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Global Warming Impacts

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Edited by Stefano Casalegno

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http://dx.doi.org/10.5772/1935
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First published in Croatia, 2011 by INTECH d.o.o.
eBook (PDF) Published by IN TECH d.o.o.
Place and year of publication of eBook (PDF): Rijeka, 2019.
IntechOpen is the global imprint of IN TECH d.o.o.
Printed in Croatia

Legal deposit, Croatia: National and University Library in Zagreb

Additional hard and PDF copies can be obtained from orders@intechopen.com

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p. cm.

ISBN 978-953-307-785-7

eBook (PDF) ISBN 978-953-51-4423-6

Meet the editor

Stefano Casalegno is an ecologist with a focus on forestry and spatial ecological modeling. He graduated at Paris Sud University in 1995 in Natural Science (Licence ès Sciences Naturelle). In 2001 he defended a PhD in ecology, GIS and remote sensing at the Institut National Agronomique Paris-Grignon (France). His research has focused on spatial-ecological modeling and the impact of climate change on vegetation. Specific research topics have included hedgerow ecology, plant insect and plant bird interactions (Univ. Paris Sud and Univ. of Bristol, Kibale Forest Nat. Park Uganda, 1996); mountain forest ecotones and vegetation belt mapping (CEFE - CNRS, France 1997, CIBNOR La Paz - Mexico 1998, INA P-G France 1999-2001); biofuels, forestation potential and forest yield estimations (INRA Versailles - MAICh Crete 2002); integrated studies for the assessment of forest condition and climate change impact on European forests (Joint Research Centre of the European Commission 2004-2008). Since 2009 Dr. Casalegno has been teaching spatial ecological modeling at different European universities.

Contents

Preface

This book addresses the theme of the impacts of global warming on different specific fields, ranging from the regional and global economy, to agriculture, human health, urban areas, land vegetation, marine areas and mangroves. Despite the volume of scientific work that has been undertaken in relation to each of each of these issues, the study of the impacts of global warming upon them is a relatively recent and unexplored topic.

Popular perceptions of climate science are dominated by one question: does man-made global warming exist? Most people would probably assume that the work of any scientist working on climate change is ultimately concerned with this question. But such perceptions could lead people to reach the conclusion that if any part of climate science is in a new, relatively exploratory stage, with many outstanding questions, then the whole edifice of climate science (equated with the theory of man-made climate change) is not on quite such a sure foundation as is often claimed. But such a conclusion would be based on a misunderstanding of the nature of the discipline. Before introducing the following chapters on the impacts of climate change – a topic which is relatively new and exploratory – it is perhaps worthwhile to indicate something of the place of such work within the broader context of climate science.

First of all, we should remember that not everything about climate science is new and controversial. I was once invited for a seminar at the CMCC (Euro-Mediterranean Centre for Climate Change) in Bologna, Italy. Afterwards I was kindly given a re-print of the 1967 book of the World Meteorological Organization on *The Nature and Theory of The General Circulation of the Atmosphere* (Lorenz, 1967). It was explained that all invited speakers to the CMCC receive this book as a gift. It serves as a reminder that the climate science of today stands "on giants' shoulders", and on a bedrock of understanding of the workings of the atmosphere and the planet as a thermal engine. This book has lost nothing of its original interest. It is not at this level that debate in climate science is focused. The topic of anthropogenic climate change is built upon these foundations.

In his introduction to the book *Vegetation Dynamics and Global Change* (Solomon and Shugart, 1993), Herman Shugart observed that the general public was already aware and understood the phenomena of long-term climatic fluctuations and the consequent fluctuations and changes of ecosystems on earth. The idea of short-term anthropogenic change was then the main focus of controversy: "*What is novel – newsworthy to the public and challenging to the scientist – are observations of shorter time scale, relatively rapid changes in atmospheric and surface features of the earth, and the strong evidence that some of these changes are being induced by human activities. It appears that we are producing measurable changes in major earth systems, but we have relatively little knowledge as to how the earth systems actually operate*".

