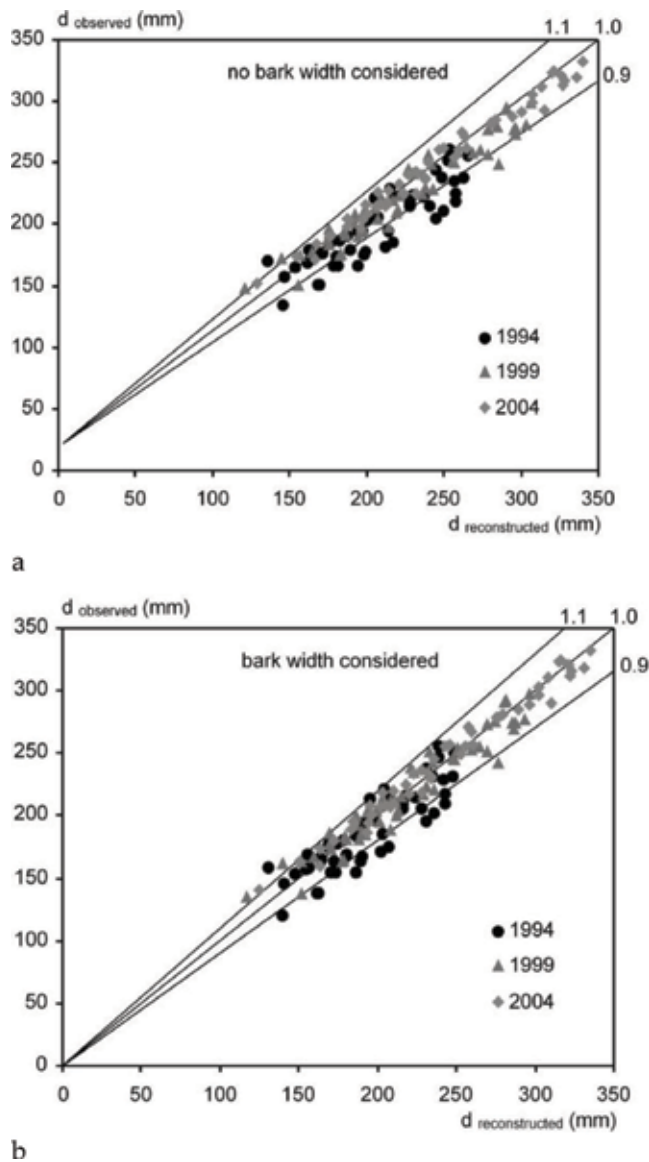


Figure 6. The diameter reconstruction based on three periods with 5 years applying Eq. (2) for plot 2 when no bark width is considered (a) and considered (b) is represented. Data points refer to single trees for year 2004 (grey, rectangular), 1999 (grey, triangle) and 2004 (circular, black). Solid black lines refer to 1:1, 1:1.10 and 1:0.9 reference lines (equal diameter, +10% and -10% deviation, repetitively).

2009, 2004, 1999 and 1994. **Table 2** provides the overview of minimum, maximum and average difference when comparing reconstructed (h_{rec}) and observed (h_{obs}) heights for Scots pine and Norway spruce ($h_{rec}-h_{obs}$). The results indicate higher average differences in mixed than mono-specific stands for both species. For Scots pine, the average difference exceeds 1 m in 1999,

	2009			2004			1999			1994		
	<i>mixed</i>	<i>pp</i>	<i>mixed</i>	<i>pp</i>	<i>mixed</i>	<i>pp</i>	<i>mixed</i>	<i>pp</i>	<i>mixed</i>	<i>pp</i>	<i>mixed</i>	<i>pp</i>
Norway spruce												
<i>n</i>	52	40	52	40	52	40	52	40	51	40	51	40
<i>avg ± sd</i>	-2.26 ± 1.83	-0.15 ± 1.51	-2.02 ± 2.01	-0.15 ± 1.77	-1.8 ± 2.01	0.47 ± 1.82	-1.71 ± 1.87	0.49 ± 1.98				
<i>min</i>	-5.84	-4.25	-6.30	-3.82	-5.90	-3.51	-4.96	-3.70				
<i>max</i>	3.00	2.55	3.61	3.00	4.55	4.08	4.72	4.63				
Scots pine												
<i>n</i>	37	32	37	32	37	32	37	32	37	32	37	0
<i>avg ± sd</i>	0.54 ± 1.18	-0.02 ± 1.34	0.73 ± 1.25	0.09 ± 1.2	0.98 ± 1.24	1.13 ± -1.8	1.22 ± 1.18	0.6 ± 1.05				
<i>min</i>	-1.72	-2.21	-1.54	-1.78	-1.88	-1.80	-1.65	-1.81				
<i>max</i>	2.99	3.18	3.00	2.94	3.29	2.88	3.41	2.83				

Represented are the minimum (min), maximum (max) and average difference (avg) with its corresponding standard error (avg ± se) for both species in mixed (mixed) and mono-specific stand (pp). Minimum, maximum and average values are given in m.

Table 2. An overview of the average difference between reconstructed and observed tree heights (in m) for the years 2009, 2004, 1999 and 1994.

vshowing an increasing tendency from 2009 to 1994. The accuracy in mono-specific stands is similar to those of the mixed stands. The standard deviation is only marginally different over time in both stand types. By contrast, Norway spruce shows larger differences in the behaviour of mono-specific and mixed forest stands. While the result for the former is comparable to those of Scots pine, the latter show a much higher deviation. Moreover, from 2009 to 1994, we detect a decrease in the average difference. The standard deviations are similar in both cases.

2.3.3. Stand level evaluation

For testing the effects of reconstruction at stand level, we evaluated permanent research plots. In a first step, based on 5-cm dbh classes, 25% trees per class are randomly chosen for parameterising Eq. (1). Here, we used four periods with 5 years. The cumulative diameter increment refers to the consecutive surveys of the selected trees, and the diameter for the non-selected trees was reconstructed based on parameterisation of Eq. (1). For each tree, the retrospective heights were calculated applying the method described earlier. We used the yield table from Assmann und Franz [40] and Wiedemann [13] to derive the quadratic mean heights. Following the methods for diameter and height reconstruction, we created a tree list for the years of survey for the last 20 years. Each plot was evaluated as described earlier. In addition, all plots have been evaluated based on the recorded observation. Thus, we compared both results with respect to the quadratic mean diameter and its corresponding height, basal area per hectare, volume stock per hectare and their increment. **Table 3** provides the overview of comparing reconstructed with observed stand characteristics for the overall time range. **Table 3** shows the results of comparing reconstructed with empirical recorded tree list at stand level. The results for quadratic mean diameter, DQ (cm) and its corresponding height, HQ (m), basal area, BA ($\text{m}^2 \text{ha}^{-1}$) and volume stock, V ($\text{m}^3 \text{ha}^{-1}$) per hectare, basal area, IBA ($\text{m}^2 \text{ha}^{-1} \text{yr}^{-1}$) and volume, IV ($\text{m}^3 \text{ha}^{-1} \text{yr}^{-1}$) increment per hectare and year are demonstrated. Here, we used the relation referenced at empirical observation, for example, $x_{\text{recon}}/x_{\text{obs}}$ with x either DQ, HQ, BA, V, IBA or IVA. The upper and lower confidence intervals (CI_{upper} and CI_{lower}) have been calculated based on the 95% significance level. For each attribute, we detect no difference for the last 20 years at stand level.

	min	max	avg ± se	CI_{upper}	CI_{lower}
DQ	0.74	1.04	0.98 ± 0.02	1.02	0.94
HQ	0.81	1.09	1 ± 0.02	1.04	0.97
BA	0.81	1.06	0.97 ± 0.02	1.01	0.94
V	0.85	1.02	0.98 ± 0.01	1.01	0.95
IBA	0.87	1.4	1.06 ± 0.04	1.14	0.98
IV	0.8	1.27	0.96 ± 0.03	1.02	0.91

Relations between reconstructed and observation are represented for quadratic mean diameter (DQ), its corresponding height (HQ), basal area per hectare (BA), volume per hectare (V), basal area increment per hectare (IBA) and volume increment per hectare (IV). The minimum (min), maximum (max), average, (avg), standard error (se), upper (CI_{upper}) and lower (CI_{lower}) confidence interval are shown.

Table 3. Results of the comparing stand level and yield characteristics for 15 permanent forest research plots considering tree lists for real observation and reconstruction for 20 years.

3. Discussion

Long-term experiments are irreplaceable for forest science. They are the unique way to study long-term dynamics at tree and stand level and can reveal the cause-effect relationships of various treatment options as they are established under controlled, *ceteris paribus* conditions. However, for dealing with many urgent topics such as mixing effects, climate change, transition from pure to mixed stands or introduction of foreign tree species, long-term experiments are simply not available. Moreover, networks of such experiments, including multiple countries, are rare. In this case, temporary plots with a back-tracing of their history by increment coring or stem analyses are a makeshift to get ad hoc data for new upcoming topics, not covered by existing long-term experiments. The proposed method reconstructs recent tree and stand characteristics based on a given survey and increment cores. Occurring stumps and standing dead wood can be considered when the year of removal (calendar year) and the corresponding dbh are available. In principle, this allows to extend the application from fully stocked stand towards treated stands. The reconstruction is mainly based on diameter increment provided by the increment cores; therefore, it is of special importance that they are representative for the diameter range, ideally at tree species level. For diameter reconstruction, the implemented models differently reflect the relationship of diameter and its cumulative increment. However, its selection is crucial and should be inspected before, for example, validation based on increment cores. In addition, for tree species with a high variability of bark width, for example, Douglas fir, its consideration will increase the accuracy. To this extent, the height reconstruction is species-specific and based on a standardised height curve system. This approach requires (species-specific) quadratic mean height for the reconstruction interval. Here, yield tables of the corresponding species are used; however, any other sufficient method will extend the application, for example, in case of missing yield tables. For example, felling sample trees and measuring shoot lengths [39] are expensive and difficult to realise, in particular, for broadleaved species. Another possibility is the use of artificial time series. In contrast to real-time series (long-term observations), they use measurements of plots covering different age classes and are spatially closed [36, 41]. However, the probability of finding suitable plots varies between the tree species under investigation and may be difficult to realise. The results of validation demonstrate that the method is applicable for recent stand development, for example, 5–10 years. With any larger time interval, the inaccuracy may increase, in particular, for managed forests where trees are regularly removed and no information regarding stumps is available beyond 10–15 years. However, the proposed method serves for both analysing and modelling mixed species stands. In a first step, mixed species stands need to be better understood in their structure and functioning. In order to design the establishment and management of mixed species stands, models that take into consideration relevant and known mixing effects are required. Such models will be essential tools for the development of silvicultural prescriptions by scenario analysis and for the quantitative formulation of guidelines. The introduced methods provide data such as stand structure and growth rates, which are essential for parameterisation of individual tree growth models [42]. Next steps will be to analyse how many trees of which size need to be sampled, cored and measured in order to reliably reconstruct the stand dynamics. The methods introduced here for retrospective

analysis of stem growth might be extended to reconstruction of crown and root growth. The restriction of retracing the tree and stand development more than 10–20 years earlier might be overcome by the establishment of artificial age series. If temporary plots of, for example, age 20, 40 ... 100 years are established and analysed retrospectively over 20 years, an artificial time series of tree and stand growth can be compiled, which overcomes the restriction of a retrospective analyses from just one plot far backwards.

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Establishment, Regeneration, and Succession of Korean Red Pine (*Pinus densiflora* S. et Z.) Forest in Korea

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Abstract

Seed production of Korean red pine (*Pinus densiflora* Siebold & Zucc.) was ranging from 25 to 27 seeds/m² with a viability averaging between 42 and 44%. Seed dispersal reaches about 80 m. Germination rate of seed varied from 19 to 90%, and survival rate of seedling varied from 0 to 30% depending on moisture condition in field experiment. Survivorship curve of the pine population showed type III. Species composition of the pine forest was characterized by possessing plants with resistant capacity to water deficit such as *Rhododendron micranthum*, *Vaccinium hirtum* var. *koreanum*, *Spodiopogon sibiricus*, and *Lespedeza cyrtobotrya*. Ecological longevity of the pine was about 140 years based on mean age of gap makers. Natural maintenance of the pine forest depended on disturbance regime, which is dominated by endogenous factor. Natural regeneration of the pine forest is possible only in a very restricted site such as ridgetop with thin and infertile soil condition. Therefore, active and systematic management is required for artificial regeneration of the forest as is known in silvicultural method. Pine gall midge damage accelerated succession of the pine forest to the deciduous broadleaved forest dominated by oak except on the ridgetop where the forest can be maintained naturally.

Keywords: Korean red pine, life history, natural regeneration, pine gall midge damage, silviculture, succession

1. Introduction

Pinus densiflora S. et Z. (Korean red pine) has a home range that includes the Korean Peninsula, northeastern China, the extreme southeast of Russia, and the Japanese Archipelago [1]. Its

latitudinal range on the Korean Peninsula is from Mt. Halla, on Jeju Island in South Korea (33° 20' N), to Jeungsan, in North Korea (43° 20' N) [2]. The height of this tree is 20–35 m. The pine prefers full sun on well-drained, slightly acidic soil. The needle leaves are 8–12 cm long, with two per fascicle. The cones are 4–7 cm long [3].

The most favorable soil type for this species is well-drained sand or gravel that is weathered from granite and eroded by storm waters during the monsoon months in summer [4]. With such a wide range of tolerance, Korean red pine normally occurs on the thin and infertile soils of rock outcroppings, weathered rocks, ridge tops, and the sandy or pebble shores of streams [5]. It also can grow well in disturbed soils along both mountain slopes and bases after forest thinning or brush removal near human settlements [6–9].

These Korean red pine forests are valued by Korean people for numerous amenities to basic life (e.g., material for buildings and ships, and oils such as terpenes), as well as for aesthetics, recreation, and biological diversity [10–13]. Therefore, the expansion of these forests, through artificial plantings and maintenance, has been encouraged by Korean governments since early in the twentieth century [14]. However, natural stands of Korean red pine have declined to only about one-third of their extent currently for several reasons, including over-exploitation under Japanese occupation (1910–1945), the Korean War (1950–1953), pest defoliation, wildfire, and negligence [5]. Such losses are a concern among forest managers in Korea because of the reduction in forest products and biological diversity [15].

This pine produces pollen that is wind dispersed [16]. It takes 3 years to complete its reproduction cycle [17]: female bud formation is initiated in the summer, pollination occurs the following spring, and seeds mature in the fall a year later. After 40–60 years, relative growth in diameter and height slows as a lognormal [18]. Cone production may begin at 7 years in isolated tree; it is delayed to 11–18 years when trees form stands [18]. On exposed rocky ridges, some trees survive to ages beyond 140 years [19].

According to pollen analysis, pine forests began to replace deciduous broad-leaved forests about 6500 years ago and it was accelerated 2300 years ago in the southwestern part, and 1400 years ago in the eastern part of the Korean Peninsula [20, 21]. This range expansion was in response to an increase in fire frequency associated with rising temperatures and agricultural activities [20, 21]. The persistence of these temperate pine forests in Korea has been speculated to be a result of the pine's adaptation to and dependence upon dry weather from fall through spring [20, 22, 23], the availability of large areas with coarse-textured soils [22, 23], and frequent disturbance by human activities [6, 20]. Disturbances were envisioned as creating gaps in the forest canopy and exposing bare soil that favored seed germination while coarse-textured soils would induce drought sufficient to limit competition from oak and other species [19, 22]. With a shift toward fossil fuels for heating homes, the kinds of disturbances that once perpetuated Korean red pine are now lacking [6, 24]. Clear felling or other alternatives serve the same role as fire [18].

It is useful to evaluate life history attributes of the species to clarify ecological characteristics of a species. The critical stages in a plant's life cycle are those having to do with reproduction, seed dispersal, germination, seedling establishment, and population dynamics including regeneration after disturbance [4, 19, 25–27]. If conditions for successful regeneration occur infrequently, then successful maintenance of a population is less assured because a favorable seed year must correspond with an appropriate disturbance. Knowledge of interannual variation in seed production and the distribution of age classes of trees can address the importance of synchronous events in perpetuating tree populations [28, 29]. Adequate dispersal is necessary to occupy new habitats and to expand a population [30–32]. Although seeds may germinate, seedling establishment may occur only under specific microclimatic and edaphic conditions that provide adequate moisture, light, and nutrients, without harmful pathogens and herbivores [29, 33].

Although most species in the genus *Pinus* grow well under high radiation [34, 35], the initial establishment stage is more sensitive to the availability of soil moisture than radiation [35, 36]. Because the Korean Peninsula customarily experiences a long dry season from fall to spring [37], it is worth to monitor of responses of plant on water stress at the time of germination and seedling establishment.

Korean red pine forest is the representative forest in Korea, which is not only familiar well with climate and soil but also economic value is very big in Korea. Therefore, a study on life history of the pine forest is required indispensably in order to clarify formation, maintenance mechanism, and transition process of forest, which occupies 2/3 of the whole national territory in Korea [4, 19].

Grime [38] divides life history into mature and regeneration phases in the life history strategy of plant and clarifies the duration and mechanism of each stage by dividing the latter stage into seed release, disposal, dormancy, and maturation of seedling. It is very difficult to clarify in detail each stage of the life history because perennial woody plant with long longevity has a very long life cycle. A serial regeneration process occurring after disturbance in the mature forest can provide critical information [39].

This chapter aims to clarify the whole life cycle from birth as a seed to regeneration and/or succession of Korean red pine forest as the representative forest community in Korea. To arrive at the goal, we analyzed the process by organizing this chapter as 10 sections including production and dispersal of seed, germination rate, survival rate of seedling, survivorship curve of Korean red pine population, species composition of Korean red pine community, disturbance regime in Korean red pine forest, regeneration of Korean red pine forest in natural condition, natural regeneration of Korean red pine forest disturbed by air pollution and by applying silvicultural method, and succession of Korean red pine forest damaged by pine gall midge.

This paper was prepared by reediting papers that prof. C.S. Lee and his colleagues had published to date.

2. Methods

2.1. Seed production

Seed production was tallied by counting the number of seeds fallen into twelve 1 m² seed traps made from nylon netting that were positioned 1 m above the soil surface. Seeds were collected over 3 years from 1 May 1985 to 30 April 1987.

2.2. Seed dispersal

Seed dispersal was measured using five seed traps per point, set at 0 (beneath the seed source), 5, 10, 20, 30 and 40 m distance from the exposed edge of the 70-year-old stand.

2.3. Emergence and survival of seedlings on forest floor

One hundred seeds were sown on the surface and at 1.0 cm depth at the 30–40-year-old stands at 3 cm × 3 cm spacing. All seedbeds were covered with a 0.5 cm thick layer of pine litter and had five replicates. Germination rate was obtained from percentage of the number of seedlings emerged to the number of sown seeds. The survival of seedlings was measured by tallying the number of live seedlings at 1-week intervals from the 5th week after sowing.

2.4. Survivorship curve

Survivorship curve of Korean red pine population was obtained by plotting density of Korean red pine investigated in stands with different ages including the number of germinable seed as a beginning cohort.

2.5. Species composition

The differences in species composition among Korean red pine forest and several oak forests, which form the late successional forest, were compared by applying NMDS ordination [40]. Vegetation survey was carried out by recording the cover class of the plant species appearing in the survey plot of 20 m × 20 m size [41]. Cover degree of each species was converted to the median value of percent cover range in each cover class. Relative coverage was determined by multiplying by 100 to the fraction of each species to the summed cover of all species in each plot [42]. The relative coverage of each species was then regarded as the importance value [43]. Finally, a matrix of importance values for all species in all plots was constructed and it was subjected to nonmetric multidimensional scaling (NMDS) for ordination [40] and detrended correspondence analysis (DCA) for ordination [44].

2.6. Disturbance regime

Disturbance regime is defined here the pattern of death of dominant individuals (canopy trees) in a community [45]. Disturbance regime was investigated based on death type of gap makers divided into three kinds of standing dead, uprooted, and stem broken.

Longevity of Korean red pine was determined from mean age of trees died naturally. Age was confirmed by counting annual rings on discs cut from dead tree.

Size of gap was obtained by applying equation of ellipse after measuring long (L) and short (S) radius of gap as the follows. $Area = \pi/4 \times L \times S$ [45].

2.7. Regeneration of Korean red pine forest

Natural regeneration of Korean red pine forest was confirmed by analyzing age class distribution of pine trees forming the forest. Age of sapling was determined by counting the number of nodes. Age of mature tree was obtained by counting the number of annual rings extracted at 30 cm above ground level by using increment borer. Age class distribution diagrams were depicted by the frequency distribution of each class divided at regular intervals. Growth of annual ring was measured with calipers under a dissecting microscope with a 0.05-mm precision.

Responses of plant on gap formation were analyzed by measuring height growth of saplings appeared within gap and branch growth of mature tree surrounding the gap. Height and branch growths were obtained by measuring node length of sapling and of branch cut from mature tree, respectively. Growth equations of height and branch were obtained from relationship between the accumulated years and growth values. The year of gap formation was determined from the year that height growth of saplings in gap and annual ring growth of trees surrounding the gap increased abruptly.

Crown projection diagram was prepared by connecting margins of canopy measured from 8 directions for canopy tree appeared in quadrat installed in study site. Spatial distribution of major species was prepared by plotting X- and Y-coordinates of woody plants appeared in the quadrat. Stand profile was prepared by carefully depicting major plant species appearing in a belt transect installed in 5 m width.

2.8. Succession of Korean red pine forest

Succession of Korean red pine forest damaged by pine gall midge was investigated by analyzing coverage changes of major plant species appeared in Korean red pine stands with different damage stages and healthy pine stands and oak forests as reference stands. Coverage was surveyed by applying Domin-Krajina scale [46].

Vegetation change was analyzed by classifying vegetation layer. Analysis on successional change was reinforced by applying ordination method.

Duration of coning was investigated by counting the number of cones classified by node (year) of branch cut from pine trees in Korean red pine forests, which are in the first and the second stages of pine gall midge damage. Fifty individuals per site were selected as sample trees in four sites.

3. Seed production and dispersal

Annual seed production in the 70-year-old pine forest was consistent, ranging from 25 to 27 seeds/m² with a viability averaging between 42 and 44% (Table 1).

Period	Seeds collected from twelve 1 m ² seed traps	Germinated seeds	Germination rate (%)
1985	301	127	42.2
1986	321	142	44.2
1987	296	126	42.6

Table 1. Interannual seed production recorded under a 70-year-old Korean red pine stand.

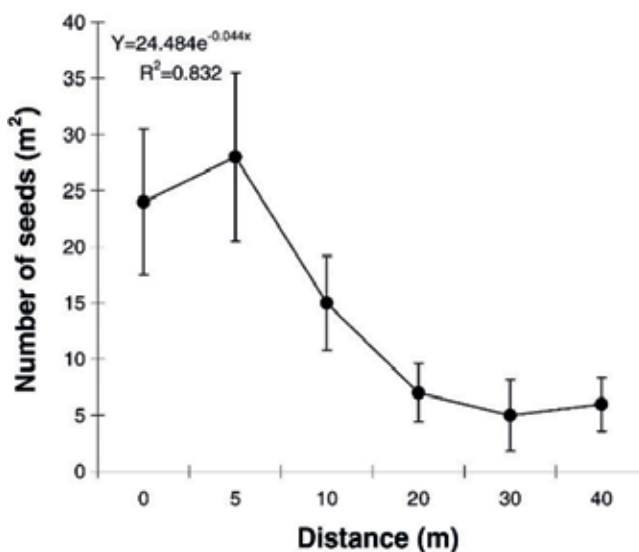


Figure 1. Changes of the number of seeds fallen in seed traps installed by distances from seed source stand. Equation on graph indicates relationship between distance and the number of seeds collected at each distance.

The number of seeds collected in traps set at varying distances from the seed source decreased exponentially out to 40 m (**Figure 1**). The exponential relationship developed between seed number and distance from the edge of the forest indicates by extrapolation that the maximum seed gravity dispersal would be about 80 m.

4. Germination

Germination of seeds sown on the soil surface varied from a high of 90% on the irrigated open (IO) treatment to a low of 19% on the open ground (OG) treatment. Germination rates on the canopy gap (CG) and closed canopy (CC) seedbeds were, respectively, 30 and 42% in 6 weeks after sowing (**Table 2**). Germination rates of seeds placed at 1 cm depth followed a similar response on the different seedbeds with only the OG and CG showing a significant difference from that measured on the soil surface (**Table 2**).

Seedbeds	Germination rate (%)		P
	Soil surface	1 cm depth	
Irrigation, full exposure	89.8 ± 3.9	90.2 ± 4.4	0.88
Open ground	19.2 ± 4.1	29.6 ± 5.3	0.0001
Canopy gap	30.0 ± 4.0	40.0 ± 5.0	0.0005
Closed canopy	42.0 ± 3.4	42.4 ± 3.6	0.88

Table 2. Mean (%) and S.D. of seed germination from 100 per 9 cm² that were sown on the soil surface and at 1 cm depth across a range of selected seedbeds.

5. Seedling survival rate

Of those seeds that germinated, survival varied from 99% on IO treatment to 0% on open ground (OG) (Figure 2). The best survival without irrigation was observed under the closed canopy (about 30%), although growth of seedlings (not shown) was higher for those that survived in canopy gaps.

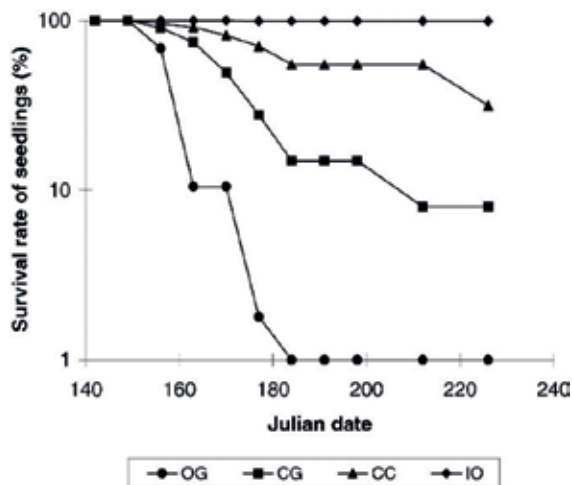


Figure 2. Survivorship curves of seedlings germinated on the different seedbeds on forest floor of the Korean red pine stand. Irrigated and exposed with soil supplement (IO), open ground (OG), canopy gap (CG), and closed canopy (CC).

6. Survivorship curve

Survivorship curve of Korean red pine population was shown in Figure 3. The number of germinable seeds was about 1,420,000 per ha and densities of 5, 28, 43, 80, and 130 years

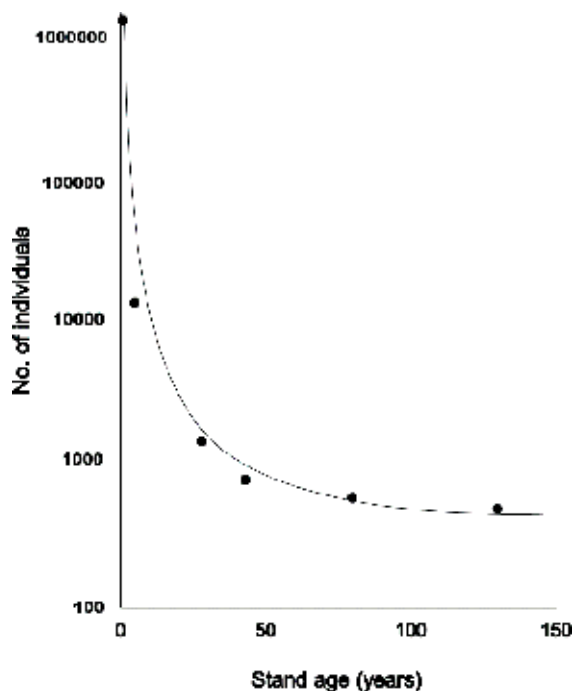


Figure 3. Survivorship curve of Korean red pine population.

old stands were shown as about 14,300, 1500, 800, 600, and 500 individuals/ha, respectively. Expressed the result as a semi-logarithmic graph, survivorship curve of Korean red pine population was shown in type III, which has the greatest mortality early in life, with relatively low mortality for those surviving this bottleneck [47].

7. Species composition of *P. densiflora* community

As the result of stand ordination based on vegetation data (Figure 4), stands of Korean red pine community were clearly divided from stands of oak communities and thus showed a difference in species composition. *Rhododendron micranthum* Turcz., *Vaccinium hirtum* var. *koreanum* (Nakai) Kitam., and *Lespedeza cyrtobotrya* Miq., which appear characteristically in the Korean red pine community but does not appear in the oak communities, dominate the difference.

Korean red pine community established on those sites usually forms pure stands. If any oak individuals are invaded to those sites, they usually showed severe desiccation damage on their leaves during spring dry season from May to June that experiences every year in Korea with Asian monsoon climate and consequently did not form erect stem as well as high stature of tree level (Lee, C.S. personal observation). *Rhododendron micranthum* Turcz., *R. mucronulatum* Turcz., *Fraxinus sieboldiana* Bl., and *Lespedeza cyrtobotrya* Miq. dominated shrub layer and *Carex humilis* var. *nana* (H. Lev. et Vaniot) Ohwi, *Spodiopogon sibiricus* Trin., *C. lanceolate* Boott, and *Arundinella hirta* Tanaka dominated herb layer of the Korean red pine community.

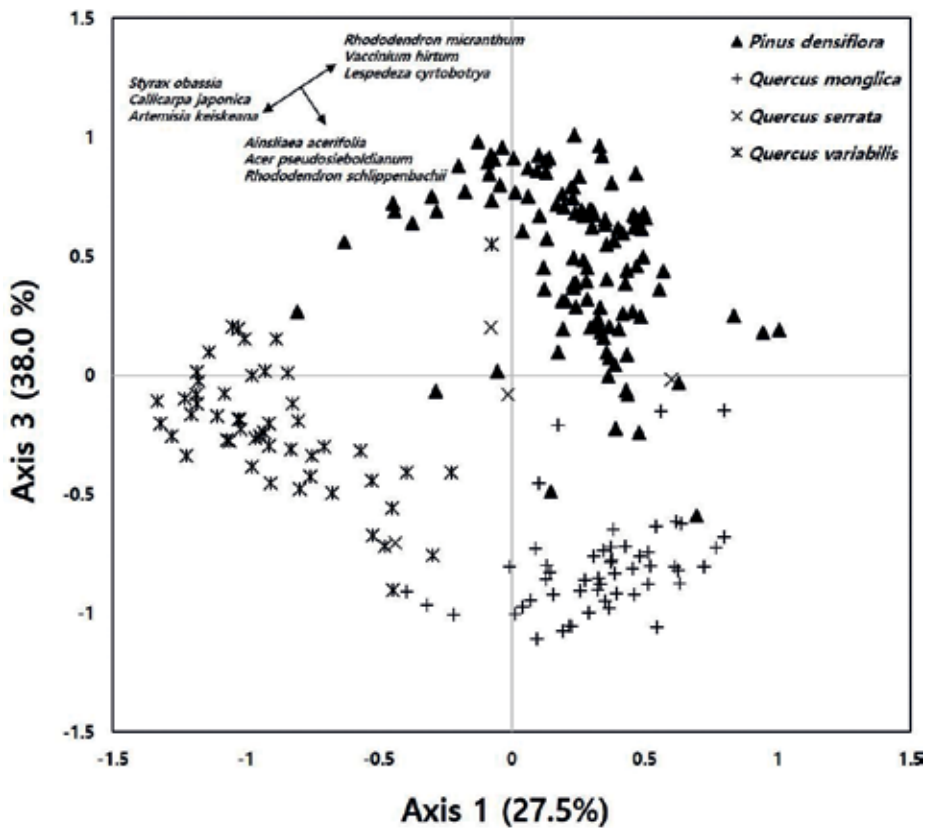


Figure 4. Stand ordination based on vegetation data collected from Korean red pine and oak forests.

Difference of species composition was also shown among oak communities. *Acer pseudosieboldianum* (Paxton) Kom., *Rhododendron schlippenbachii*, Max., and *Ainsliaea acerifolia* Sci.-Bip. of Mongolian oak (*Quercus mongolica* Fisch.) community and *Styrax obassia* S. et Z., *Callicarpa japonica* Thunb., and *Artemisia keiskiana* Miq. of Chinese cork oak (*Q. variabilis* Blume) community dominated the differences (Figure 4).

8. Disturbance regime

Disturbance regime was investigated in the sites such as ridgetop with dry and infertile soil where the Korean red pine forest is maintained as an edaphic climax (Photo 1). Standing dead type occupied the highest percentage and uprooted and stem broken types tended to be followed although a little difference exists depending on site (Table 3).

In general, both endogenous factors related to senescence of plant and exogenous factors such as typhoon, tornado, heavy snow, rainfall, and so on influence on death of gap makers. But if exogenous factors influence more strongly, frequency of uprooted or stem broken types increases in death type of gap maker [48]. In this respect, cause of disturbance in this Korean red pine forest would due to endogenous factors rather than exogenous ones.



Photo 1. Photos showing sites where Korean red pine forest is maintained naturally.

Sites	Death patterns of gap-makers		
	Standing dead	Uprooted	Stem broken
Youngwol	37 (53.6%)	19 (27.5%)	13 (18.8%)
Mt. Wolak	33 (63.5%)	10 (19.2%)	9 (17.3%)
Mt. Songni	5 (100.0%)	–	–
Uljin	3 (75.0%)	–	1 (25.0%)
Mt. Gaya	10 (71.4%)	3 (21.4%)	1 (7.2%)

Table 3. Death pattern of gap-makers in the Korean red pine forests.

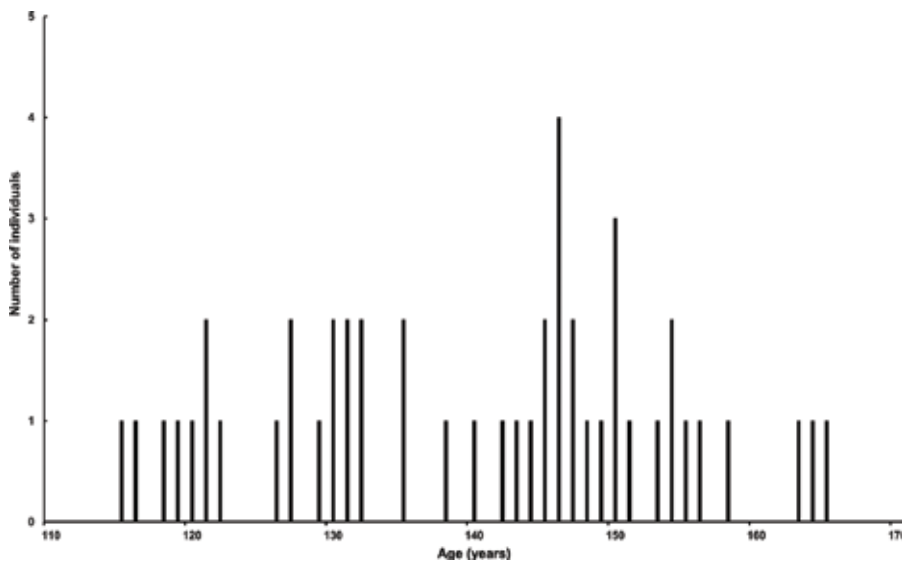


Figure 5. Age distribution of gap makers.

Gaps formed naturally in a forest is usually occurred by cooperative actions of both senescence of plant and exogenous factors [45, 48, 49]. Based on the fact, we can regard gap makers died by natural disturbance as trees that their longevity expired. Thus, we estimated ecological longevity

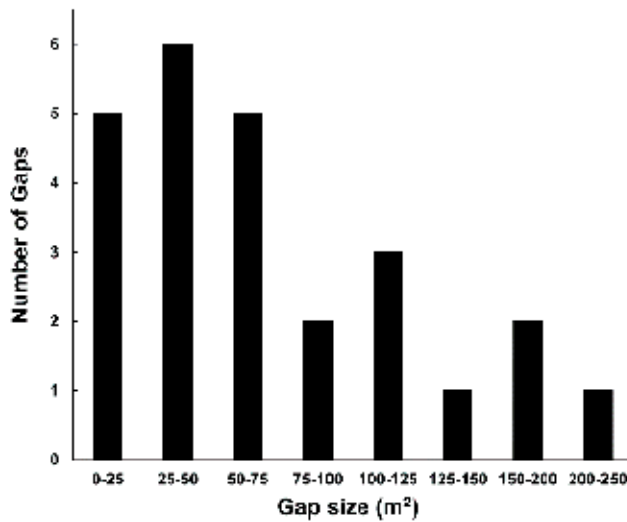


Figure 6. Frequency distribution of size class of gaps formed in *Pinus densiflora* forest.

of Korean red pine from age distribution of gap makers. Ages of gap makers ranged from 116 to 165 years and mean age was ca. 140 years (**Figure 5**). In most forest vegetation around the world, longevity of dominant species ranges from 100 to 1000 [50–53] and it is known that mean longevity of tree species forming temperate deciduous forest is about 300 years [54]. Compared with this information, longevity of Korean red pine was shorter, the reason would due to not only life history trait that the pine is early successional species [55, 56] but also poor environmental condition of site where the Korean red pine forest is maintained in an edaphic climax [19].

In a size class frequency distribution diagram of gaps occurred in the Korean red pine forest (**Figure 6**), gap size ranged from 20 to 235 m². Among them, 25.1–50.0 m² class occupied the highest frequency as 21.4% and below 25.0 m² and 50.1–75.0 m² classes (each 17.9%), 100.1–125.0 m² class (10.7%), 75.1–100.0 m², 150.1–175.0 m², and 175.1–200.0 m² classes (each 7.1%) and so on followed.

9. Natural regeneration of Korean red pine forest

Age distribution diagrams investigated in the Korean red pine stands of three sites where gap is formed due to disturbance and of one site without gap showed the reversed J-shaped pattern (**Figure 7**). This result implies that seedlings are recruited vigorously in these sites and the Korean red pine forest could be maintained continuously [57, 58]. Compared the periods that seedlings are recruited and gaps are formed, seedling began to be recruited in advance of gap formation. Seedlings appeared in Korean red pine forest where gap was not formed yet as well and thus support advance recruitment of pine seedlings.

But the non-gap site showed a difference from gap sites. Age of saplings was restricted below 10 years and dead individuals also appeared in non-gap site. This results suggest a necessity

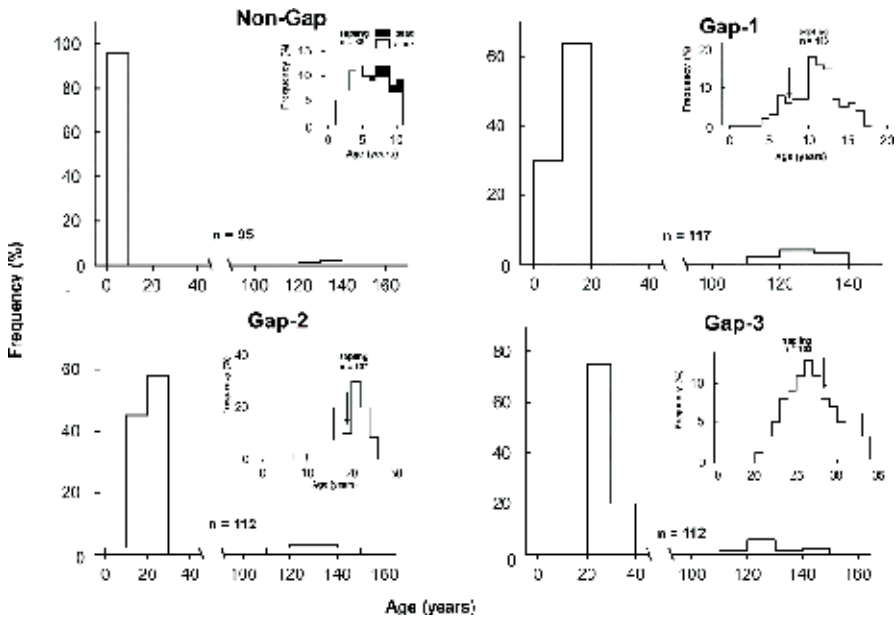


Figure 7. Age distribution diagrams of *Pinus densiflora* population in Korean red pine stand with gap and without gap (non-gap). In each diagram, lower diagram indicates age distribution of all the individuals including mature trees and regenerating young trees and saplings and upper diagram indicates that of the only regenerating individuals. Vertical arrows indicate the estimated year of gap formation. This result shows that many regenerating individuals were recruited in advance of gap formation. Sapling group established in a Korean red pine stand without gap reinforces the result. N numbers indicate the number of trees surveyed. Vertical arrows indicate the estimated year of gap formation.

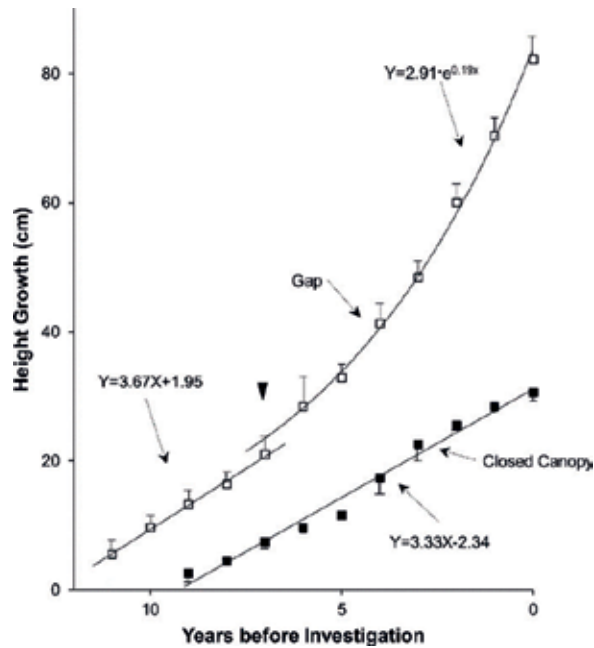


Figure 8. Height growth of saplings of *Pinus densiflora* within gap and under the closed canopy. Vertical arrows indicate the estimated year of gap formation.