Now, twenty-five years after the 1986 initiation of the International Geosphere-Biosphere Program by the International Council of Scientific Unions – a milestone in climate change research – we have accumulated a huge body of scientific data, models and literature, and our understanding of global warming has much advanced. While the anthropogenic origin of climate change still remains a matter of controversy in some quarters, we can say that there has been a sea-change in positions taken on this question. The skepticism of the majority of scientists and the general public on both climate change and its anthropogenic origins has been substantially reversed.

But even as it becomes harder to question the thesis of anthropogenic climate change, there are still many other issues that remain less well-understood, full of questions, and potentially controversial. The impacts of climate change fit into this category.

Back in the early to mid 1990s, Solomon and Shugart (1993) was an important reference for myself and many colleagues as we started to explore the field of ecology and climate change. The volume focused on the importance of scale in global studies and, in particular, on the prediction of the response of global ecosystems and patterns of vegetation to a change in climate. At that time, the response of forests to global climate change was one of the most hotly contested issues in the greenhouse effect debate.

Today, questions about the impacts of climate change still abound, though the focus is increasingly on understanding what climate change means in practice for human societies and natural ecosystems. This book thus focuses not on the part of climate science that deals with the understanding and modeling of the climate fluctuations, but on climate change impacts. It focuses on the simulation of future impacts, on the assessment of changes that have been observed in recent years, and on proposals and debates relating to future development and mitigation strategies.

The purpose of this book is to provide the reader with an overview of global warming impacts in different fields. In Part 1 authors focus on economic impacts. One chapter examines the issue of GDP and CO2 emissions at the global scale, while another examines local changes in the economy of Galicia, Spain. Part 2 deals with global warming and human health. One case study is concerned with an emerging viral disease, *Nephropathia epidemica* in Europe, whilst the other focuses on changing patterns of malaria transmission in Kenya. In Part 3, two chapters describe research on impacts and future scenarios for European and Japanese metropolises that has used machine learning techniques. In Part 4, studies on global warming and agriculture are presented. These include analyses of changes in crop production systems in Costa Rica (agroforestry) and China (rice), and two studies on the eco-physiology of crops, the first on the effect of changing night temperatures on rice, and the second reviewing known impacts of climate change and possible technical countermeasures for a range of key crop species. In the fifth and last part, five chapters focus on global warming and ecological changes. Included are a case study on impacts on forest trees species in Japan, two different case studies on sea level rise and mangroves (one on changes to a specific mangrove population in Taiwan, the other on general morphological and anatomical adaptations of mangroves to rising sea level). The final two chapters focus on global warming and sea ecosystems. One on fur seals' and sea lions' vulnerability and the other on changes in algae species composition and distribution.

We believe that scientists working in the field of global warming have much to benefit from the ideas and findings of studies in different disciplines that are linked to the same background of climate science. However, the need to work across disciplines creates a potential for difficulties of communication. This is why the authors of this book were asked to maintain a rigorous scientific methodology and a relatively broadly understandable terminology. This is to facilitate the exchange of ideas between different scientific areas of application.

The contributions to this book come from authors working in research centers, hospitals and Universities spread across almost all continents – a global science produced globally. We received contributions from Europe (Spain, Italy, The Netherlands, Germany, Belgium), from East Asia (Japan, China, Taiwan), from the Americas (Canada, USA, Mexico, Costa Rica, Peru, Brazil) and from Kenya in Africa.

The chapters of this book offer a broad overview of potential applications of global warming science. As this science continues to evolve, confirm and reject study hypotheses, it is hoped that that this book will stimulate further developments in relation to the impacts of changes in the global climate.

I acknowledge the contribution of each of the authors of this volume and I am grateful for their professional cooperation. For their help in the revision process, I am also very grateful to Dr. Stelios Rozakis from the Economic department of the Agricultural University of Athens; to Dr. Giovanni Sitia from the Division of Immunology, Transplantation and Infectious Diseases at San Raffaele Scientific Institute, Milan, Italy; to Tim Bending; and to Victoria O'Brien at the Department of Geography, Friedrich-Alexander University Erlangen, Germany.