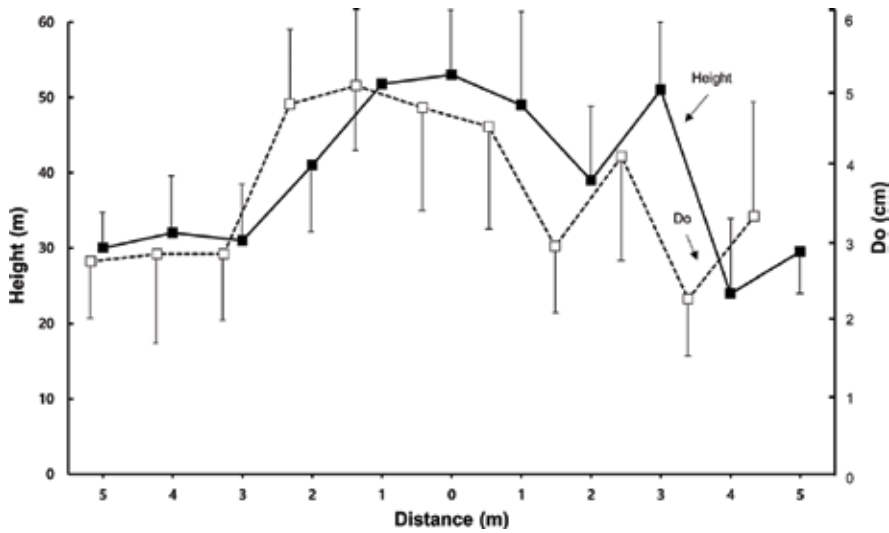


Figure 9. Changes of height, diameter (D_o) and density of saplings of *Pinus densiflora* according to the distances from the center of gap. 0 m indicates the center of gap.

of gap formation for natural regeneration of the Korean red pine forest. In fact, not only shade intolerant species dominated forest but also shade tolerant species dominated forest necessitate gap formation for natural regeneration [59].

Growth of saplings established in advance gap formation showed a linear growth before gap formation but the growth was accelerated exponentially since gap formation (Figure 8). This result implies that gap formation promotes the growth of saplings established in gap and consequently contribute to natural regeneration of the Korean red pine forest.

Both height and diameter of saplings were larger at the center of gap and tended to be smaller as move toward the margin of gap (Figure 9). It was interpreted that the differences in height and diameter of saplings appeared along the distances from the center of gap would be a response on the spatial differences of light intensity [19].

10. Regeneration process of Korean red pine forest

The regeneration process that gap occurred from a disturbance is closed, is different depending on the disturbance regime such as scale or intensity. If the disturbance scale is small and the intensity is not severe, the gap is closed by branch growth of mature trees surrounding the gaps. But if the disturbance scale is large and the intensity is severe, regeneration is progressed by height growth of saplings established within the gap or replaced by different kinds of forests [45].

Growth of saplings growing within gap showed a big difference from that of saplings under closed canopy without gap (Figure 8). The growth was similar to each other before gap formation, but the difference between both got larger after gap formation. Growth of the former showed a linear growth before gap formation but the growth was accelerated as exponential

one since gap formation (Figure 8). Meanwhile, growth of the latter maintained a linear growth without any difference before and after gap formation (Figure 10).

Compared branch growth of mature pines surrounding the gap with that of mature pines, which form a closed canopy without gap, growth of the former showed an increasing trend although the difference was a little, whereas that of the latter was vice versa (Figure 10). But a difference between both was not so big.

Mean size of gaps occurred from death of one individual was 28.3 m² and the radius of gap of this size was about 3 m [19]. As annual mean branch growth of mature trees surrounding the gap was 6.5 cm per year, 46 years were required to close the gap by branch growth of this level (Figure 11) [19].

Height of the tallest tree measured in the sites where Korean red pine forest can be maintained naturally, was about 20 m and annual maximum height growth of the tree was about 60 cm. Meanwhile, height growth of saplings within the gap showed an exponential growth ($Y = 2.92 e^{0.19x}$) as was mentioned above. Based on the results, Lee [4] hypothesized that exponential growth of saplings is progressed until the annual growth is arrived at 60 cm, annual maximum growth and since then, maintains the growth rate continuously. To arrive at 60 cm/year,

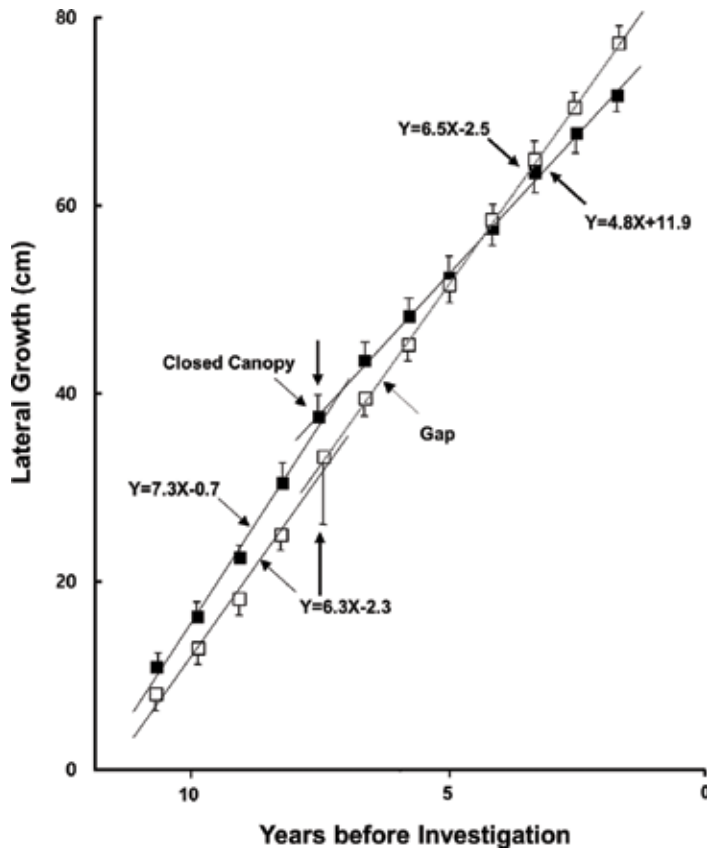


Figure 10. Branch growth of mature trees of *Pinus densiflora* bordering on gap and those on *Pinus densiflora* forest of the closed canopy. Vertical arrows indicate the estimated year of gap formation.

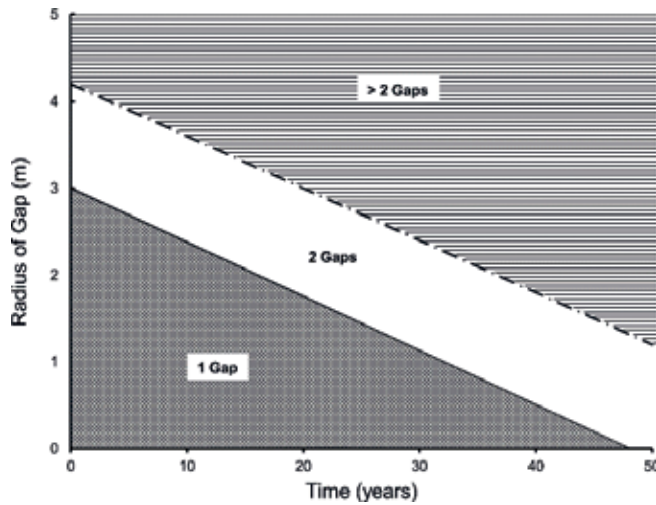


Figure 11. Decreasing curves of gap area. 50 years on X-axis indicate the year required for the saplings to enter the forest canopy. Straight lines inclined to the right indicate the case in which gap area is decreased by the branch growth. When these lines meet X-axis, it means that gap is closed and X-value at the moment indicates the year required for the gap to be closed. 1 gap, 2 gaps and >2 gaps indicate gaps formed by the death of 1, 2, and more than 2 trees.

the annual maximum height growth rate by the exponential growth of the level, 22 years are required and height of saplings at that time reaches about 2 m. Since then, if the saplings reach the canopy level, 20 m, by annual maximum growth rate, 60 cm, 30 years are required more [4]. Synthesized those results, it is calculated that 52 years are required until saplings grow to mature trees, which form overstory canopy by height growth (**Figure 11**) [4]. Compared years required for gap filling by height growth of sapling and branch growth of mature tree, the gap formed by death of one individual would be closed before the saplings within gap arrive at the canopy by height growth if multiple gap events are not occurred there (**Figure 11**).

This result was similar to that of Lee and Kim [18], which was carried out in the Korean red pine forests with different stand ages. But the growth rate, in particular, in early stage was very slow compared with the result of Lee and Kim [18]. This slow growth would due to that they were in the shading state under the closed canopy as individuals established in advance of gap formation. In fact, it is known that growth of individuals established through advance regeneration is very slow in most trees including shade tolerant trees [26].

On the other hand, size of gap formed by death of two individuals becomes 56.6 m² and the radius is 4.2 m, calculated the size by hypothesizing as twice of gap size occurred from death of one individual. About 65 years are required to close the gap of this scale by branch growth of trees surrounding the gap (**Figure 11**). Consequently, the gaps formed by death of more than two individuals would be regenerated by height growth of saplings established within gap before the gap is filled by branch growth of surrounding trees [4].

Based on the size class frequency distribution of gaps (**Figure 6**), large gaps occupied about 80% of total gaps. From this result, it was estimated that regeneration of the pine forest is usually achieved by growth of seedling established within the gap in these sites where pine forest can be maintaining continuously.

But as was mentioned above, gentle and endogenous factors dominate the disturbance regime in this region. Therefore, we have to find a background that large gaps are formed. It is known that most large gaps are originated from multiple gaps due to overlapped disturbance events [34, 45]. In general, gaps formed naturally are small ones, which are occurred from death or uprooting of one individual at first. Canopies of trees composing a forest are connected with each other before gap formation and thereby inflow of wind into forest interior is blocked effectively. But if the canopy is opened due to a disturbance, the effect of wind is flowed into the forest interior easily and thus the effects of following disturbance become stronger. Consequently, trees around the gap become more susceptible to disturbance [45]. Moreover, if a tree grows and becomes a mature tree, growth stage of the other trees surrounding the tree are also in similar stage because age range of trees composing the pine forest is narrow and thus close an even-aged stand. This result could be a causal factor that multiple gap is occurred [60].

11. Regeneration of pine forest treated artificially

In managing pine forests for timber, silvicultural methods are applied. The methods are classified three types depending on harvesting method, which is the method of removing products from a forest to make room for a new generation of trees. Clearcutting method is removing the mature stand completely and is usually applied in the upper slope in Korea. Seed trees is usually remained on the ridge above upper 80% in the slope length (**Figure 12, Photo 2**).

The seed tree method is removing most of the mature overstory and leaving a portion standing. Mature trees left in low density function as a seed source only. The residuals from this cut are too few and scattered to provide shelter (**Figure 12, Photo 2**).

The shelterwood method involves the removal of most of the mature stand at the end of the rotation, but a portion of the mature stand is left standing. The shelterwood method serves three basic purposes: firstly, to prepare the stand for production of abundant seed, secondly, to modify the environment in a way that promotes germination and survival of the selected species, and finally, to build up the amount and size of advance regeneration to ensure the prompt restocking of the new stand following overstory removal. The shelterwood method involves a sequence of three cuttings: firstly, preparatory cuttings make the seed trees more vigorous and set the stage for regeneration. Secondly, establishment/seed cuttings open up enough vacant growing space to allow establishment of the new regeneration. Finally, removal cuttings are uncover the new crop to allow it to fill the growing space [61].

These silvicultural methods are usually applied in the sites beyond the range that natural regeneration of the Korean red pine forest is possible to ensure higher productivity. But the sites are covered with trees including oak competitively superior to Korean red pine. Therefore, in order to achieve successful regeneration of Korean red pine forest as a shade intolerant, management of undergrowth including oak sprouts is required in the level that can expose mineral soil beyond creating gap in the overstory in Korea [18].

Age distribution diagram in the Korean red pine stands treated by applying silvicultural methods for timber production showed a reverse J-shaped pattern that young trees were

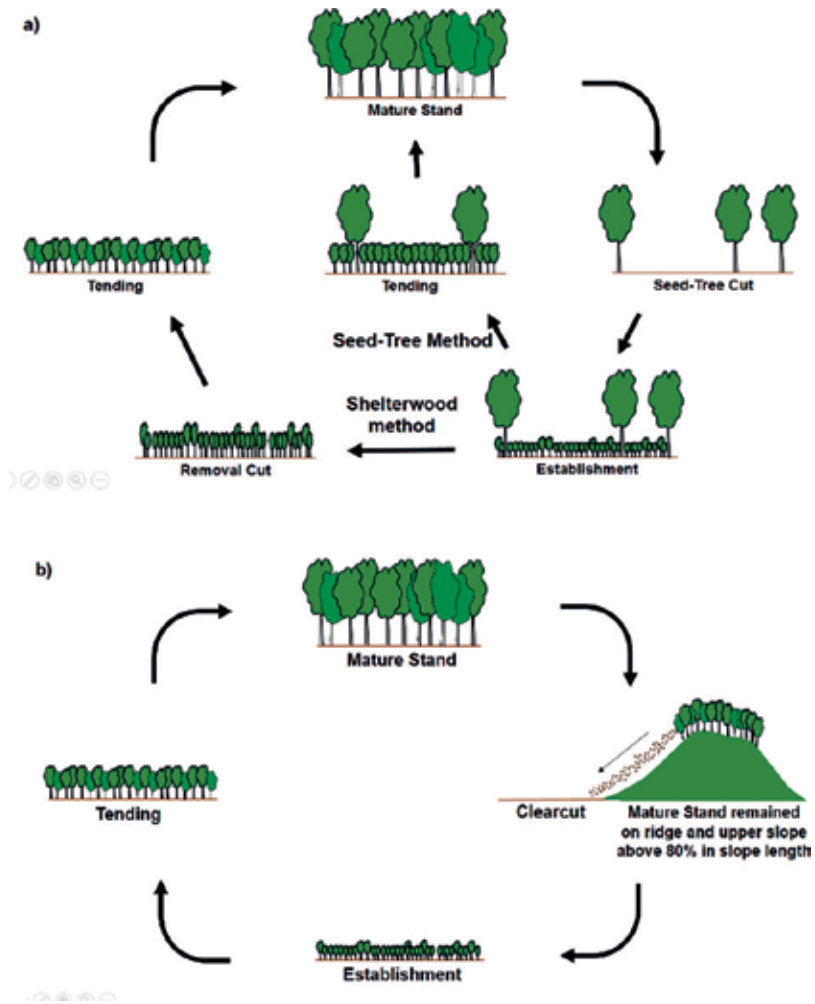


Figure 12. A diagram showing examples of the seed tree and shelterwood (a), and clearcut (b) regeneration methods.



Photo 2. Photos showing cases that the seed tree and shelterwood (a), and clearcut (b) regeneration methods are applied.

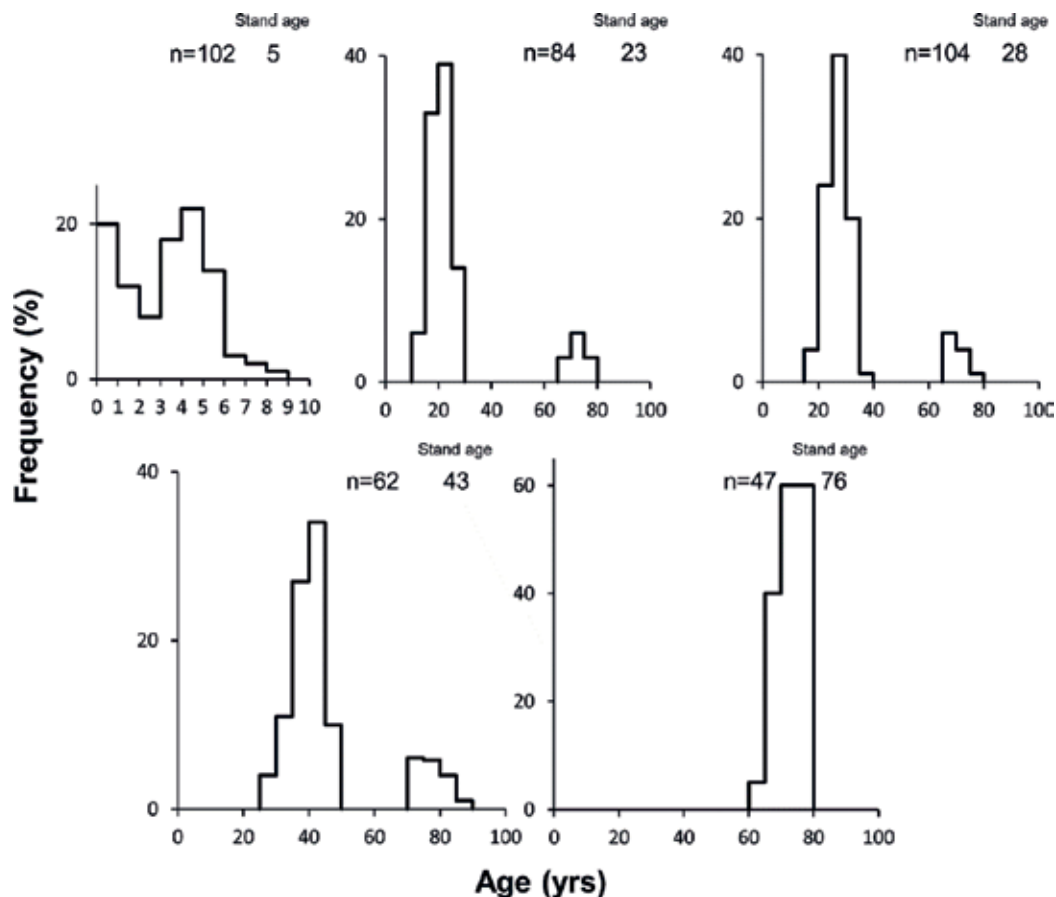


Figure 13. Age distribution diagrams of *Pinus densiflora* population in Korean red pine stands treated by silvicultural method. N numbers indicate the number of trees surveyed. Stand ages were estimated from the median value of peaked age class of regenerating successor tree population.

recruited vigorously except 76 year-old mature stand. Age distribution diagram is composed of two peaks of seed tree group and successor tree group recruited after treatment except 76 year-old stand and each cohort tends to a normal distribution (**Figure 13**). Based on age distribution range of successor group of the diagrams, period that recruitment is continued, was about 20 years.

12. Regeneration of Korean red pine forest damaged by air pollution

Dynamics of the Korean red pine forest damaged by air pollution were investigated around the Yecheon industrial complex, a representative industrial complex in Korea [62]. Annual ring growth of pine trees, which survived from air pollution damage, was suppressed for about 10 years since 1974 when industrial facilities began to be operated in this area but since then such suppressed growth tended to be recovered (**Figure 14**). It was supposed that the suppressed growth was originated from air pollution and that improvement of growth

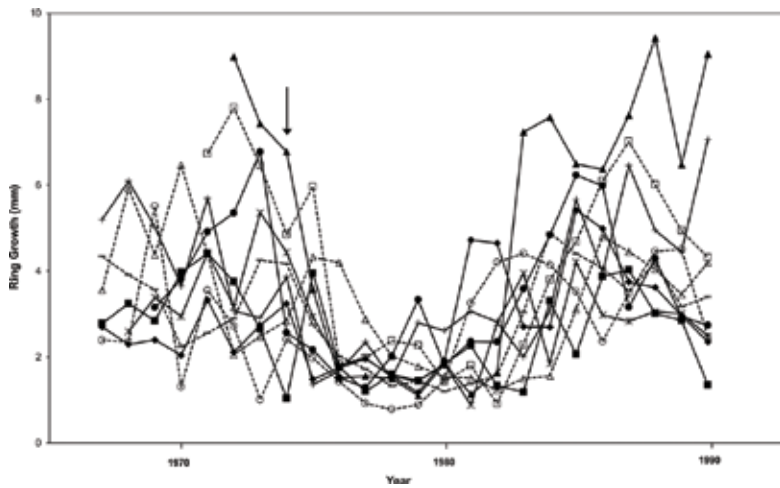


Figure 14. Yearly changes of annual ring growth in the mature Korean red pine. Vertical arrow indicates the year when the Yecheon industrial complex began to be operated. Symbols indicate different individuals.

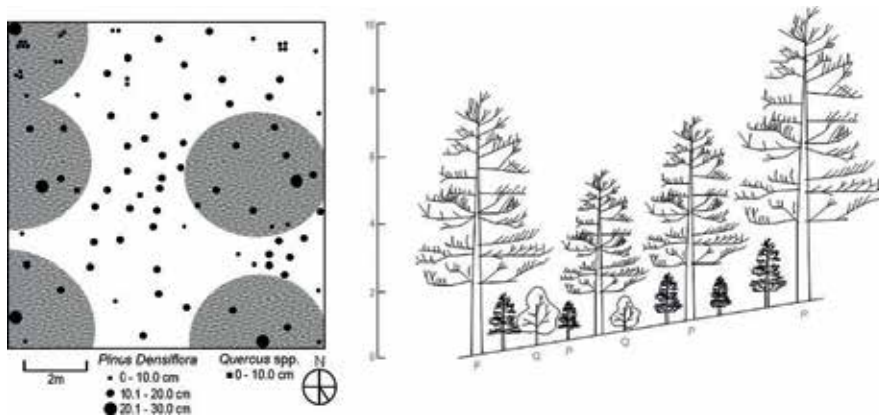


Figure 15. Crown projection and spatial distribution (left) and stand profile (right) of major species in a *Pinus densiflora* stand regenerated after air pollution damage. Shaded parts indicate canopy area of the seed trees survived from pollution damage. Circular and rectangular dots indicate pine and oak saplings, respectively. P: *Pinus densiflora*, Q: *Quercus* spp.

since then was due to release from competition by selective death of neighboring trees as well as mitigation of air pollution [62]. Therefore, physiognomy of the pine stands showed a mosaic pattern composed of different patches like stands regenerated by applying silvicultural method (refer to **Photo 2**). Spatial distribution pattern of individuals and stand profiles prepared there were similar to those of pine stands regenerated after natural and artificial disturbances (**Figure 15**). In an age class distribution diagram (**Figure 16**), ages of the pine trees ranged from 1 to 33 years. Among those individuals, those from 10 to 15 years old occupied more than 40% and the period when those individuals were recruited corresponded to the period when annual ring growth of the pine trees survived from air pollution was suppressed (**Figures 14** and **16**). This result suggests that this pine stand of mosaic pattern is the product of air pollution damage and natural regeneration of the damaged pine forest.

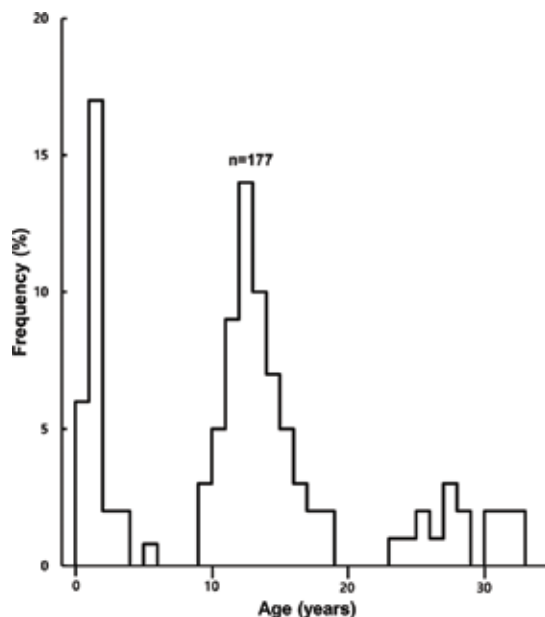


Figure 16. Age distribution diagram of *Pinus densiflora* population in a Korean red pine stand regenerated after air pollution damage. N numbers indicate the number of individuals surveyed.

13. Succession of pine forest damaged by pine gall midge

Changes of the Korean red pine forest damaged by pine gall midge (*Thecodiplosis japonensis* Uchida & Inouye) were investigated by classifying into four damage stages of the first (infested 3 years ago), the second (infested 8 years ago), the third (infested 13 years ago) and the fourth (infested 18 years ago). Damage stage were determined by the damage class and the years lapsed after outbreak.

Annual ring growth began to decrease from the first stage and decreased greatly in the second stage after infestation by pine gall midge (**Figure 17**). Reproduction based on coning was usually for 3 or 4 years and until 7 years after infestation (**Figure 18**). Many damaged pines died and their coning was interrupted in the second stage.

Coverage of pine in the Korean red pine forest damaged by pine gall midge decreased to 10% in the third stage and disappeared in the fourth stage. The pine forest was replaced by oak forest (**Figure 19**). Replacement of damaged pine forest was made by rapid growth of oaks released from suppression of overstory pine due to pine gall midge infestation.

As the result of ordination (DCA) based on vegetation data, stands tended to be arranged depending on the damage stage and thus reflected above mentioned change (**Figure 20**). Damaged pine forests of the third and the fourth stages were arranged near the oak forests and were located far from the healthy and the damaged pine forests of the first and the second stages. But the results in the shrub and herb layers were not so differently from that in the tree layer. That is, floristic composition of tree layer in the third and the fourth stages was changed but that of undergrowth was not.

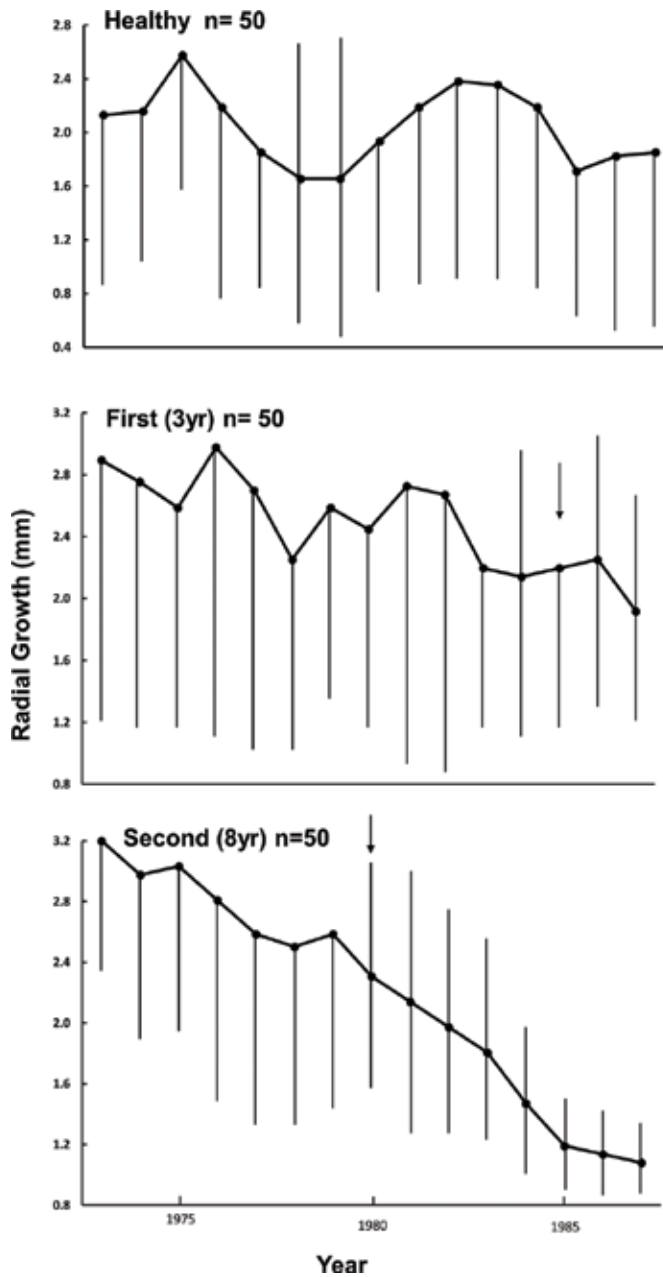


Figure 17. Yearly changes of radial growth of the Korean red pine in the healthy pine forest and the damaged pine forests of the first and second stages. Vertical arrows indicate the year that damage was begun. N numbers are the number of trees surveyed. Healthy, first, and second indicate Korean red pine stands non-infected and infected of the first and second stages, respectively. Vertical lines indicate standard deviation.

As was shown in above mentioned results, pine gall midge damage led to succession of the Korean red pine forest to oak forest during short period within 20 years. That is, pine gall midge damage accelerated succession as in the case of chestnut blight [63].

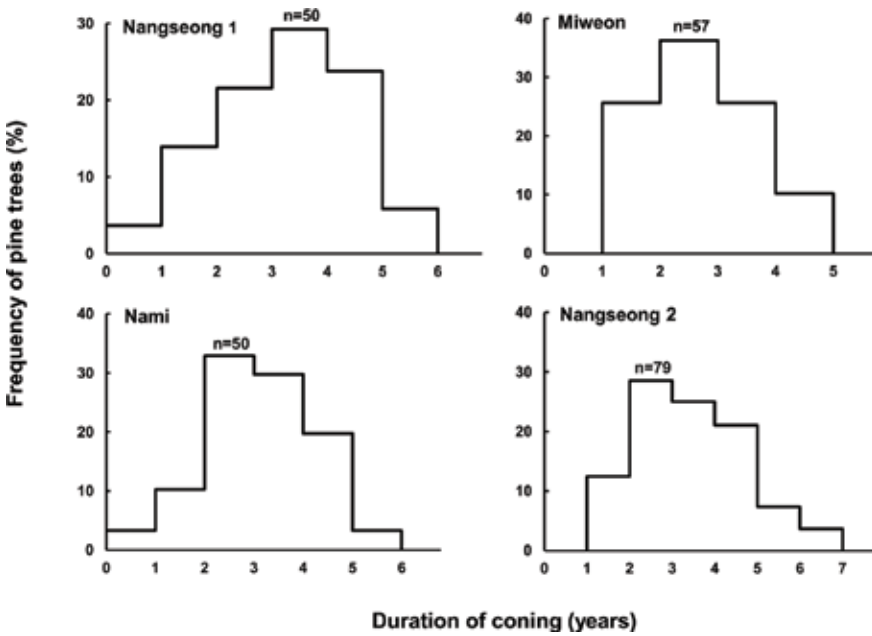


Figure 18. Frequency distribution of trees with different duration of coning in the Korean red pine stands of the first and the second damage stages. N numbers are the number of trees surveyed. Nangseong 1 and 2, Miweon indicate names of sites surveyed.

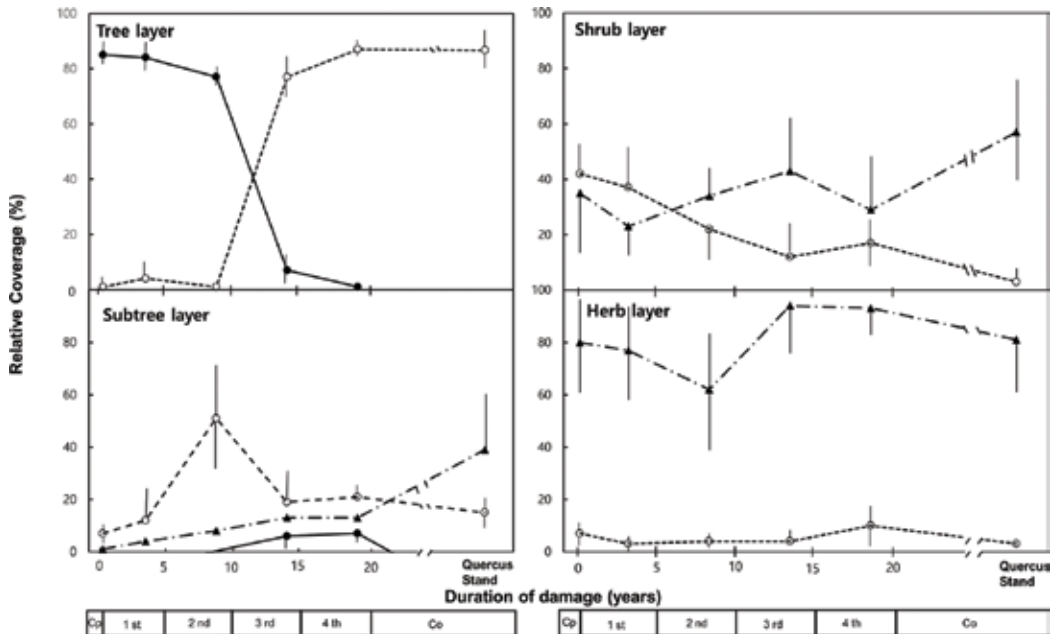


Figure 19. Changes of coverage along the period that pine gall midge damage continued. Cp: Control plot of pine, 1st, 2nd, 3rd, and 4th: Infected pine stands of the first, second, third, and fourth damage stages, co: Control plot of oak. N numbers indicate the number of individuals surveyed.

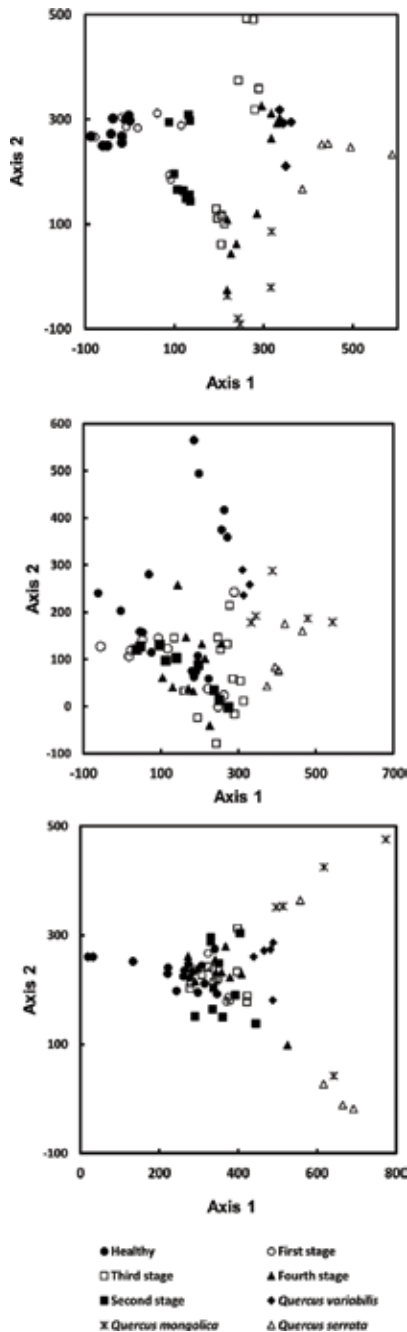


Figure 20. DCA ordination of stands based on vegetation data obtained from Korean red pine stands with different pine gall midge damage stage.

But vegetation change occurred in the Korean red pine forest as a response on pine gall midge infection was different depending on topographic condition [64]. The result is due to that dry and infertile condition of the ridgetop site are not suitable for inhabitation of pine gall midge [65]. Vegetation change was occurred in most areas except ridgetop and replacer trees

were different depending on slope aspect and elevation. Mongolian oak and Chinese cork oak dominated vegetation change on Northern and Eastern and Southern and western slopes, respectively. On the other hand, Konara oak dominated vegetation in lowland [64].

14. Conclusions

Pinus densiflora grows throughout the whole national territory of the Korean Peninsula and the community is the representative forest community as it is one of the forest communities occupying the most extensive area. Korean red pine forest showed the life history traits typical of the forest, which is in the early successional stage. Seed production was consistent without a mast year and survivorship was shown as type III. Natural maintenance of the forest was possible only in the restricted sites such as rock outcroppings, weathered rocks, ridgetops, and the sandy or pebble shores of streams where can escape competition with oak forests composing the late successional stage in the region. Natural regeneration of the Korean red pine forest in those sites depended on disturbance regime, which is dominated by endogenous factors. The forest had dominated forest ecosystem in Korea in the past that artificial disturbance for the forest ecosystem was severer than the present days. But the area that Korean red pine forest occupies declined greatly due to socio-economic change in these days in Korea. In particular, reduction of human interference for forest and infection of alien pest occurred in a continued series in the order of pine caterpillar (*Thaumetopoea pityocampa* (THAUPI)), pine gall midge, and pine wilt disease (*Bursaphelenchus xylophilus* (Steiner & Buhner) Nickle) dominated such changes. The former induced succession of the Korean red pine forest to the deciduous (cool temperate zone in northern and central parts of the Korean Peninsula) and/or evergreen (warm temperate zone in southern part of the Korean Peninsula) broadleaved forests dominated by oaks and the latter accelerated the process [6, 24]. However, other trends are also detected in these days. Climate change expands not only the distributional range of the Korean red pine forest to higher elevation [66] but also growing season beyond the normal growing season from April to early July [67].

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Conflict of interest

This paper was prepared by reediting papers that prof. C.S. Lee had published [4, 5, 18, 19, 62, 64, 68].

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Litter Fall and Forest Floor under Conifer Stands: Silviculture Consequences - A Review

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Abstract

Litter fall is an important part of nutrient cycle in forest ecosystems. Conifers are traditionally considered to be less-suitable nutrient cycling improvers and/or maintainers compared to broadleaves. Long-term observations plus information from both domestic and international publications showed an important role of conifers in process of accumulation and decomposition of the forest floor. Our results also show relations between litter fall and forest floor amounts due to thinning. From silviculture point of view, the knowledge of nutrient cycling is essential to optimize tree species composition using appropriate techniques for forest regeneration and thinning.

Keywords: Norway spruce, *Picea abies*, Scots pine, *Pinus sylvestris*, European larch, *Larix decidua*, thinning

1. Introduction

Soil fertility is being maintained and/or improved via litter fall partly. To evaluate impact of tree species on forest soils, knowledge of forest floor development and its properties is essential. The properties of forest floor layers are attributable to tree species composition and soil properties that are developed under conditions of different climates. The forest floor consists of three particular layers (see [1, 2]). Forest floor humus amount is typically a result of many years' litter fall [3].

These layers were described [2]: L-litter at the surface consisting of shed foliage and other plant matter that is mostly undecomposed which means that particular organs can be recognized

(**Figure 1** and **Figure 2** on the left); F-layer of partly decomposed plant remnants, recognizable organs and parts still prevail, the matter of unrecognizable origin is already present including soil biota remnants, presence of fungi is obvious (**Figure 2** in the middle); H-humus consisting of mostly heavily decomposed matter excepting partly recognizable remnants of roots (**Figure 2** on the right). Mineral topsoil below H layer is called an organic-mineral soil; it contains 20–30% of humus and are 5–30 cm deep [2]. Waterlogging contributes to development of deeper (even 50 cm) peaty horizon [2].

The main measure to avoid development of overstocked, dense and thus less-stable stands is thinning. Thinning reduces standing aboveground biomass as the residues are left on site and/or removed from the stand and used commercially. Both approaches affect production of litter fall; the former one, however, increases the annual litter fall in the year of thinning. Thinned stands' forest floors have better conditions to be decomposed more quickly. On the other hand, the trees left on the site have more space and sources to grow that affects growth rate, amount of biomass which increases litter production again.

Sampling of litter fall was conducted using litter collectors in stands of various age on sites both of long-term forested and former agriculture origins. The very beginning of the litter collectors' installation is the stage of the young canopy closure when the oldest needles fall, ground vegetation declines and new forest floor starts to accumulate on the soil surface (**Figures 3** and **4**). Forest floor sampling was done using steel frames (25 × 25 cm in size) to separate the three enclosed L, F and H layers. The review was based on published studies dealing with both litter fall and forest floor produced and developed by three conifers: Norway spruce, Scots pine and European larch. If available, more information from



Figure 1. Sampling of forest floor L layer using steel frames (25 × 25 cm) in Norway spruce stands.



Figure 2. Sampling of forest floor under Scots pine stands—horizons L—litter (left), F—fermentation (in the middle) and H—humus (right).



Figure 3. Litter fall collectors in young Scots pine stands.



Figure 4. Litter fall collectors under control (above) and thinned (below) Norway spruce stands.

unpublished results being relevant to the topic was added. The objective of the study was to gather information on relationship between the three important conifers and the development of forest floor. Authors pointed out, that contrary to popular believes, coniferous litter fall itself should not be considered a single factor contributing to acidity of forest floor.

2. Norway spruce [*Picea abies* (L.) Karst]

Norway spruce does not always develop the worst forest floor conditions [4] though worsening of soil properties was also found (see [5]) which is frequently the reason for converting the species composition or restoration of mixed-species stands [6]. Norway spruce showed its capability of developing similar forest floor properties compared to other tree species [7]. Also unexpected trends were found as Mareschal et al. [8] found higher pH of topsoil (0–5 cm) under 34-year-old Norway spruce compared to stands of Douglas-fir, Corsican pine, European beech and 150-year-old beech-oak coppice while base saturation was the lowest under conifers. Annual litter fall differs according to tree species. Augusto et al. [9] reported litter falls of Scots pine > sessile and English oaks = Norway spruce > Douglas-fir > European beech > European hornbeam > birch amounting 3.9, 3.7–3.8, 3.8, 3.4, 3.5, 2.9 and 2.2 Mg.ha⁻¹. year⁻¹ in descending order respectively. Hobbie et al. [10] found an interesting relationship between increased accumulation of coniferous forest floor (silver fir, Norway spruce, Scots and Corsican pines) and content of calcium that seemed to favor earthworms' abundance in calcium-rich small-leaved linden and both sycamore and Norway maple forest floors. Authors of [11] reported higher C/N and accumulated forest floor under Norway spruce compared to English oak.

Development of forest floor relatively higher in nutrients is crucial on nutrient-poor sites [12]. For example, excessively low phosphorus was estimated in large areas in the Jizera Mts., North Bohemia (see [12], p. 83) and Norway spruce forest floors can be higher in phosphorus compared to deciduous broadleaves [13]. More phosphorus was reported from under Norway spruce, European larch and mountain pine compared to silver birch and rowan [13] in the Jizera Mts. Also our unpublished results confirmed more phosphorus under spruce compared to Carpathian birch in the Hrubý Jeseník Mts., North Moravia.

Worse forest floor conditions were frequently attributable to air-pollution load. Kantor [14] found lower forest floor pH under Norway spruce compared to Scots and Corsican pines and broadleaves (European aspen, European beech, silver birch and goat willow) under heavily SO₂-polluted conditions near Trutnov-Poříčí power plant in 1986–1988. More acidic soil and 10 times heavier forest floor was found under Norway spruce compared with linden [15]. Greater accumulation of forest floor is reflected by higher C/N (see [11]). Higher C/N and more phosphorus under Norway spruce were also reported by Dušek et al. [16] compared to small-leaved linden. Also our other unpublished results from Norway spruce and small-leaved linden confirmed the conclusions in [16]. Norway spruce forest floor properties are frequently reported as worse compared to deciduous broadleaves [5, 17–20]. Compared to evergreen conifers, Norway spruce was found to be the same acidifier as Sitka spruce, Scots pine [9], as blue spruce, Serbian spruce [14] and also as silver fir [21] or contributed to worse conditions than white pine [5] or Douglas-fir and silver fir [17].