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Part 1

Economic Impacts of Global Warming at Global and Local Scales

1

Global Warming and Its Economic Effects on the Anchovy Fishery and Tourism Sector in North-Western Spain

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1. Introduction

In recent years much evidence has been gathered on climate change and its impact on different sectors and systems. Global warming is one of the main threats to sustainable development and, consequently, one of the most significant environmental challenges in the last decades affecting the economy, health and social welfare. It is necessary, therefore, to identify evidence of the impact of global warming on biodiversity and carry out an economic evaluation. In the specific case of marine ecosystems, changes in rainfall frequency and intensity, acidity, water temperature, wind, dissolved CO_2 and salinity, combined with anthropogenic nutrient and toxin contamination, can affect water quality both in coastal regions as well as in the open sea. All of this will consequently affect the productivity of the marine environment. And given that fishing is one of the economic activities which critically depend on natural conditions or characteristics, the influence of environmental changes on fishing is notably higher than that which might occur in other primary activities. Furthermore, climate has a vital impact on the tourism and recreation sector and, therefore, this sector will be affected by any changes in climate.

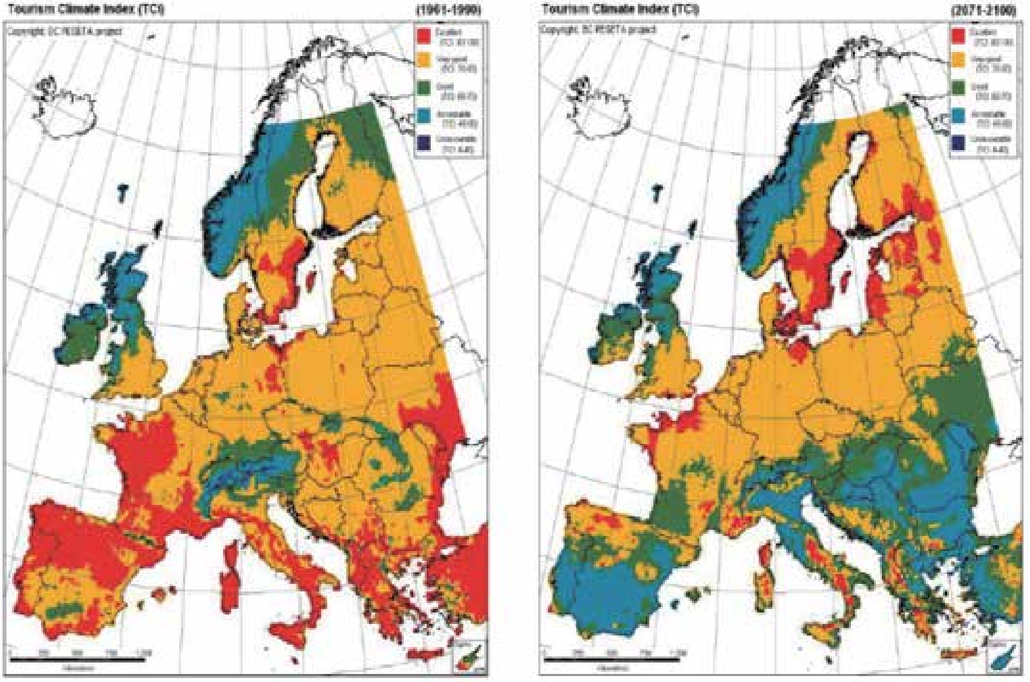
In this chapter, we assess the possible economic effects (losses or gains) of global warming on some of the main economic activities in north-western Spain. The economy of this region specialises in products derived from fishing and aquaculture as well as tourism, among others (IGE – Galician Statistics Institute-, 2010), and both activities are extremely sensitive to environmental conditions. It is highly probable that global warming will alter the intensity and conformation of ocean currents, affect marine organisms and generate coastal alterations (IPCC, 2007). Such environmental changes will have important repercussions on these economic activities.