Thinned Norway spruce stands showed longer living crowns and comparable annual litter fall to nonthinned ones [22]. Nonthinned control plots have greater forest floor amounts than the thinned ones [3, 22]. Norway spruce forest floor accumulates along with the age of stands. 30–40-year-old nonthinned stands showed exceptionally high L + F + H dry-mass values amounting 50–70 Mg.ha⁻¹; the values were comparable to other Norway spruce stands of similar age representing particularly 800–1200 kg of nitrogen, 70–90 kg of phosphorus, 80 kg of potassium, 230–370 kg of calcium and 80–160 kg of magnesium [23].

Although the Norway spruce can aggravate acidity of soil, the forest floor and topsoil properties depend not only on the presence of the tree species, but also on synergistic confluence of all biota ecosystem component and environmental conditions of the site. It was Binkley [24] who asked “Why is acidification assumed to be a degradation?” Also Singer, Munns [25] pointed out that acidic soils are typical of conditions “where high rainfall and free drainage favor leaching and the biological production of acids.” Norway spruce is a main commercial species on many forest sites from middle altitudes to mountains. Growing Norway spruce becomes risky in conditions of beech with oak and beech sites due to ongoing climate change; Norway spruce, however, remains an important tree species at highland beech with fir, beech with spruce and mountain spruce with beech and spruce sites [26].

3. Scots pine (*Pinus sylvestris* L.)

The topics concerning nutrient cycling are in focus of both researchers and forestry practice due to increasing amounts of logging residues used for energetic purposes (e.g. [27]). Nutrition sustainability is even more important because Scots pine is grown frequently on nutrient-poor, sandy sites and is typical producer of recalcitrant litter. Kantor [14] found Scots pine forest floor less acidic compared to spruces under SO₂-polluted conditions at the end of 1980s. Scots pine was ranked as similarly acidifying tree species compared to Norway spruce and Sitka spruce [9]. Scots pine forest floor properties can be, however, also improved by mixing it with spruce [28, 29], birch [28], beech and oaks [30–32]. Also beech under-planting can improve both amount and diversity of mycorrhiza fungi [33]. Barba et al. [34] reported significant change in forest floor formation as Scots pine is being replaced by Holm oak due to forest die-off. The positive changes in forest floor properties were attributable to soil biota changes; the shift from recalcitrant pine needles input to more palatable oak leaves was important [34]. Keeping pine site fertile is expected from deciduous admixed tree species (see [28, 30–32, 34]).

Young 30-year-old Scots pine stands produce 2–8 Mg.ha⁻¹ of litter fall annually. Nitrogen represents ca 0.6% which is a mean input of N totaling 24 kg.ha⁻¹.year⁻¹ [35]. The amount of litter fall increases significantly with increasing basal area and also with reduction of suppressed understory trees [35]. Annual litter fall can be decreased after thinning of the young pines over 8 following years [35]. Nitrogen content (%) is not affected, therefore lower amounts of nitrogen (kg.ha⁻¹) in the thinned stand representing 75% of nonthinned control stand litter fall is attributable to removal of litter producers, the trees [35]. If salvage cut is done within the no-thinning stand, litter fall amounts can be equal or even lower than that of the thinned treatment [35]. Annual litter fall can be affected also by climate, which is that the mean temperatures correlate with the annual amounts of litter positively while precipitation correlates

negatively [35]. There was also a relationship found between the latitude and content of nutrients such as nitrogen and phosphorus [36]. Also litter higher in nitrogen along with increasing annual actual evapotranspiration was documented [37]. Higher fraction of recalcitrant pine litter was found at sites with higher long-term mean annual temperature [38].

Scots pine needle litter fall decreased along with age was reported [39]. Contrary to this, Berg et al. [40] published a logistic litter fall model showing greater amounts of litter fall in old (over 120 years) than in young (ca 20 years old) stands. Mean needle litter fall is ca 3.9 Mg.ha⁻¹ annually and forest floor litter layer totals between 13 and 45 Mg.ha⁻¹ [9, 39]; the poorer sites the less litter occurs. The pine forest floor accumulates a less favorable thick humus form of moder-mor type that does not enrich topsoil layers with humus very well. Topsoil high in organic matter develops preferentially under the woody species where higher abundance of earthworms occur [41]. Novák et al. [42] reported 70–123 Mg.ha⁻¹ of forest floor layers (L + F + H) under 79-year-old pine stands. The most of forest floor amount was found below no-thinning treatments [42]. The decreased litter fall after thinning in pure Scots pine stands on very poor sites can contribute to development of nutrient deficient forest floor [43]. This can be mitigated by planting deciduous soil improvers (see [28, 30–32, 34]. For instance, neighboring broadleaved stand dominated by European beech accompanied with silver birch, European hornbeam and small-leaved linden showed the top layer (L) of forest floor higher in nitrogen, magnesium, potassium and calcium than Scots pine L in Moravian Sahara near Bzenec, South Moravia. Pine needles were higher in phosphorus. Decomposed FH layers under broadleaves were more base-saturated compared to pine ones ranging between 71 and 81% and 43 and 68%, respectively. The same pattern was found for plant-available phosphorus, potassium, calcium and magnesium. On the other hand, both A and B mineral horizons showed a reverse trend for phosphorus (higher under pine) and comparable base cations content under both broadleaves and pine.

4. European larch (*Larix decidua* Mill)

Humification of litter horizon of larch forest floor was comparable with spruce and slower compared to alder, birch and Scots pine under 25-year-old stand [44]. Podrázský et al. [45] found more than 27 Mg.ha⁻¹ of forest floor under European larch while neighboring wild cherry and small-leaved linden accumulated 4 Mg.ha⁻¹; the stands were 60-year-old. The forest floor of European larch origin was lower in base cations (particularly potassium and magnesium) and higher in nitrogen and phosphorus [45]. Below-larch topsoil higher in plant-available phosphorus compared to silver birch, red oak and Norway spruce was found also in [4].

Greater accumulation of larch forest floor is also confirmed on former agricultural land. For example, increased carbon along with age of Siberian larch stands compared to downy birch on volcanic soils of abandoned heath land was found [46]. A thicker L horizon under larch was reported compared to spruce in 53-year-old stands at formerly cultivated site of 600 m altitude [47]; both deeper F and H horizons' differences were not significant. Larch litter layer

was higher in potassium while topsoil was lower in phosphorus and 10–20 cm soil lower in magnesium despite the same soil showed higher pH KCl and base saturation. There is a question if the differences were attributable to legacy of former agriculture [47].

Podrázský and Štěpáník [4] found more acidic soil under European larch than silver birch, red oak and Norway spruce on nutrient-poor, former agricultural soil at middle altitude. Later, [48] the same 28–37-year-old stands of silver birch, red oak, European larch and Norway spruce were compared, less favorable conditions under larch were reported again. There were found, for instance, the lowest pH, base saturation and plant-available nutrients contents excepting phosphorus [48].

In 50-year-old larch stand on former agricultural land, the LF layer of forest floor was higher in calcium and magnesium, the FH layer was lower in potassium and 0–10 cm topsoil was lower in phosphorus than neighboring Norway spruce stand. Larch topsoil showed also significantly lower C/N [49]. Also another experiment with first-generation European larch forest floor (unpublished results) showed L horizon higher in magnesium and potassium and lower in calcium than spruce. H horizon was higher in all the three base cations under larch. Both H forest floor and topsoil showed the same pH under larch and spruce.

More acidic humus under larch was found also on long-term forested soils in Sweden as lower pH was reported under Siberian larch compared to silver birch and Norway spruce [50]. On the other hand, Eriksson and Rosen [51] reported forest floor of 35-year-old Japanese larch higher in calcium, magnesium, potassium and nitrogen compared to that of grand fir and Norway spruce; no differences were obvious in the mineral soil. We found also more calcium, potassium, magnesium, the same concentrations of phosphorus, nitrogen and slightly less carbon in European larch forest floor than Norway spruce (unpublished results). The forest floor carbon under stands of European beech, Douglas-fir, Scots pine, English oak and Japanese larch was compared in the Netherlands [52]. The values varied between 11.1 Mg.ha⁻¹ for beech and 29.6 Mg.ha⁻¹ for larch; carbon stocks were lower at managed locations than at unmanaged ones [52].

European larch is also used successfully on post-mining sites [41, 53]. The 29-year development of forests on brown coal mining heap increased significantly dry mass of forest floor under larch compared to broadleaves (oak, linden and alder) and nonsignificantly compared to Scots pine with black pine mixture; the greatest forest floor was accumulated under mixture of Serbian and blue spruce [41]. In the same study, a significant and positive correlation was found between the total soil carbon storage and earthworm density and occurrence of earthworm casts in topsoil [41]. From this point of view, larch was comparable with oak, nonsignificantly higher than other conifers and significantly lower than linden and alder [41]. Similar trends were confirmed by Józefowska et al. [53] on two Polish post-mining sites. Significantly lower biological activity (earthworms, enchytraeidae) and microbial C biomass were found under 30-year-old larch stand compared to broadleaves (oak, birch, alder); biological activity under pine was comparable [53].

Heavy thinning of 20-year-old larch stands reduced significantly litter fall (**Figures 5 and 6**) in the thinned treatment compared to nonthinned control [54]. If used as a substitute tree species in formerly air-polluted Czech mountains, the biomass from thinning for chipping



Figure 5. Litter fall collectors in young European larch stands.

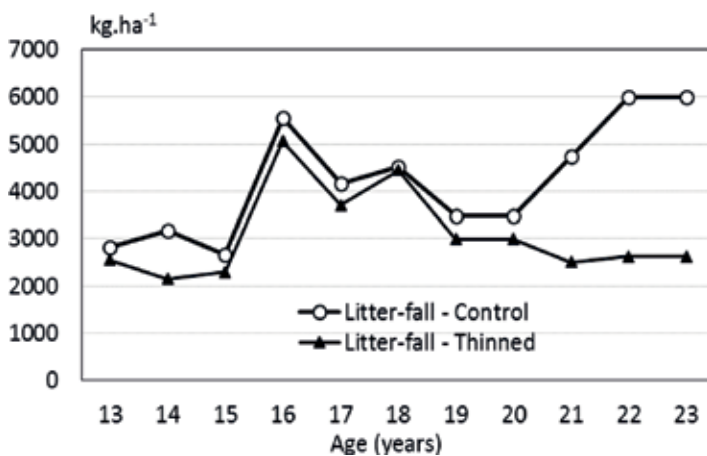
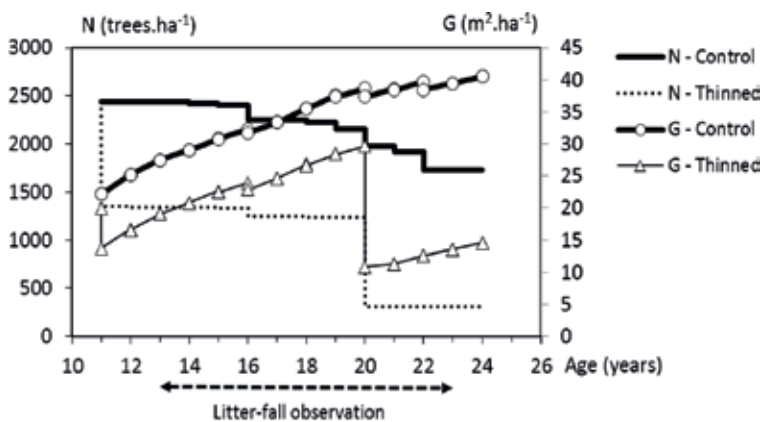


Figure 6. Heavy thinning (above) of 20-year-old European larch stand affected annual litter fall (below); litter fall was slightly higher on control plot after the first thinning at the age of 11 (above); heavy thinning did not decreased litter fall of the thinned treatment substantially, however, that one on control plot increased which made a great difference.

should be limited to stem-wood use only and the remaining aboveground biomass (particularly needles, twigs and branches) should be left on site to be decomposed [55].

5. Silvicultural implications and conclusions

Norway spruce is an important commercial conifer in Central Europe; it grows well on fir-beech to spruce vegetation domains; however, it is also capable of surviving on more sites excepting the flooded ones [56]. Wind, snow, biotic agents and air pollution threaten the Norway spruce stands even in its optimal growing conditions [56].

Scots pine is also important commercial tree species in Central Europe; it is common on natural pine sites, hillside, acidic, gleyic and water-logged sites from lowlands to highlands [56]. Scots pine can be also used as a preparatory pioneer species to restore forest in less-favorable environment such as abandoned sand quarries and so on.

European larch is often used as accompanying tree species on many sites from middle to mountain altitudes [26]. Its forest floor properties are similar to those of evergreen conifers. European larch is not expected to be a soil improver. Larch grows well also outside the original area and is successfully used in mixed stands.

Thinning of young conifer stands can affect annual litter fall over years. Additionally, early thinning increases the decomposition rate and positively impacts on nutrient cycling. The effect is as long as the thinning has been intensive. In case of light or medium thinning, crown biomass increases over a few years and, consequently, amount of litter fall under control and thinned stand becomes comparable again.

Besides the known effects of thinning on quality of production, stability, throughfall and so on, it was confirmed that it is a silviculture measure to influence litter conditions in conifer stands significantly.

However, existing results should be continually verified by following (and replicated) research at all sites where expected climate change is to affect conifers' growth.

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Conifers in Mountains of China

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Abstract

China has the largest area of mountains of all countries, with about 70% of land territory covered with mountains and plateaus. Thanks to vastness, mountainousness, highly heterogeneous habitats and long history of biological evolution, China boasts of extremely high biodiversity (more than 30,000 species of seed plants). The objectives of this chapter are to investigate conifer species and to analyze their multi-dimensional distribution in China. Our conclusions include: (1) China has 244 species of conifers belonging to 32 genera in 4 families (*Pinaceae*, *Cupressaceae*, *Podocarpaceae* and *Taxaceae*), accounting for 38.37, 49.29 and 66.67% of the global totals, respectively; (2) there are totally 115 conifer species endemic to China, falling in 23 genera of 4 families; (3) conifers and coniferous forests are widely distributed in China, from north to south and from east to west, more prominently in its numerous and high mountains and plateaus; (4) some conifer species appear even at very high elevations, e.g., *Juniperus tibetica* forests at 4800–4900 m above sea level in the southeastern Tibetan Plateau; and (5) China has established a large number of nature reserves and promulgated and implemented a series of laws and regulations to protect its rare and precious conifer resources.

Keywords: conifer, endemic species, Tibetan plateau, mountain forests, altitudinal zonation

1. Introduction

China is located in the southeast of the world's largest continent—the Eurasian continent, and characterized by vastness, mountainousness and high heterogeneity. With a land area of 9.6 million km², it is the third largest country in the world; about 70% of its land territory is mountains and plateaus, especially such high mountains and plateaus (**Figure 1**) as the

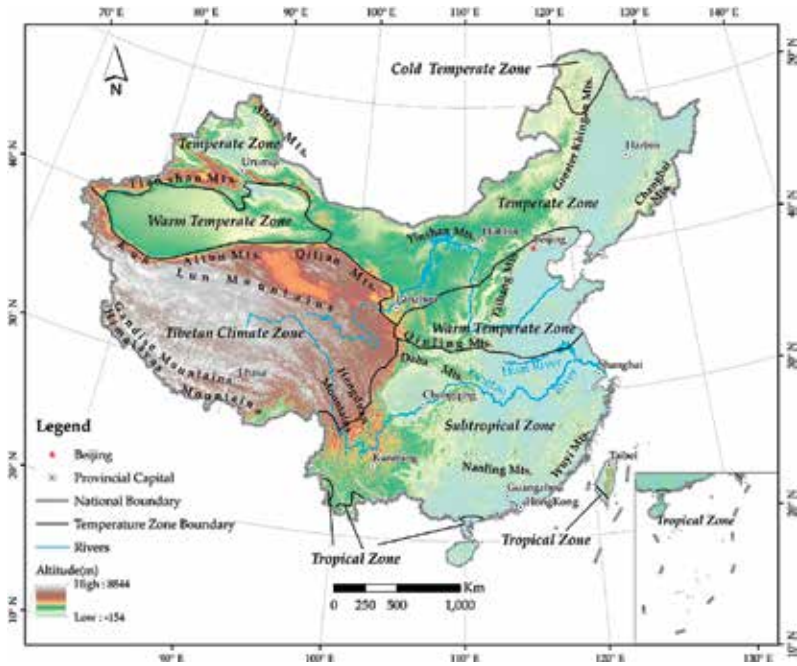


Figure 1. Distribution of the main mountain ranges in China.

Himalayas, the Kunlun Mountains, the Tianshan Mountains, the Tibetan Plateau, and so on. China is virtually a country with the largest area of mountains in the world. Its lowest point is at 154 m below sea level in the Turpan Basin of Xinjiang, and the highest point is the top of Mt. Everest (8844 m).

These many mountains, especially those extending east-west, contribute greatly to the climatic and landscape patterns of China. The Qinling Mountains form the boundary between temperate and subtropical climate regions; the Yinshan Mountains set apart temperate and warm-temperate climate in Inner Mongolia; the Tianshan Mountains are the natural border of temperate and warm-temperate desert areas in Xinjiang. While in Northeast China, the north-south stretching Greater Khingan mountains serve as the boundary between sub-humid and semi-arid regions. These mountains strengthen China’s north-south and east-west areal differentiation, shaping its climate and vegetation patterns into their present states.

The most prominent feature of the geography of China is the differentiation of three realms: the eastern monsoon realm, the northwestern arid realm, and the Tibetan frigid realm (Figure 2). The formation of this pattern of three realms is mainly the effect of the Pacific monsoon from the southeast in the warm season and the Mongolian cold air flows in the cold season. The eastern monsoon realm is divided, by the Qinling-Daba Mts.-Huai River, into southern and northern parts. Therefore, the Qinling-Daba Mts. are also regarded as China’s north-south transitional zone. To the south are subtropical and tropical regions, with an annual mean precipitation of 800–2000 mm. To the north are temperate areas with sub-humid and semi-arid moisture conditions, and their annual mean precipitation is only between 400

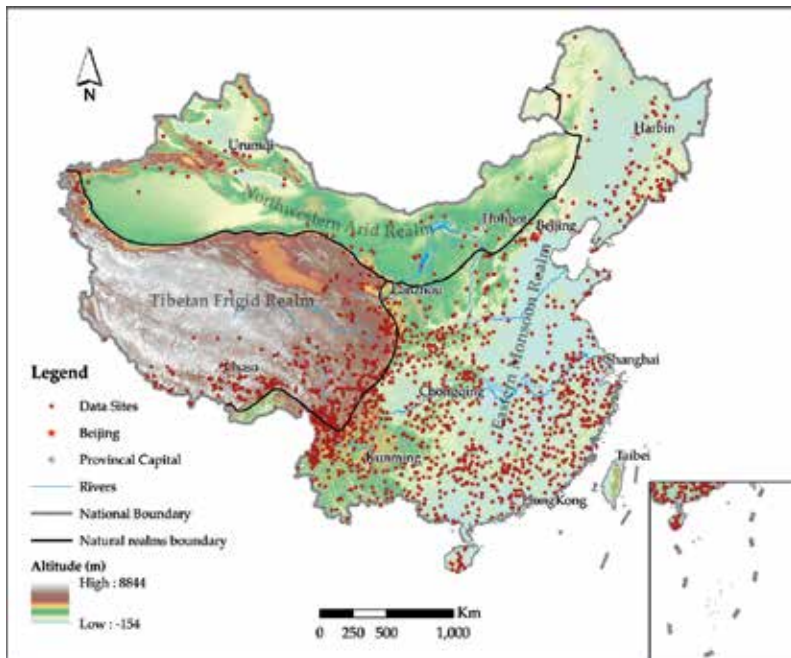


Figure 2. Conifer species occurrence in mainland China (data downloaded from gbif.org).

and 600 mm and slightly higher in the northeast and in the upper parts of mountains. The northwest arid China features the alternativeness of high mountain ranges and desert basins or the mountain-basin systems, with an annual precipitation usually between 50 and 200 mm, but much higher (>500 mm) in its high mountains. The Tibetan frigid realm is characterized by high elevation of averagely 4500 m above sea level (a.s.l.) and alpine climate, and it shows great variation in moisture from southeast to northwest, namely, from humid to extremely arid conditions. This pattern was ever referred to as “Tibetan Zonation,” a spatial dry-wet pattern just like that of China as a whole.

Thanks to extensiveness and numerous towering mountains, China shows not only sharp and complex areal differentiation but also outstanding altitudinal zonation in large mountains. In other words, zonal and azonal factors interplay to give rise to highly heterogeneous and varied habitats, landscapes and vegetation types. In the east, climate types transit in succession from cold temperate, temperate, and warm temperate in the north to subtropical and tropical climate in the south. From southeast to northwest, forest, forest-steppe, steppe and desert appear in succession. The frigid Tibetan Plateau shows, from southeast to northwest, an alternation of montane forest, alpine meadow, alpine steppe and alpine desert. In the northern flank of the long-stretching Tianshan Mts., such altitudinal belts could be clearly identified, from the bottom, montane desert, montane steppe, montane coniferous forests, alpine meadow, sub-nival and nival belts. In Mt. Namjag Barwa of East Himalayas, nine altitudinal belts can be recognized from tropical rainforest at the bottom upward to the nival belt at the uppermost part. In addition, the mass elevation effect leads to much higher air

temperature in the interior of the Tibetan Plateau than the free air on the same elevation above the lowlands around the plateau [1]. As a result, conifer forests could grow at elevations of up to 4800–6900 m a.s.l. in the southeastern Tibetan Plateau [2], that is, the globally highest forest, at least 1000 m higher than even in the southern flank of the Himalayas.