A considerable number of studies have been carried out internationally which have aimed to assess the economic effects of climate change on these activities. Among other references in the case of fishing, we would underline the following: Arnason (2005) evaluates the possible impact of climate change on Iceland's fishery production, proposing different scenarios involving temperature increase; along the same lines, Eide (2005) analyses the possible impact on the Barents Sea fisheries; Gallagher (2005) makes an application to the New Zealand cod fishery, differentiating between zone and fishing method; Röckmann

(2005) analyses the effects of possible changes in salinity on the Baltic cod fishery; Sissener & Bjorndal (2005) study the effect of climate change on the migratory patterns of the Norwegian herring; Arnason (2006) proposes a theoretical model into which he introduces the risks deriving from global warming; Briones et al (2006) develops a model applied to small pelagic species in fisheries in India, the Philippines and Thailand; Hannesson (2006) analyses the effects of warming on the Norwegian herring fishery; Herrick et al (2006) make an application to the sardine fishery in north-American Pacific waters; and Garza-Gil et al (2011) evaluate the effects on the Ibero-atlantic sardine fishery.

In relation with the references which study the complex relationship between climate change and tourism, most of them point out that not only will the volume of tourism flows change but the destinations as well (Smith, 1990, 1993); Viner & Agner, 1999; Maddison, 2001; Lise & Tol, 2002; Scott *et al.*, 2004, 2005; Hamilton *et al.*, 2005a, 2005b; Gómez Martín, 2005; Bigano *et al.,* 2006, among others. In Europe, we would underline the PESETA study (European Commission, 2007) to evaluate the impacts forecast in Europe for the time periods 2011-2040 and 2071-2100, and which predicts that summer climate conditions will change radically and that the zone that currently has excellent conditions (the Mediterranean) will be displaced northwards (figure 1). In the case of Spain, the Spanish Climate Change Office reaches similar conclusions, predicting a "Mediterraneanisation" of the north of the peninsula and the aridization of the south (Ministry of the Environment, 2005). This result is particularly relevant for the research carried out, as we will see that for Galicia tourism flows come directly from the rest of Spain and this Mediterraneanisation of the north might generate a change in direction to the north from the current flows to the south. In this respect, the analysis by Bigano *et al.* (2004), which points out that approximately 86% of total tourism is the domestic or internal tourism of each country, is confirmed when we analyse the tourism flows from the rest of Spain to the north-west of the country. It should also be pointed out that, given the volume of domestic tourism, the analysis of the effects of climate change has in general dealt with international tourism, obviating internal or domestic tourism (Seddighi & Shearing, 1997; Coenen & Van Eekeren, 2003).

For this chapter and in relation with fishing activity, the study case chosen is the anchovy (*Engraulis encrasicholus*) fishery, it being a hugely important pelagic species for the fisheries sector in the region analysed. The pelagic species would be among those most affected by the impacts of climate change on seas and oceans due to the high level of instability and sensitivity to environmental impacts. These species are especially sensitive to temperature changes and the upwelling of nutrients in the marine environment. Therefore, any water temperature variation will have repercussions to a greater or lesser extent on these species' reproduction levels. In particular, we assess the possible economic effects of global warming on this fishery and sea surface temperature management is introduced into the management problem. This variable allows us to gather evidence of climate change and its repercussion on ecosystems and marine species, which are the bases of fish reproduction functions (McGowan *et al.*, 1998; Levitus *et al.*, 2000; IPCC, 2001; Stenevik and Sundby, 2007). Other variables, such as the frequency and intensity of rainfall, acidity, dissolved carbon and salinity, are also prone to experience environmental changes; however there is a high level of correlation between all of these variables. In this study, we describe the evolution of fish biomass, based on the sensitivity of the species' growth function with respect to fluctuations in oceanographic conditions (through the sea temperature), and will analyse impacts on the economic yield of the fishery deriving from a possible change in the temperature conditions



Source: PESETA Project (www.jrc.es/docs/Tourism.html) cited in EEA (2007).

Fig. 1. Simulations for summer tourism en Europa for 1961-1990 (left) and 2071-2100 (right), based on high emissions scenario of IPCC A2.

of the marine ecosystem. We will apply a bio-economic model for evaluating these effects on the fishing profits.

With relation to tourist activity, the physical changes in the coastal landscape, in the availability of certain resources or basic provisions (water, energy, food, etc.), in risks to health (new illnesses, effects of extreme temperatures) and the risk of catastrophic events (droughts, floods, storms and extreme weather conditions) are some of the consequences of climate change that will directly influence tourism. We assess the possible effects of global warming on tourist visits to the north-west of Spain. The analysis is based on prior qualitative information gathered on expected changes in the climate at different times of the year in Spain, the main source of tourist demand in the region studied. A prior description or zero scenario of tourism flows to the region is carried out. On this basis, changes in tourist preferences to estimate how the new climate scenario will affect tourist travel to the region are analysed. The methodology used consists of a field study based on direct methods using questionnaires presented to a representative sample at the source market. The objective market chosen was Madrid, the main tourist source market for the north-west of Spain. Climate is hugely important in the satisfaction or dissatisfaction of tourist visits at present and, in consequence, the choice of destination.

The structure of the chapter is as follows: in section 2, we will analyse the effects of climate change on the anchovy fishery, while section 3 deals with effects on tourist activity. Lastly, in section 4, we will sum up the study's main conclusions.

2. Effects of climate change on the anchovy fishery

Given that fishing activity is one of the economic activities which most critically depends on natural conditions or characteristics, the influence of environmental changes on fishing is notably higher than that which might occur in other primary activities (Hannesson 2006). It is assumed with some degree of probability that global warming will alter the intensity and disposition of ocean currents, and the effect of this, among others, will mean an increase in ocean temperatures, variations in salinity levels and changes in upwellings (ACIA 2004; IPCC 2007). The impacts will differ according to ecosystems and coastal or ocean zones, and will affect different groups of organisms, from phytoplankton and zooplankton to fish and algae (Ministry of the Environment 2006). Among these organisms, pelagic species (and, in particular, small pelagic species), on account of their high level of instability and sensitivity to environmental impacts, will be among those most affected by the impacts of climate change on seas and oceans. The small pelagic species are target species for the majority of the Spanish fleet, in general, and for the north-west in particular; and, of these, the anchovy is important on account of its high commercial value. For this reason, any significant modification in anchovy biomass levels can affect fishermen's net profits. We will begin by describing the situation of this fishery.

2.1 The situation of the fishery

The Spanish purse seine fishery in the Atlantic is made up of 491 vessels, of which 346 fish in north-western Cantabrian waters and the remaining 146 in the waters of the Canary Islands and the Bay of Cadiz (MAPA, 2008). It is one of the fleets with the most vessels operating in these waters, second only to the artisanal fleet, and it targets small pelagic species, among which are the sardine, horse mackerel, mackerel and the anchovy (MAPA, 2008; Ibermix, 2007). The Spanish purse seine fleet in the North Atlantic is made up of relatively homogenous vessels insofar as their technical characteristics are concerned, with an average capacity of 34.2 GT, power of 151.8 Kw per vessel and a length of 21m. The average life of the fleet is 20 years, with a crew of 8 per vessel. All of the vessels use nets made from synthetic materials, they are equipped with hydraulic haulers and electronic fish detectors.

Regarding the management, in general there are no specific regulations from the European Union. Given the poor situation in which the anchovy has found itself over the last years, a precautionary TAC was implemented for several years and a moratorium for this species has been in place in the Bay of Biscay since 2005. The Spanish government uses input control (area restrictions, entrance restrictions and gear regulation) and, in addition, some regional governments implement output control for some species (maximum catches per fishing day in the case of the anchovy).