Thanks to large area, heterogeneous habitats and long history of biological evolution, China boasts of extremely high biodiversity (more than 30,000 species of seed plants), only next to Malaysia (45,000) and Brazil (40,000). As for the diversity of pteridophytes, China ranks No. 1, about 52 families, 204 genera, 2600 species. Gymnosperm has totally 13 families worldwide, of which only *Araucariaceae* and *Sciadopitys* are missing and other 11 families can all be recognized in China, including 42 genera and 323 species [3–5].

China's conifers amount to 244 species, occupying 66.67% of the total in the world. So, China has an outstanding position in global conifer diversity and protection. As for China itself, conifers have widespread distribution, especially up to surprising 4800–4900 m a.s.l. and are absolutely significant for its biodiversity conservation and ecological security.

The objectives of this chapter are to generalize conifer species, China-specific conifers and their three-dimensional distribution, to explain their distribution patterns, and to show China's effort in protecting its conifer diversity and resources. We first give a statistics of conifer family, genus and species in China, including those endemic to China, and briefly show their geographic distribution; then we display their characteristics in different temperature zones; next, we especially analyze the altitudinal pattern of conifers in China mainly by taking "mass elevation effect" into account; finally, we show what China has done to protect its diverse and precious conifer resources.

2. Conifers and endemics in China

2.1. Conifers in China

In terms of Christenhusz's taxonomy [3–5], China has 244 species of conifers (including subspecies, varieties and forms) belonging to 32 genera in 4 families (*Pinaceae*, *Cupressaceae*, *Podocarpaceae* and *Taxaceae*), accounting for 38.37, 49.29 and 66.67% of the global totals, respectively. The largest conifer family in China is *Pinaceae*, including 137 native species (56.14% of China's total) with 73 species endemic to China (63.47% of China's endemic conifer species) (Table 1).

2.2. Geographical distribution of conifers

Conifers are quite unevenly distributed in China. Their diversity is relatively low in Northeast China and high in Southwest. This distribution pattern is caused by many factors, including geologic histories, biotic histories and evolution, contemporary environments, and so on [6]. The major genera of conifers take on such geographical patterns as follows:

Pinaceae consists of 11 genera widespread in China, with the Himalayas-Hengduan mountain region as the center of distribution and differentiation. Comparatively, *Pinus*, *Picea* and *Abies*

Family name	Genera	Endemic genera	Species	Endemic species
<i>Pinaceae</i>	11	3	137	73
<i>Cupressaceae</i>	14	4	61	25
<i>Taxaceae</i>	5	1	28	12
<i>Podocarpaceae</i>	2	0	18	5
Sum	32	8	244	115

Table 1. Number of conifer genera and species in China.

are almost throughout the country; *Larix* is mainly in the northernmost, up to north latitude of 72–75°; *Pseudotsuga* and *Tsuga* are mainly distributed in the subtropical or tropical mountains in the Himalayas and south of the Qinling Mountains [7, 8].

Cupressaceae contains 15 genera in China, mostly occurring in the Hengduan Mountains of the eastern Qinghai-Tibet Plateau but scattered in the Northeast and Northwest of China. *Juniperus* has the largest number of species (33) in this family and more than half of these species are distributed in the Hengduan Mountains, Yunnan-Guizhou Plateau and the eastern Qinghai-Tibet Plateau [9].

Taxaceae includes five genera in China. *Cephalotaxus* is widely distributed in southeastern Tibet, Hainan and Taiwan. *Taxus cuspidata* is only seen in northeastern China. Other species of *Taxus* are found between the Qinling Mountains and the Pearl River, in eastern Taiwan and in western Tibet. *Torreya* trees are scattered in coniferous and broad-leaved forests in southern China. *Amentotaxus* can be found south of the Qinling Mountains, expanding from Taiwan westwards to southeastern Tibet and southeastern Yunnan [10].

Podocarpaceae has only two genera in China, with *Dacrydium* mainly distributed in Hainan Island and *Podocarpus* south of the Yangtze River and east of the Hengduan Mountains [10].

2.3. Conifers endemic to China

There are totally eight conifer genera endemic to China, and seven of which are monotypic genera except *Cunninghamia* [11]. *Pinaceae* contains three endemic genera, *Cathaya*, *Nothotsuga* and *Pseudolarix*. *Cupressaceae* contains four endemic genera, *Cunninghamia*, *Glyptostrobus*, *Metasequoia* and *Taiwania*. *Pseudotaxus* is the only endemic genus in *Taxaceae*. There are totally 115 conifer species endemic to China belonging to 23 genera of 4 families (Table 2). *Pinaceae* and *Cupressaceae* rank the top two families in terms of the number of endemic species, making up 63.47 and 21.73% of all endemic species, respectively.

2.4. Geographical distribution of conifer endemic genus

The complexity and diversity of regional climate and landform could affect directly or indirectly the speciation, differentiation, migration of Chinese endemic conifers [12]. Known for highly topographic heterogeneity, southwestern China is the hotspot of endemic conifers [11, 13]. The general distribution of endemic genera of conifers in China is as follows:

Family	Genus	Endemic species	Family	Genus	Endemic species
Pinaceae	<i>Pseudotsuga</i>	4(5)	Cupressaceae	<i>Cupressus</i>	5(6)
	<i>Keteleeria</i>	7(10)		<i>Chamaecyparis</i>	2(3)
	<i>Abies</i>	18(26)		<i>Juniperus</i>	12(33)
	<i>Larix</i>	7(11)		<i>Thuja</i>	1(2)
	<i>Pinus</i>	15(43)		<i>Glyptostrobus*</i>	1(1)
	<i>Tsuga</i>	5(8)		<i>Taiwania*</i>	1(1)
	<i>Picea</i>	14(26)		<i>Metasequoia*</i>	1(1)
	<i>Pseudolarix*</i>	1(1)		<i>Cunninghamia*</i>	2(2)
	<i>Cathaya*</i>	1(1)		Taxaceae	<i>Torreya</i>
<i>Nothotsuga*</i>	1(1)	<i>Cephalotaxus</i>	5(10)		
Podocarpaceae	<i>Podocarpus</i>	5(16)	<i>Amentotaxus</i>		2(4)
			<i>Pseudotaxus*</i>	1(1)	

Notes: genera with asterisk (*) are endemic to China; numbers in brackets mean the species number of each genus. Genera without species endemic to China are not shown in this table.

Table 2. Number of endemic conifers for each genus in China.

2.4.1. *Cathaya*

Cathaya, with only one species of *Cathaya argyrophylla*, is discontinuously distributed in southeastern Sichuan Basin, eastern Yunnan-Guizhou Plateau, and northeastern Nanling Mountains, usually between 900 and 1900 m a.s.l. Mostly seen on steep cliffs or in gaps of bare rocks, this species grows in communities or as mixed forests with *Quercus engleriana* and *Cyclobalanopsis glauca* [5, 9, 10, 14].

2.4.2. *Nothotsuga*

Nothotsuga is a monotypic genus (*Nothotsuga longibracteata*), usually growing in subtropical mountains with a warm, humid, cloudy and foggy climate, for example, in the Fanjing Mountains of Guizhou province, the Mang Mountains of Hunan province, and the Nanling and Wuyi Mountains of Fujian province. It appears on elevations between 400 and 2000 m a.s.l., and is mixed with *Tsuga chinensis* var. *tchekiangensis*, *Fokienia hodginsii* and other evergreen broad-leaved trees [5, 9, 10].

2.4.3. *Pseudolarix*

Pseudolarix, also a monotypic genus (*Pseudolarix amabilis*), is an ancient relic species. It ever grew in northern China between latitudes of 33°N and 52°N, but nowadays only appears on warm and rainy mountains in the warm regions of the middle and lower reaches of the Yangtze River. Its upper limit is 1500 m a.s.l., and it could be seen in coniferous or broad-leaved forests [5, 9, 10].

2.4.4. *Cunninghamia*

Cunninghamia contains two species. *Cunninghamia lanceolate* grows south of the Qinling Mountains, especially in the deep valleys of southwestern China. In the Dabie Mountains in the middle of China, it occurs only to 700 m a.s.l., but up to 1800 m a.s.l. in Mt. Emei of Sichuan Province. *Cunninghamia konishii* appears in central and northern Taiwan, taking on patches of pure forest or being scattered in *Chamaecyparis obtusa* forests [5, 9, 10, 15].

2.4.5. *Glyptostrobus*

Glyptostrobus has only one species of *Glyptostrobus pensilis*. It adapts to warm and humid environment below 1000 m in subtropical low mountains, appearing in a wide extent from Taiwan in the east to Yunnan province in the west and northwards to Shandong province [5, 9, 10].

2.4.6. *Metasequoia*

Metasequoia has also only one species of *Metasequoia glyptostroboides*. It is a relict species with strong adaptability, appearing in mountainous areas of moderate warm temperature, rainy climate and acidic yellow soil, with a very limited geographic distribution mainly in southwestern Hubei and little in Chongqing and Hunan [5, 9, 10].

2.4.7. *Taiwania*

Taiwania contains one species of *Taiwania cryptomerioides* Hayata. It grows in a cool and humid climate with fertile acidic soil, mainly in Taiwan and southwestern Asia, for example, the Gaoligong Mountains in northwestern Yunnan and the mountains in southeast Guizhou. Vertically, it is distributed in evergreen broad-leaved forests at an elevation of 1600–2800 m a.s.l [5, 9, 10, 16].

2.4.8. *Pseudotaxus*

Pseudotaxus is a monotypic genus, that is, *Pseudotaxus chienii*. Its distribution areas extend along the Nanling range, from southern Zhejiang in the east, to northern Guangxi in the west. It usually appears in subtropical evergreen broad-leaved forests at an altitude of 500–1500 m a.s.l [5, 9, 10].

3. Areal distribution of conifers in China

3.1. The spatial distribution of conifers in China

Conifers and coniferous forests are rather diverse and complex in China due to its vast and mountainous territory. They show quite different in different climatic zones. The cold-temperate coniferous deciduous mixed forest is composed of eight or more formations in China; the dark coniferous forest, mainly Spruce and Fir trees, has more than 26 common formations; while *Pinus*-dominant formations amount to 13 and could develop in several climatic zones.

Based on the vegetation map of China and its geographic pattern (1:1,000,000) [17], the spatial distributions of conifers in China were divided into five vegetation types as follows:

3.1.1. Cold-temperate and temperate mountain conifer forests

The main species are *Larix*, *Abies* and *Picea* for the cold-temperate and temperate conifer forests of China, with 17 plant communities including *Larix gmelinii*, *Pinus sibirica*, and *Abies nephrolepis* forest. Its distribution areas extend from 53°33'N southward to the Qinling Mountains and the Dadu River in Sichuan, from the Changbai Mountains westward to the Tianshan Mountains, with the highest distribution at 4000 m a.s.l. They are mainly concentrated in mountains of Northeast China (Greater Khingan Mountains, Zhangguangcai Range, Changbai Mountains, etc.), of North China (Mt. Wulingshan, Mt. Wutai, Yanshan Mountains, Mt. Guandishan, Mt. Hengshan, etc.), and of Xinjiang and Inner Mongolia (Altay Mountains, Tianshan Mountains, Qilian Mountains, Helan Mountains and Yinshan Mountains), and in the Qinling- Daba Mountains of central China [10, 17].

3.1.2. Temperate conifer forests

Temperate coniferous forests are mainly distributed in the plain, hill or low mountain areas of the warm temperate zone in China, including the middle and lower reaches of the Yellow River and the Southern Xinjiang, roughly between the Yinshan Mountains in the north and the Qinling-Daba mountains in the south. The constructive species are *Pinus* and *Platycladus*, and the main communities *Pinus tabulaeformis*, *Pinus densiflora* and *Platycladus orientalis* forests. *Akamatsu* appears in the offshore of Shandong Peninsula, and *Pinus tabulaeformis* in the Qinling-Daba Mountains. *Platycladus orientalis* and *Juniperus* forests could extend up to an elevation of 2500 m in the mountains of the northwest arid China [10, 17].

3.1.3. Subtropical conifer forests

The subtropical coniferous forest can be subdivided into deciduous-coniferous mixed forest and evergreen-coniferous mixed forest according to their life forms. In the deciduous-coniferous mixed forest are mainly *Metasequoia glyptostroboides*, *Glyptostrobus pensilis*, *Pseudolarix kaempferi*, *Taxodium distichum* and *Taxodium ascendens*, occurring south of the Qinling Mountains. This type of forests is seldom in purely natural state. The evergreen-coniferous forest is widely distributed in subtropical and tropical regions of China, with dominant component of *Pinus*, *Picea*, and *Cupressus* and with such main communities of *Pinus massoniana*, *Cunninghamia lanceolata* and *Cupressus funebris*. Subtropical evergreen conifer forests are normally distributed below 1500 m in the eastern China and up to 2000–3000 m in the western subtropical areas [10, 17].

3.1.4. Tropical conifer forests

Tropical conifer forest is mainly distributed in the tropical flat ground, hills and low mountains in China, with a limited area in Hainan, southern Guangdong and southeastern Guangxi. *Pinus latteri* and *P. roxburghii* are the main species. *Pinus latteri* appears up to

600 m, at most to 800 m, in mountains, and only to 200 m in hills. *P. roxburghii* only occurs between 1800 and 2300 m in the Gyirong Basin of southeastern Tibetan Plateau [10, 17].

3.1.5. Subtropical and tropical mountain conifer forests

Distributed in relatively high mountainous areas south of the Qinling Mountains, generally from 1000 to 4500 m, tropical and subtropical mountain conifer forests include species of *Pinaceae*, *Taxodiaceae*, and *Cupressaceae* and about 30 types of communities such as *Pinus griffithii*, *Larix chinensis*, *Tsuga dumosa*, and so on [10, 17].

3.2. Main spatial limits for conifer distribution

Fourteen typical conifer associations from five vegetation types were selected to specify conifer spatial distribution limits. Associations 1–4 are from cold-temperate and temperate mountain conifer forests, association 5 from temperate conifer forests, associations 6–9 from subtropical conifer forests, association 10 from tropical conifer forests, and the other four (11–14) from subtropical and tropical mountain conifer forests [10, 17].

3.2.1. *Larix gmelinii* forest

The *Larix gmelinii* forest, mainly distributed in the Greater Khingan Mountains, is the largest larch forest in Northeast China and even in China. It is actually the southward continuation of bright coniferous forests in Eastern Siberia in Russia. It is zonal vegetation north of Yakeshi, Heilongjiang Province (49°20'N), but southward it turns into vertical zonal vegetation along the Greater Khingan Mountains. Further southward, it forms a transition zone with *Larix principis*, mixed with small patches of *Larix olgensis* and *Hailin larch* forest. *Larix gmelinii* forest also appears in the low-wetland as azonal vegetation between the Greater Khingan Mountains and the Lesser Khingan ridge. Further southward through Wandashan to Zhangguangcai mountains, near the Laoyeling Mountains (about 42°30'N), it forms a transitional zone with *Larix olgensis* and then is completely replaced by *Larix olgensis* forest. It is generally below 1200 m in the northern slope and below 1400 and 1550 m in the south slope of the Greater Khingan Mountains.

3.2.2. *Larix olgensis* var. *changpaiensis* forest

Larix olgensis var. *changpaiensis* is endemic to China and mainly appears in the Changbai Mountains in Jilin province, usually as stable pure forest. Just as *Spruce* and *Abies* in subalpine zone, it adapts to cold and humid climate and could also grow in low swamps or swampy areas where other tree species are difficult to grow.

3.2.3. *Pinus sibirica* forest

The *Pinus sibirica* forest is only distributed in the northwesternmost corner of Xinjiang which is virtually the southernmost limit of natural *Pinus sibirica* forest. As a cold-resistant continental species, it often appears at the upper parts and even upper limit of forest belts.

3.2.4. *Picea schrenkiana* forest

Picea schrenkiana is one of the most widespread forest species in the mountains of desert zones in Asia. In China, it appears in the northern flanks of the Tianshan and Western Kunlun and in the Western Junggar Basin. Usually as one-species pure forest, it appears on shadow slopes at elevations between 1600 and 2800 m in the northern flank of the Tianshan Mountains and 2500–3600 m in some valleys of the northern flank of West Kunlun.

3.2.5. *Pinus tabulaeformis* forest

Pinus tabulaeformis is endemic to China, widely distributed in the mountains of the warm temperate region in north China, namely, from the Yinshan Mountains southward to the Qinling Mountains. In the Qinling Mountains, it appears between 1400 and 2000 m. Further southward, it is replaced by *Pinus massoniana* forest.

3.2.6. *Pinus massoniana* forest

The *Pinus massoniana* forest is the largest and most widely distributed conifer community in subtropical China. Its distribution extends from the Qinling Mountains in the north to the Leizhou Peninsula in the south. It meets *Pinus yunnanensis* forest in its westernmost areas and tropical *Pinus latteri* forest in its southernmost distribution area. It can also be found in central Taiwan. It grows usually below 1000 m or even 800 m a.s.l.; further upward, it is replaced by *Pinus tabulaeformis*, *Pinus henryi* and *Pinus armandii* forests.

3.2.7. *Pinus yunnanensis* forest

Pinus yunnanensis is a common and important conifer species in the Yunnan-Guizhou Plateau. It is also a typical representative community of the western dry subtropics. Its distribution extends to Guangxi province and Tibetan Plateau. Mostly distributed between 1500 and 2800 m a.s.l., it can lower to about 1000 m and ascend to 3500 m. In the middle-south Yunnan Plateau, it is replaced by *Pinus khasya* forest.

3.2.8. *Pinus taiwanensis* forest

The *Pinus taiwanensis* forests are one of the representative communities in the subtropical mountains of east China. Mainly distributed in the subtropical mountains of Taiwan, Fujian, Zhejiang, Jiangxi, Anhui, Hunan and Hubei provinces, they especially can be met in the northern and southern flanks of the Dabie Mountains. Their most suitable distribution area is within 400 km off the coastline. Vertically, they occur on elevations above 600 and 800 m, at most up to 1750 m.

3.2.9. *Pinus armandii* forest

Pinus armandii constitutes a typical mountainous coniferous forest in the western subtropics of China. It is mainly distributed in Sichuan, Yunnan, Guizhou provinces and the Qinling-Daba Mountains. Its altitudinal distribution shows a trend of northward lowering, for example,

about 2500–3000 m in southwestern Sichuan and northwestern Yunnan, 2000–2500 m in western Guizhou, 1500–2400 m in the Qinling-Daba Mountains, and 1000–2200 m in the warm temperate zone.

3.2.10. *Pinus latteri* forest

This type of forest is a typical community in tropics. Mainly distributed in southern Guangdong, Hainan and southeastern Guangxi, its altitudinal range is normally below 600 m (800 m) a.s.l. in mountains, and even below 200 m in hills.

3.2.11. *Larix chinensis* forest

Larix chinensis forests are mainly distributed in the Qinling Mountains, especially in Mt. Taibai. Vertically, it is above the *Abies* forest and below alpine shrub-meadow, basically at elevations between 3100 and 3500/3600 m, and serves as treeline species in its distribution areas.

3.2.12. *Larix potaninii* forest

Larix potaninii is the main component of deciduous-coniferous forests in northwestern Sichuan, the Three-parallel-rivers areas, Tibetan Plateau, and the Taohe basin of Gansu province, roughly north of 30° north latitude. It appears on elevations of 3700–4200 m in west Sichuan and the southeastern Tibetan Plateau (down to 3000 m in some river valleys), and 2900–3300 m in the Taohe river basin of Gansu province.

3.2.13. *Abies fargesii* forest

The *Abies fargesii* forest is mainly distributed in the whole Qinling-Daba Mountains in central China. It is a special community of *Abies* in the subtropical mountains, with a relatively low elevation, normally between 2500 and 3000 m in central Qinling Mountains of Shaanxi province, at 2700–3052 m in Shennongjia of northwest Hubei province, at 2400–3600 m in Minshan, Micangshan and Dabashan of Sichuan Province, and at 1800–2100 m in the Funiu Mountain of Henan province. This indicates an increasing trend of its altitudinal distribution from northeast to southwest.

3.2.14. *Abies spectabilis* forest

The *Abies spectabilis* forests appear in the eastern and central Himalayas. In China, they are mainly distributed in Bomi, Nyingchi, Medog, Milin, Cuona, Yadong, Nyalam, and Gyirong of southeastern Tibet. Their altitudinal range is from 3400 (3200) to 4100 (4500) m.

4. Altitudinal distribution of conifers in mountains of China

China is the largest mountain country of the world, with about 70% of its land area being mountains or plateaus. Thanks to their extremely complex and varied environment, mountains usually provide quite diverse habitats for territorial plant species and, as a result, serve

as hotspots of biodiversity and endemic species [18]. Floras in mountains are relatively less disturbed by human activities in China, as in other countries. China's primary conifer forests are mainly distributed in mountains, and their altitudinal distribution is an important dimension to fully understand conifers of China. The following sections explore the conifer distribution pattern along elevation and its possible influencing factors by taking "mass elevation effect" into account.