This fleet targets pelagic species, in this case, the sardine and the anchovy. The anchovy has been subject to a precautionary TAC in area VIIIc for several years, but since the collapse of this species in 2005, the European Union established a moratorium (ICES, 2008). Stock biomass has been low because recruitment has been low since 2002, and the fishery has been closed since 2005. There are no indications how long the low recruitment will last and whether a continued low SSB will reduce future recruitments. Biologists consider it likely that the closure of the fishery over the last few years has led to an increase in the abundance of older anchovy, and because of the very low recruitment in 2008, the contribution of older fish to spawning in 2009 will be crucial. The fishery was opened again in 2010 and the EC implemented a TAC of 7,000 tons. In any case, the harvest control rules for anchovy are currently under development. Under the rules being considered, a TAC is set on the basis of the estimated spawning biomass and may be set for the whole period July–June, with or without a provision to revise it at the beginning of the year based on the results of juvenile surveys. The criterion for accepting these rules as precautionary would be that the rule implies a low risk of reducing the SSB to a level which may imply further reduction in recruitment (ICES, 2008). Other supplementary measures (area closures, minimum landing size) may be considered in addition to TACs.

Year	**Sea Surface Temperature (°C)**	**Anchovy Biomass (tons)**	**Catches in Spain (tons)**
1987	16.08	34128	15308
1988	16.13	51754	20302
1989	16.62	30193	16558
1990	16.61	81330	40759
1991	15.86	43675	25556
1992	16.02	18286	41051
1993	15.88	117981	42377
1994	16.08	79257	38019
1995	16.45	97017	43071
1996	16.32	78517	38968
1997	16.76	71573	27632
1998	16.64	124322	42579
1999	16.50	102308	34668
2000	16.41	132228	39496
2001	16.48	113063	49247
2002	16.24	46391	26313
2003	16.62	41317	15864
2004	16.36	52016	22205
2005	16.49	24413	5643
2006	16.51	37141	6244
2007	16.54	49579	6595
2008	16.56	36532	6457

Source: Own compilation from ICES (2008) and, for the temperature, Spanish Centre for Higher Scientific Research.

Table 1. The fishery.

The landings of this species were on the increase up to the year 2000, after which they dropped until the temporary closure of the fishery was imposed on account of poor stock recruitment in preceding years (table 1). For application purposes, we will not bear in mind the data corresponding to the period 2005-2008 due to the moratorium established by the European Commission for this stock, given that it is not the usual situation in the fishery. In figure 2, we can observe the variability that exists in the evolution of the biomass. However, in general, and except in the middle years of the period, as the sea surface temperature in this zone increased, the biomass dropped in the same way as catches, especially in the last years of the period analysed. And in table 2 we can observe the correlation matrix between these three variables, from which it can be gathered that variations in the sea temperature generate variations of the opposite kind in biomass and catches.

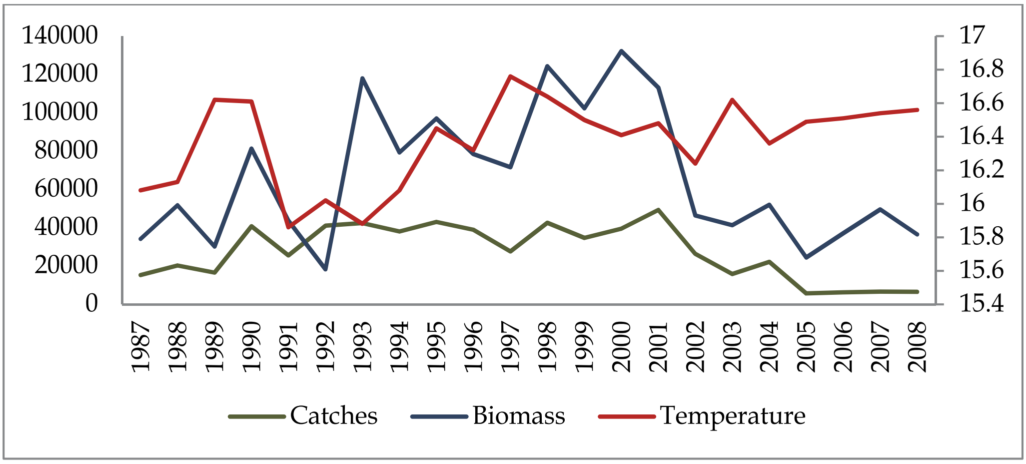


Fig. 2. Evolution of fishery. 1987-2008.