4.1. Conifer species richness along elevation

Conifer records in mainland China (**Figure 2**) were downloaded from GBIF [19] using the *dismo* [20] package in R. After removing duplicate data and excluding data without position coordinates or scientific names, a total of 3158 records are used to analyze their altitudinal distributions (**Figure 3**). These records involve 215 species belonging to 34 genera in four families (*Cupressaceae*, *Pinaceae*, *Podocarpaceae*, *Taxaceae*). This type of data for mainland China from GBIF is less than the existing relevant data in China.

The elevational range of conifer species is from 0 to 4900 m, and 50 m is taken as an interval to acquire data of species numbers; and 98 elevational sections were divided to count species richness at each interval. The results are shown in **Figure 3(a, c)**. Species diversity decreases monotonically upwards, with a fluctuating rate. The diversity decreases fast below 1300 m a.s.l., remains roughly stable from 1300 to 3300 m a.s.l., and decreases relatively slowly above 3300 m a.s.l. Conifers of different families show varied altitudinal diversity patterns. The species diversity curve has a bulge between 2000 and 3500 m for *Pinaceae*, but the species diversity decreases continuously upwards for *Cupressaceae*, *Podocarpaceae* and *Taxaceae*, at varied rates.

Cupressaceae has the broadest altitudinal distribution, from 0 to 4900 m a.s.l. Its richness is relatively steady and small below 3000 m a.s.l., whereas a surge in richness occurred on the elevation of about 3000 m, and its richness occupies three quarters of the total at treeline ecotone. *Pinaceae* has a similar vertical range as *Cupressaceae*, making up about 20% of the total richness from 1800 to 4900 m a.s.l., and reaching the highest proportion at elevations between 2500 and 3500 m. *Podocarpaceae* has the narrowest vertical distribution, mainly below 2000 m. It accounts for about half of the total diversity below 200 m, but its relative contribution decreases upwards as *Taxaceae*'s and *Pinaceae*'s richness increases. *Taxaceae* contributes more than a quarter of the total species richness between 800 and 3000 m; yet, its contribution declines below and above these elevations.

4.2. Altitudinal distribution of conifer families

Conifers have different highest distribution elevations along latitude (**Figure 4**), achieving the highest roughly at 30° north latitude. *Pinaceae* can grow up to 4700 m at 28° north latitude, with *Abies* at the highest elevation. *Juniperus* of *Cupressaceae* appears even at 4900 m a.s.l., the highest treeline position, at approximately 30° north latitude. *Podocarpus* of *Podocarpaceae* can be up to 4000 m a.s.l. at 25° north latitude, but *Taxus* of *Taxaceae* to its highest elevation of only 2000 m a.s.l. at 28° north latitude.

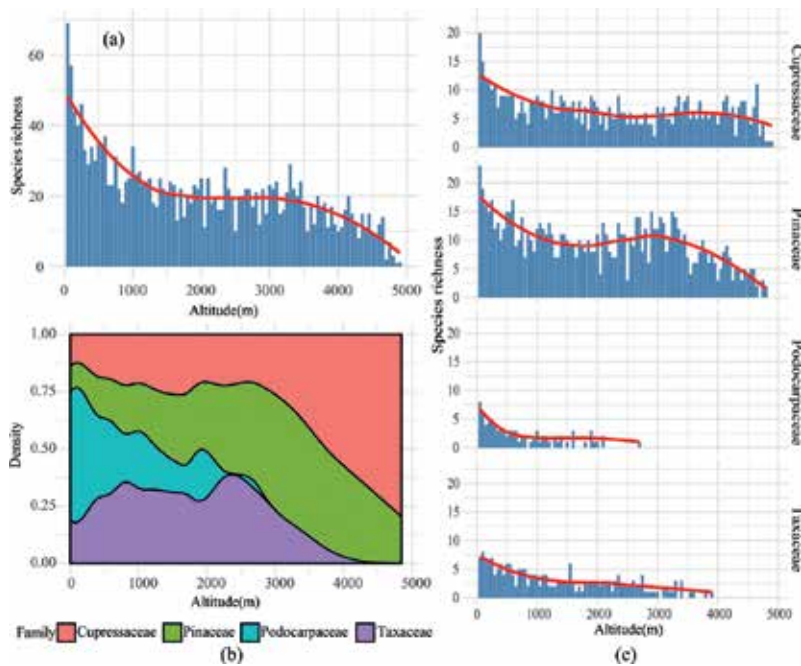


Figure 3. Species richness along elevation in mainland China. (a) The overall distribution pattern of conifers along elevation; (b) the percentage of different conifer families along elevation; (c) distribution pattern of four conifer families along elevation.

Figure 5 demonstrates that the four families all reach their highest distribution at around 100° eastern longitude. *Podocarpaceae* and *Taxaceae* appear only east of 95° east longitude; while *Pinaceae* and *Cupressaceae* are widespread with their highest distribution between 90 and 100° east longitudes.

4.3. Conifers in treeline ecotone

As is well known, leaves get smaller with increased elevation as a mean of adaptation to harsher environment. In other words, needle-leaved plants are comparatively more competitive than any other woody plants in treeline ecotone; so, treeline-forming species are almost all conifers [21, 22]. In China, at treeline ecotones are mainly *Pinaceae* and *Cupressaceae* [22]. In the eastern monsoon realm (**Figure 2**), *Larix*, *Picea* and *Abies* of *Pinaceae* constitute the main species of the upper treelines. In the north of the realm, *Larix*, such as *Larix gmelinii*, occurs in the Greater Khingan Mountains, *Larix principis-rupprechtii* in Mt. Wutai and the Taihang mountains, *Larix chinensis* on Taibai Mts. in the middle of the Qinling range; westwards from Taibai Mts. appears *Larix potaninii*. In the south of the realm, *Abies* of *Pinaceae* is the main treeline species in the Jade Mountains of Taiwan. In the northwestern arid realm of China, *Picea schrenkiana* forms the upper treeline species in the Tianshan, *Picea crassifolia* in the Qilian Mountain, and *Larix sibirica* in the Altay Mountains. In the Tibetan Frigid realm, all upper treelines are characterized by *Juniperus*, with *Juniperus tibetica* at the world-highest treeline site (4900 m) in the southeastern Tibetan Plateau [2].

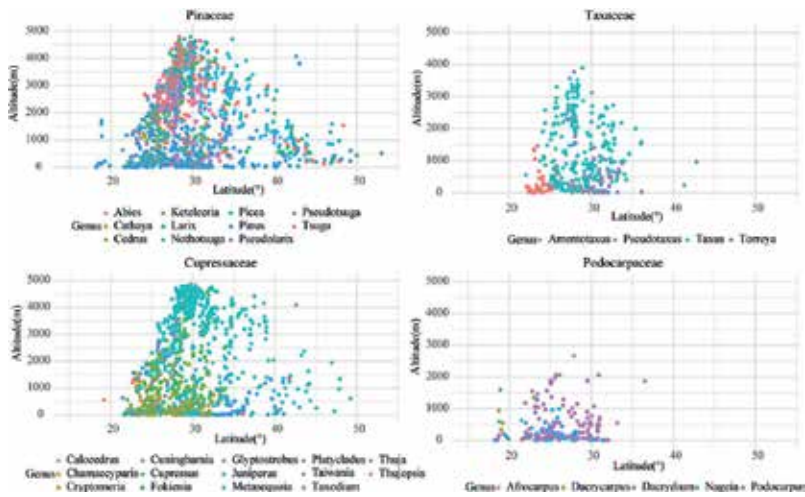


Figure 4. Altitudinal distribution of conifer families along latitude in China.

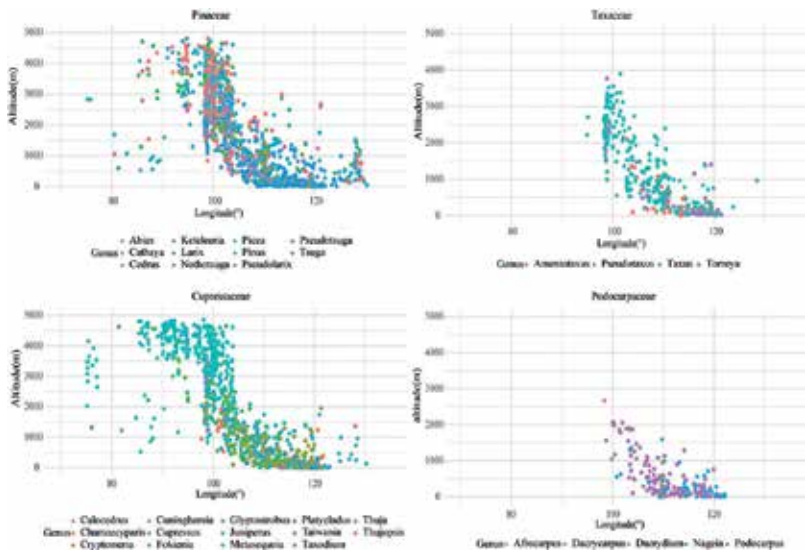


Figure 5. Altitudinal distribution of conifer families along longitude in China.

4.4. Mass elevation effect and the altitudinal distribution of conifer treelines

Mass elevation effect (MEE) is one of the most significant factors influencing the altitudinal distribution of treelines [23]. It is virtually the results of the thermodynamic effect of mountain masses or the heating effect of mountain massifs [24], leading to higher temperature in the interior than in the outside of mountain masses on the same elevations at similar latitudes. MEE is most prominent in the lofty and immense Tibetan Plateau (averagely 4500 m). Its magnitude is closely related with MEE intra-mountain base elevation (IMBE), and it can be quantified by developing a ternary linear regression model with IMBE, latitude and continentality as independent variables. It has been shown that IMBE, latitude and continentality

could together explain 92% of global treeline elevation variability, with IMBE contributing the most of 52.2% to the altitudinal distribution of global treelines [23]. Thanks to MEE, the 10°C isotherm for the warmest month and the warmth index of 15°C month, which roughly coincide with alpine treelines, are as high as 4600–4700 m a.s.l. in the southeastern Tibet Plateau [1], more than 1000 m higher than in surrounding lowland areas.

We collected 364 treeline sites of China from the dataset [23] to explore the contribution of MEE to the distribution of conifer treelines by developing a regression model with treeline elevation as the dependent variable and the other three variables (latitude, continentality and base elevation) as independent variables. The multiple regression model is as follows:

$$TL(m) = a \times Lat + b \times K + c \times BaseAlt + d \quad (1)$$

where TL is treeline elevation, Lat latitude, $BaseAlt$ Base altitude, K continentality; a , b and c are coefficients of independent variables, d is constant term.

Continentality is calculated based on Gorczynski's formulas [25]:

$$K = 1.7 \times A / \sin \phi - 20.4 \quad (2)$$

where K is continentality, ϕ latitude, and A the difference of mean temperature of the warmest and coldest months. Monthly mean temperature data were extracted from interpolated climate surfaces at a spatial resolution of 30 arcs (equivalent to 860 m) provided by the WorldClim database [26].

The regression is analyzed by using R, and the results are shown in **Table 3**.

The regression model is as follows:

$$TL(m) = -24.77 \times Lat - 30.95 \times K + 0.54 \times BaseAlt + 4783.76 \quad (R^2 = 0.7843, p < 0.001) \quad (3)$$

Variance inflation factor (VIF) is used to detect multicollinearity of the three variables, and the results showed low multicollinearity (**Table 3**). To analyze the prediction accuracy of the multiple regression model, Shapiro-Wilk normality test of standardized residual was performed. The result shows that $W = 0.9953$ and $p\text{-value} = 0.3141 > 0.05$, proving the correctness of the regression model.

The contribution rate of base altitude is as high as 49.81%, showing that MEE contributes the most to the altitudinal distribution of conifers in China. Continentality and latitude are the second and the third influential factors with contribution rates of 33.28 and 16.90%, respectively. The contribution rate of base elevation we calculated is very close to the results by Zhao et al. [23] (52.2% for global scale and 50.4% for north hemisphere).

4.5. Conifer elfin forest in China

Conifer elfin forests develop under very severe environmental conditions, usually at the uppermost sections of treeline ecotones or pseudo-treelines with cold or harsh habitats. Most of conifer elfin forests are formed mainly by *Pinus pumila* in China [27]. *Juniperus* is another

variables	C1	C2	CR (%)	t value	p value
(Intercept)	4783.76	—		29.54	<0.001
Base altitude	0.54	0.51	49.81	17.82	<0.001
Latitude	-24.77	-0.17	16.9	-3.33	<0.001
continentality	-30.95	-0.34	33.28	-6.12	<0.001

Notes: C1 and C2 refer to Unstandardized Regression coefficients and Standardized Regression coefficients, respectively; CR is Contribution rate, is the respective proportion of absolute C2 to their absolute sum.

Table 3. Multiple linear regression model of treeline sites.

main component of elfin forests, such as *Juniperus squamata* scattered above the *Abies* treeline of the Jade Mountains, which can be compared with the *Abies*-formed treelines in the Tibetan Plateau, indicating the difference of dominant species between them.

5. Conifer protection in China

5.1. Evaluation and directory of endangered species

In the 1980s, Chinese government introduced the criteria of conservation status developed by the International Union for the Conservation of Nature (IUCN) to evaluate the situation of endangered native species. The National Environmental Protection Bureau of the PRC¹ and the Chinese Academy of Sciences jointly published the *List of Rare and Endangered Species in China* in 1987, which evaluated 388 endangered species including 65 species of coniferous trees in terms of IUCN's grades of endangered species (endangered, rare and vulnerable) [28]. In 1991, *China Plant Red Data Book* (vol. 1) was published to expound in detail the characteristics and endangerment causes of all listed species [29]. In 1999, the State Council issued the *List of National Protected Wild Plants* (vol. 1), covering a total of 285 species and 51 conifer species. Its second volume, already under discussion, will include further 1615 species.

The Ministry of Environmental Protection released the *Red List of Biodiversity in China* in 2013, which evaluated the endangerment level of almost all wild higher plants in China. The list involves 202 species of conifers, of which 109 are endemic to China; a total of 16 species are critically endangered (CR), half of which are the *Pinaceae*; 29 species are endangered (EN), 10 near threatened (NT), 56 vulnerable (VU). In addition, some national protected species of class I are still in critical condition, such as *Abies beshanzenensis*, *Abies yuanbaoshanensis* and *Pinus squamata*, most of which are still endangered, such as *Cathaya argyrophylla*, *Abies fanjingshanensis*, *Taxus fauna*, and so on, and the rest are vulnerable. However, among the 45 conifer species in CR and EN, 9 in CR and 13 in EN are still not in the national protected list. To further

¹The National Environmental Protection Bureau of the PRC (1984–1998) was predecessor of Ministry of Environmental Protection (2008–2018), and now the Ministry of Ecology and Environment.

strengthen species protection, the government launched the Rescue and Protection Program for Plant Species with Extremely Small Populations (PSESP), and carried out a 5-year rescue for 120 species, including 14 conifer species, mostly in CR or EN.

5.2. Conifer protection

5.2.1. On-site conservation

China has established a large number of protected areas to conserve its high biodiversity, especially its all rare or endangered species, including nature reserves, forest parks, national parks, scenic areas and geo-parks. By 2015, nature reserves of different levels amount to 2740 in mainland China, covering an area of about 1.4659 million km², about 15.31% of the total land area. A total of 256 nature reserves involves the protection of conifers and covers an area of 47,200 km², 64 (about 1/4) are at the national level and occupy 50.25% of the total area. Geographically, conifer-related nature reserves cover almost all China's provinces. Heilongjiang province in Northeast China possess the most (23), followed by Hunan (22) in the middle south, Guizhou (22) and Yunnan (20) in the southwest (**Figure 6**).

5.2.2. Off-site conservation

The introduction and cultivation of rare and endangered species in botanical gardens and their specialized gardens (areas) are considered an effective method of species conservation, a supplement to on-site conservation. China has developed 164 botanical gardens, about one-fifth of the global total, to nurture about 20,000 species, some 60% of its whole flora [30]. Approximately half of conifer taxonomy in China are rare species and need off-site conservation. The repeated cultivation of species in different botanical gardens can effectively reduce the transmission of pests and diseases caused by larger populations [31]. China's main six botanical gardens (South China Botanical Garden, Wuhan Botanical Garden, Beijing Botanical Garden, Nanjing Botanical Garden, Guilin Botanical Garden and Lushan Botanical Garden) have covered almost all rare conifer species, especially *Taxus chinensis*, *Cathaya argyrophylla*, *Pinus kwangtungensis*, *Pseudotsuga chienii*, and so on [30, 32].

5.3. Laws and regulations

In order to protect forest ecosystems including conifers, China has promulgated and implemented Environmental Protection Law, Forest Law, Grassland Law, Nature Reserve Regulations, Regulations on the Protection of Wild Plants and so on, which have formed a relatively comprehensive legal system. The State Council issued in May 1987 the Chinese Program for Natural Protection, the first macro guidance document for protecting natural resources and environment in China [33]. In December 1993, China became the member of the State Parties of the Convention on Biological Diversity (CBD). The government even formulated and implemented the "China Action Plan for Biodiversity Conservation", "Outline of National Ecological Environment Protection Plan", "National Plan for the Protection and Utilization of Biological Species Resources", and has organized a series of key plant protection projects [34].

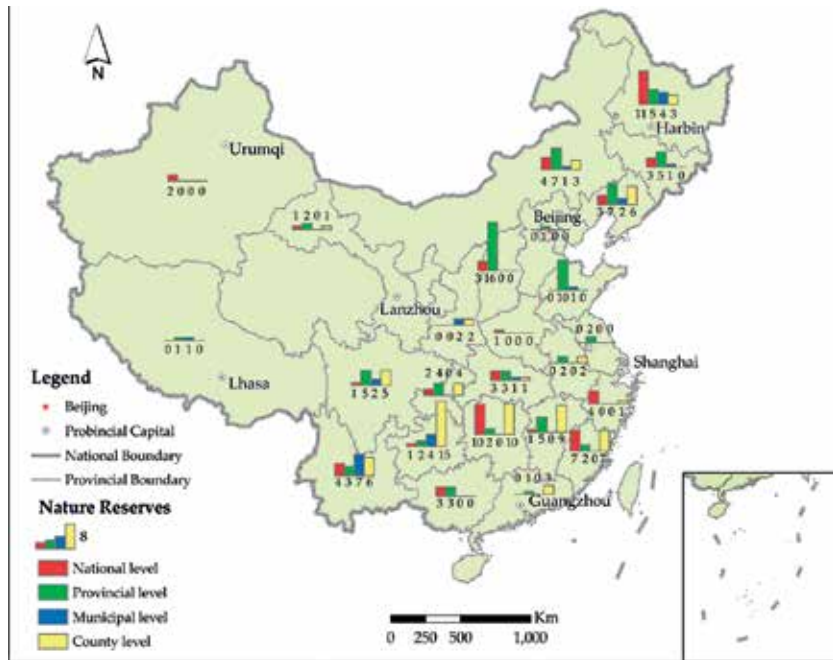


Figure 6. Number and distribution of conifer-related nature reserves in mainland China.

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Why Forest Plantations Are Disputed? An Assessment of Locally Important Ecosystem Services from the *Cryptomeria japonica* Plantations in the Darjeeling Hills, India

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Abstract

This study explored locally important forest products generated from different plantation forests. A comparison was made between monoculture and mixed stands in terms of understory plant species richness and number of forest products collected by local communities in the Darjeeling Hills of India. The results showed that forest-dependent communities collect an array of forest products from mixed stands compared to the monoculture stands but understory plant species richness was not significantly different between these two types of forest plantations. This study suggests that a single management strategy alone (e.g., mixed species plantations), could not produce an array of forest products expected by local communities, which requires a mixture of different types of strategies. Limited plantation management activities that were confined during the first 3 years after plantation were the major determinants of such homogeneity in the Darjeeling hills.

Keywords: monocultures, mixed stands, plantations, ecosystem services

1. Introduction

1.1. Forest plantations and ecosystem services

Forest plantations, particularly the plantations of exotic conifers, are one of the contentious issues when considering bio-diversity conservation and supply of ecosystem services. Usually, the large-scale monocultures, particularly those established by replacing natural forests, are the concerns of environmental lobbies [1]. In agrarian communities in which forest products

are considered as an important input of farm-household production functions, monocultures are likely to receive negative responses. This is because monocultures tend to have the least positive consequences for bio-diversity [2]. An increasing abundance of single planted species literally decreases the availability of other native species. Plant species richness and ecosystem services are so intricately linked that a change in the state of one of these variables can be expected to have an impact on the other [3].

It is likely that the establishment of a species-poor forest (i.e., a monoculture plantation) affects the interaction of local forest dependent communities and the forest in a negative way even though silvicultural options to enhance biodiversity in forest plantations do exist [4]. Even if silvicultural options are applied, they may never reach the levels of biodiversity that a native forest holds.

There are sufficient plantation management options available to manipulate attributes of the planted landscape [5, 6]. These forest management activities can enhance the production of multiple ecosystem services. These services are direct or indirect benefits that ecosystems provide to people [7]. Compared to monocultures, mixed plantation systems of native species are widely acknowledged to provide a wide range of benefits such as increasing production and stability, bio-diversity conservation and rehabilitation of degraded ecosystems [4, 8, 9].

Generally, local communities have the perception that the benefit derived from forest plantations relies on the species composition [10], and forest managers can expect positive responses by transforming forest plantations from monocultures to a mixture of species. However, having a single strategy of a mixed-species plantation may not address all social and environmental issues that arise due to monocultures. In this context, a broader understanding of complex plantation forestry practices and purposes may significantly increase the benefits society derives from plantations and may help to balance some of the shortages in resources that mankind will face in the decades to come [5].

Accordingly, this study will assess the role of plantations in the Darjeeling Hills of India and in so doing will answer two research questions. First: do mixed species plantations enhance plant species richness? Second: is there any improvement in the supply of locally important forest products after a change in forest management strategy from monocultures to mixed plantations?

2. Materials and methods

2.1. The case of *Cryptomeria japonica* plantations in the Darjeeling Hills, India

During British rule in the Darjeeling Hills of India, Japanese cedar (*Cryptomeria japonica*) plantations were extensively established to produce the timber required for railway construction and the tea industry, but at the expense of native forests [11]. *Cryptomeria japonica* locally known as *Dhupi* in the hills is endemic to Japan and Southern China. Today, these plantations of *Cryptomeria japonica* account for one-third of the total area of the Darjeeling Hill Council

followed by tea plantations which cover 22% of the total area [12]. It is obvious that such a change in land use, especially when it affects large areas, can cause a significant change in community composition and is very likely to have a negative impact on biodiversity from the stand to the landscape level [1, 13, 14].

These plantations are occasionally portrayed as environmentally negative as they are not suitable for the production of the wide variety of locally important forest products including fuelwood and fodder [15]. For instance, rural people require fuelwood for cooking and heating; and fodder for livestock to maintain their daily livelihoods. Therefore, in rural areas local livelihoods depend highly on the diversity of the native forests and locals can experience much dissatisfaction with commercially introduced plantations. In the Himalayan region reported cases exist where this dissatisfaction has led local people to deliberately damage conifer plantations [16]. However, the magnitude and direction of forest plantations are associated with the objectives of the plantation management and the integration of socioeconomic value into the plantation system [17].

After much public debate in the early 1990s, these plantations have undergone a paradigm shift from monocultures to mixed-species plantations where an allotment of planted conifers is prohibited from being more than one-fifth of the total planted trees [12]. In 1996 following a verdict of the Supreme Court of India, a felling ban in the hill regions was imposed [18]. Consequently, forestry operations were limited to rehabilitation of the degraded areas and nurturing of the planted crops until their establishment. This period generally lasts 3 years [12]. The hill people are allowed to collect forest products (fuelwood and fodder) only from the undergrowth for their subsistence needs. However, this provision seems contradictory with one of the objectives envisaged by the National Forest Policy of 1988 [19] and the Joint Forest Management (JFM) program, which were designed to meet the demand for forest products required in forest dwellers' daily life. Collecting forest products only from the undergrowth may not fulfill the demand for forest products particularly fuelwood and small timber.

For this study, plantation blocks within the Takadah Range of the Darjeeling Forest Division, west Bengal, India, were selected. The pre-requisites to select the pool of potential plantation blocks were (1) outside of the protected areas, (2) managed under the JFM program and (3) both monocultures and mixed stands in the same landscape (aspect and altitude between 1650 and 2140 msl) with different ages of stands. Most of the sites were dominated by *Cryptomeria japonica* monocultures established between 1922 and 1981. Additionally, planting mixed species (*Cryptomeria japonica* with other broadleaved species) was in practice after 1991. All of the hills had south-facing slopes.

The selected forest blocks are being protected by local people under the JFM program. Local people are organized into Forest Protection Committees (FPCs) to protect a particular plantation block. Three FPCs including the Tinchule, the Upper Humbasti and the Takadah are protecting the selected stands. The Tinchule FPC has both forest villages and revenue villages, while other FPCs have only revenue villages. A forest village is a colony of plantation workers established by the forest department on public land, and in the revenue village land are owned by individuals.

We adopted two different methods for each research question, respectively. The first method addressed the effects of plantation management regimes on plant species richness. Plantation management regimes mean the different stand structures that result from the species mixture and tree spacing at the time of establishment and the subsequent management by local people. Silvicultural management was not carried out by the forest department. We performed an inventory where we assessed the plantations composition and structure with special focus on the main understory. The second method consisted of focus group discussions with local communities to access information on the ecosystem services (ES) extracted by them from the inventoried stands.

2.2. Plantation inventory

We applied a stratified systematic sampling method for the plantation inventory. The plantations were divided into two groups: monocultures and mixed stands. Based on the working plan for the Darjeeling forest division [12], monocultures were defined as stands with more than 90% of *Cryptomeria japonica* trees. All other stands were classified as mixed stands. Each group was further stratified into four age classes: under 20 years, 20-40 years, 40-60 years and more than 60 years. This classification was based on the suitability of the particular age-class to produce locally important forest products as preliminary discussions with key persons from the Forest Department and local NGOs including Darjeeling Earth Group, Friends of Trees Forum, WWF Darjeeling, ATREE, and Prerana RCDC. For instance, stands under 20 years old are suitable for fodder and fuel wood, 20 to <40 year-old stands are used for poles, 40 to <60 year-old trees are considered mature, and > 60 years is the harvesting age for timber. A preliminary field visit and interaction with members of the FPC and the Forest Department Range Offices were carried out to select the stands resulting in a total of 17 plantation stands of different age classes that were inventoried (Table 1).

As all plantation stands are homogenous in terms of their age, we considered a sampling size of 2% as sufficient for forest inventory. We used a nested plot design with two different plot sizes. In circular plots of 200 m² (main plot) to increase the replication by increasing number of plots. We measured the height and diameter at breast height (dbh) of each tree with a dbh of 10 cm or more and recorded the species type. In each main plot we nested three sub-plots of 9 m² (square shape) to measure the understory vegetation [20]. In these plots we estimated the total cover of the understory vegetation in percent of the total sub-plot, the cover of different growth forms (i.e., herb, shrub, climber and trees) as well as the cover of each species that covered at least 5% of the sub-plot area. We also estimated the cover of different life forms and

Stand type	Plantation type	Age group	Area (ha)	No. of main plots
Mixed	Mixed	<20 years	26.30	27
Young	Monocultures	20 to <40 years	23.40	25
Mature	Monocultures	40 to <60 years	10.12	12
Old	Monocultures	≥60 years	16.19	18

Table 1. Plantation types, age groups, area (ha), and number of main plots.

species with a cover of >5%. The understory vegetation here (i.e., trees with a dbh <10 cm) were counted and also included in the cover estimates with shrubs, climbers, and herbs.

A total of 82 main plots were laid systematically at intervals of 100 m along parallel transects that resulted in one main plot per hectare. If there was more than one transect required, when forest area is not sufficient for defined intervals, the distance between the two consecutive transects was 40 m. During the inventory, we involved local inhabitants and forest guards who helped us to identify the plants and for triangulation. We collected a herbarium of the plants that were confused and verified with local experts.

2.3. Focus group discussions

Focus group discussions (FGDs) were carried out with members of the executive committee and general members of FPCs including former plantation workers to identify the services derived from the investigated forest types. To ensure that there was a consensus about the stands, each site was visited twice with the participants before and after the FGDs. These visits (i.e., discussion walks) mainly focused on forest products collected from the particular stand as these are the ecosystem services predominantly derived from the plantations by local people for their livelihoods. A list of ecosystem services was prepared with the participants during the discussion walks and the FGD for each selected stand. Discussion walks with focus group participants also helped to reconfirm to them about the plantation stands they were talking about. Participants were asked to rank the most important ecosystem services for their livelihoods and to indicate the five most preferred species using a majority voting system for each product that they obtain from the forest. In addition to the FGDs and discussion walks, interviews were conducted with 14 local experts from divisional forest offices (6), environmental NGOs (5), and local experts (3). Key person interviews were carried out to get information on the present status of forest management, ongoing conflicts and suggestions for future improvement.

2.4. Statistical analysis

Results from the forest inventory were analyzed with a one-way analysis of variance (ANOVA). Stata 14 software was used for data analysis. The effects of species composition on undergrowth and a variety of forest products were the main interest. The plant species diversity was described by the Shannon Index [21]. The index is a quantitative measure of species diversity in a given community based on the number of species present and their abundance. It is calculated as follows:

$$H' = -\sum P_i \times \log P_i \quad (1)$$

where H' is the Shannon diversity index. P_i is the fraction of the entire population made up of species i .

Knowing the structure and diversity of the different plantation types as well as how these types are utilized for locally important ecosystem services, we wanted to know if and to what extent the different stand variables influence the availability of these ecosystem services. We

Variables	Description	Notation
Trees per ha	Number of trees (≥ 10 cm dbh)	T
Diversity index of undergrowth	Shannon diversity index of vegetation measured in sub-plots	H'u
Diversity index of main plots	Shannon diversity index of vegetation measured in main plots	H'm
Stand age	Age of the plantation stands, which was estimated based on the plantation record	A
Plantation type	Types of plantations, value as 1 for monocultures and 0 for mixed stands	PT

Table 2. Stand characteristics included in the analysis.

therefore performed a multiple regression analysis to identify the determinants of locally important ecosystem services. We selected tree density, diversity of canopy and understory vegetation, stand age and plantation type as independent variables as these are important determinants of provisioning for multiple ecosystem services [4, 22–24].

In general, the quantity of ecosystem services depends on the intensity of forest management while the variety of ecosystem services depends mainly on structural features of the stand [22, 25]. Hence, we considered the number of locally important forest products as a dependent variable. The stand characteristics tested are listed in **Table 2**.

The multiple regression was based on the following model:

$$ES = \alpha + \beta_1 T + \beta_2 H'u + \beta_3 A + \beta_4 H'm + \beta_5 PT \quad (2)$$

where ES is the number of forest products, how many types of forest products, local people were harvesting from each plantation stand, α is the constant term. β_1 to β_5 are the vectors of coefficients associated with the tested stand characteristics (**Table 2**).

3. Results

3.1. Structure and diversity of *Cryptomeria japonica* plantation types

3.1.1. Differences in the upper canopy among plantation types

A total of 54 species were recorded both in main plots and nested plots of all studied plantations. Of the total, 34 species were trees, 9 herbs, 9 shrubs, and 2 climbers. Among them, 17 species occurred in the upper canopy, which are planted as plantations were followed by clear felling. The basal area and average number of trees per ha reported in **Table 3** indicates that the stands are dense according to Takahashi et al. [26]. In the monocultures, two native broadleaved species—*Magnolia lanuginosa* and *Castanopsis tribuloides*—were observed sparsely throughout the stands. As per focus group participants, these broadleaved trees were left by the forest workers during tending operations in the past and grew profoundly and regenerated naturally. In the mixed stands, a total of 16 species were found while *Exbucklandia*

Stand type	Basal area (m ² ha ⁻¹)	Tree per ha	Ratio conifers/broadleaved	Average H' m	Average H' u
Mixed	19.3	1344	24/76	1.08	2.15
Young	54.3	772	100/0	0.16	1.93
Mature	58.7	412	92/8	0.28	1.92
Old	60.6	344	99/1	0.06	1.71

Table 3. Characteristics of the upper canopy (trees >10 cm DBH).

populnea was within 60% of all tree individuals of the main planted species followed by *Cryptomeria japonica* (22%).

3.1.2. Differences in undergrowth vegetation among plantation types

The highest number of regenerated species (36 species) was recorded in mixed stands and young monocultures. Among the monoculture stands, the number of regenerating species decreased further with the age of the stands, i.e. 30 and 26 species in mature and old monocultures, respectively. Very few species were dominant in the understory vegetation. Approximately, three-fourths of the total number of species was recorded in only less than 10% of the total sub-plots. Common herbaceous species were *Dryopteris cochleata*, *Rumex nepalensis*, and *Eupatorium adenophorum*, which were found in 99% of the total sub-plots, however these species were not used by local people. Other common species were *Porteresia coarctata*, *Eragrostis tenella*, and *Equisetum debile* (92% of the total sub-plots). *Eurya acuminata* was the highest occurring regenerating tree species and was reported in 60% of the total sub-plots.

Mixed stands showed the highest value for the Shannon Diversity Index. Among the monocultures this value decreases with the age of stands however, they were not statistically significant within monoculture stand types.

3.2. Supply and preferences for ecosystem services by local communities

3.2.1. Forest products from different plantation types

The 12th Working Plan (1997/1998–2017/2018) for the Darjeeling Division states that the main aim of forest plantations was the production of timber and small-timber. However, local people were collecting several products such as fuel wood, fodder, bedding materials, and leaf litter in these plantations (Table 4). Among them, the respondents ranked fuel wood, fodder, and poles as the main collected products. Likewise, *Cryptomeria japonica* needles were used for decoration and the local Buddhist community used the needles for incense. Bamboo and Rattan are used by local artisans to produce toys, furniture, and household articles.

In the mixed stands, people collected different types of forest products from both the canopy vegetation and the understory. Bedding materials and fodder in particular were being collected from the understory. In the case of monocultures, *Cryptomeria japonica* trees from young monocultures were suitable for poles and needles, whilst *Cryptomeria japonica* trees from mature monocultures were only useful for the needles. Most of the forest products collected

Stand type	Locally important ES
Mixed	Fuel wood, Fodder, Poles, Leaf litter, Bedding materials, Support to vegetables
Young monoculture	Fuel wood, Fodder, Leaf litter, Decorative, Medicinal herbs
Mature monoculture	Poles, Fuel wood, Fodder, Decorative
Old monoculture	Fodder, Bamboo & Rattan, Vegetables

Table 4. NTFPs collected from different stand types.

in the monocultures was from the understory. However, it was observed that local people were collecting *Cryptomeria japonica* branches for fuel wood.

Obviously, mixed plantations supplied more number of forest products than other stand type.

Shannon diversity index of upper canopy vegetation has a strong correlation with the number of provisioning products ($r = 0.994$, $P = 0.006$).

3.2.2. Preferred plant species for different forest products

Native broadleaved species were highly preferred as fuel wood and fodder, while *Cryptomeria japonica* was the first choice for pole production (**Table 5**). Local people concerned about crop raiding by wild animals in their agriculture fields stated that an increase in fruit bearing species like *Castanopsis* spp., *Machilus edulis*, and *Elaeocarpus lanceaefolius* in forest plantations would help to create a suitable habitat for wildlife and reduce animal raids on their agricultural fields.

3.3. Variables determining ecosystem services availability

The results of the multiple regression analysis to identify the determinants of ecosystem services are reported in **Table 6**. The value of R-square indicates that the Model is a good fit. There are a number of significant variables (e.g., the age of the stands, Shannon Index of the undergrowth and the upper canopy, stand type, and number of trees per plot) that determine the variety of forest products from the plantation stands.

The regression analysis showed that the number of trees per ha and the Shannon diversity index of the upper canopy have a positive association with the supply of diverse forest products. On the other hand, the variety of forest products decreases with the understory diversity index and age of the stands, particularly if the stands are monocultures.

Locally important ES	Five most preferred species
Fuel wood	<i>Quercus</i> spp., <i>Acer campbellii</i> , <i>Symplocos</i> spp., <i>Eurya acuminata</i> , <i>Macaranga</i> spp.
Fodder	<i>Ficus nemoralis</i> , <i>Maesa</i> spp., <i>Garuga pinnata</i> , <i>Quercus</i> spp., <i>Prunus nepalensis</i>
Pole	<i>C. japonica</i> , <i>Schima wallichii</i> , <i>Exbucklandia populnea</i> , <i>Symplocos</i> spp., <i>Mallotus nepalensis</i>

Table 5. The five most preferred species by the focus group participants locally important ecosystem services.

Variables	Coefficients ^a
Constant	5.96 (1.160)***
Age	-0.043(0.008)***
Diversity Index Undergrowth	-0.133(0.055)**
Diversity Index Main plot	1.140 (0.630)*
Plantation type	-2.083(0.627)***
Trees per ha	0.016 (0.005)**
R-square 0.879	Adjusted R-square 0.624

^aStandard errors in parentheses.

*, ** and *** denote significant at 10, 5 and 1% levels respectively.

Table 6. Variables that influence a variety of forest products availability.

4. Discussion

The first question our research addressed was whether mixed species plantations enhanced plant species richness. Regarding the upper canopy this question can be answered, positively. Mixed plantations showed the highest diversity index in both the upper canopy and in the understory. This can lead to a variety of benefits for plantation managers, such as the creation of structural diversity, better utilization of nutrients leading to faster growth and a higher volume of trees [27] and reducing the risk of pest outbreaks [4]. A balanced mix of native and exotic species therefore seems to be a good option when addressing the multiple demands of forest products by rural communities. For instance, native species are suitable for the production of minor forest products including fuelwood, bedding materials and fodder, and exotic species are more suited for timber and small wood including pole and veneer [25].

Understory plant communities is widely heralded as forest ecosystem drivers as they are shown to significantly contribute toward enhancing species diversity and providing habitats for wild-animals [23, 28]. In this study area, we have seen that understory plants have a significant contribution to rural livelihoods as they are the only source of daily important forest products after the felling ban. In general, the species mixture in plantations enhances undergrowth plant diversity, but it is only partially true in our study [29, 30]. As expected, the mixed stands have with a value of 2.15 (the highest Shannon index), but the difference with monocultures is not statistically significant. This might be the result of the absence of forest management activities in this study area as silvicultural treatments focusing on maintaining spatial and temporal diversity of environments usually have positive effects on species diversity of naturally regenerated plants [31–33].

Our second question addressed whether increased diversity in forest plantations will also benefit local communities in the Darjeeling Hills. First, we must state that ecosystem services other than timber were derived from all plantations types, even from those which had almost no diversity in structure and plant species (Tables 3 and 4). This opposes the perception that

forest mono species plantations in general, and *Cryptomeria japonica* plantations of Darjeeling in particular, are of no use for the diverse requirements of local forest dwellers [6, 34].

Second, we found that higher diversity of the upper canopy is correlated with a higher number of tangible ecosystem services derived from the stands. As these mixed plantation stands have not faced any structured management since being planted the increased supply of ecosystem services can be seen from the forest department's perspective as undesirable and at best being somehow directed by the local user supporting species that are important to them. As mixed stands are seen to have a great potential for producing a wide variety of forest products [22, 35], a structured and intentional management of these plantations with the enhancement of the supply of ecosystem services seems to bear a much greater potential than currently utilized. This is especially true for the enhancement of the understory diversity which seems not to depend on the grade of tree species and structural diversity in the upper canopy.

The focus group members did not perceive *Cryptomeria japonica* plantations as negative as had been generally presumed [15]. Besides timber production, the rural farmers acknowledged the use of *Cryptomeria japonica* for pole production and its potential for commercial products such as decoration and incense. Typically, rural communities evaluate the plant species based on how their economic needs are influenced by the species regardless of the origin of species [36].

If *Cryptomeria japonica* plantations in the Darjeeling Hills can contribute to local livelihoods, why is their use disputed? We see two reasons why *Cryptomeria japonica* plantations were not able to gain public support. First, the felling ban imposed in the hills enforced monocultures to become over-matured and over-stocked. Second, plantation management in the hills follows an assumption that *Cryptomeria japonica* stands do not respond to thinning and can grow equally in un-thinned stands [12]. As a consequence of both, *Cryptomeria japonica* monocultures, whether mature or young, are dense. These dense stands create a dark understory environment resulting in low plant species richness [37, 38]. This dark understory reduces the availability of forest products.

Following the imposition of the felling ban it has been almost impossible to implement forest management systems. The ban has constrained the supply of locally important forest products thereby influencing regeneration. As a result, the collection of locally important forest products became unsystematic and local people have been collecting those products from whatever was available. In addition, the mixed-species plantations are dominated by limited species and these species do not represent local preferences (Table 5). This shows that without considering local preferences, the plantations, whether mixed-species or monocultures, cannot satisfy the local needs. Since there are a number of ways that plantation management can be manipulated for greater diversity in structure and species composition [4], it needs to be assessed at the local level.

5. Conclusions

The study concludes that options to enhance the supply of tangible forest products from forest plantations for rural communities in the Darjeeling hills are far from being fully utilized. There

is a need for a mixture of different options based on local assessments with moderate management activities [39]. However, it is almost impossible to apply any silviculture options in the Darjeeling hills due to the felling ban. This study calls for further discussions on whether the felling ban was imposed to support the existing practice of absolute protection or to allow for an improvement in forest operations. The answer to this question would provide valuable information to assist in designing an appropriate strategy to optimize the socioeconomic benefits from plantations. If the answer supports the continuation of the existing practice of absolute protection, then further investigation is called for to examine the future prospects of the plantations, particularly in the matured monocultures.

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The conifer tree can lead to a wide variety of products and services. Overall, the evaluation, management and planning of the multiplicity of these forest systems requires effective and specific methods and tools in a sustainable frame of the systems and of their products and services. This book reflects the current research on conifer stands and forests. The authors, specialists in different areas, addressed several issues in forest science, focusing on the species' characteristics, silviculture and climate change; growth analysis; reconstruction of stand dynamics of mixed stands; establishment, regeneration and succession; litter-fall, nutrient cycle and silviculture; distribution and zonation; and ecosystem services provided by monocultures and mixed stands.

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