With regard to the economic parameters, we have average data for the period 1995-2006 from the European Commission (2006) and from direct interviews with fishery sector representatives. On this basis, the price per unit of catches landed (*p*) stands at 3950.01 €/ton (constant euros for 2008); the cost per unit of catch (*c*) stands at 982.7 €/ton (constant euros for 2008); and the discount rate (δ) is approximately 5%.

	Biomass	Biomass t+1	Catches	Temperature
Biomass	1.0000			
Biomass t+1	0.7923	1.0000		
Catches	0.7141	0.7428	1.0000	
Temperature	-0.4659	-0.6366	-0.6781	1.0000

Table 2. Correlation matrix among the variables biomass, catch and temperature

On the other hand, the north-west zone represents 36% of the total fishery insofar as anchovy landings for the period 1995-2006 are concerned. This will be the data we will use as a reference to estimate the variations in net profits in the face of the new climate scenario.

2.2 Methodology

Bio-economic modeling enables us to incorporate natural, environmental and institutional contributing factors, as well as typically economic factors, into a single analytical body. For the specific case of fisheries, the aim is to control the size of the fish population by limiting catches (or fishing effort) in such a way as to maximise the present value of the flow of net profits generated by the fishery over a specific time horizon and bearing in mind the dynamics of said natural resource. In this way, we can determine the extent to which society can invest (or disinvest) in the natural resource and what the appropriate extraction rate would be over time, allowing for the sustainable exploitation of said resource.

Given that we do not have data on fishing effort for this fishery, we can represent the bio-economic problem in simplified form as follows:

$$Max_h \int_0^\infty \pi(X,h)e^{-\delta t}\ dt \qquad (1)$$

$$s.a.\ \ \dot{X} = \frac{dX}{dt} = F(X) - h(t)$$

where *π(X, h) = [p - c] h(t)* represents the net profits generated by fishing in the instant t, X the fish population, h the catch rate, p the price per unit of fish, c the cost per unit of fishing, δ the social discount rate and F the natural dynamics of the fish population (or the natural growth function of the stock without considering human activity). The fundamental problem (Kamien & Swartz, 1991) consists of determining the optimal feasible control, h(t)=h*(t) con t ≥ 0, which maximises the objective function while satisfying the problem's conditions in the new climate context.

In order to resolve the problem (1), we need to previously define marine resource dynamics $\dot{X}$. This function is statistically tested on the basis of the data that exists on biomass, catches and, in our case, the sea surface temperature, generally using Ordinary Least Squares. From the data in table 1, and once the correlation matrix shown in table 2 has been obtained, the function which presents the best economic results is as follows:

$$\dot{X} = \alpha X_t + \beta X_t^2 + \gamma T_t - h_t \qquad (2)$$

The equation (2) corresponds to the logistic model, widely used in fisheries economics literature, where α, β and γ are parameters containing biological information on anchovy stock, and T denotes the sea surface temperature. The concrete results of the econometric estimation of (2) are shown in table 3. Therefore, the concrete form of this function is given by the following expression:

$$\dot{X} = 1.98\, X_t - 0.7E^{-5}\, X_t^2 - 0.03648\, T_t - h_t \qquad (3)$$

	$X_{t+1} + h_t = \alpha X_t + \beta X_t^2 + \gamma T_t$
α	1.98 (4.86)
β	-0.7 E^{-5} (-2.28)
γ	-0.03648 (-2.14)
Jb	0.3564
Q-Stat	0.0883
LM (ARCH)	0.8153
R^2	0.7982
R^2 adjusted	0.7684

Note: t-ratio between brackets. Jb is the Jarque-Bera statistic of the normality test; Q-Stat is the Ljung-Box statistic used in the correlation test; LM (Lagrange multiplier) is the one used in the heteroscedasticity test; and AIC is the statistic used in the prediction error model.

Table 3. Econometric results for growth function of anchovy biomass.

In this way, the *Hamiltonian* function in usual terms (current moment t) associated with problem (1) is given by the following expression:

$$H\,(X, h, t;\, \mu) = (p - c)h_t + \,\mu\,(\alpha X_t - \beta X_t^2 - \gamma T_t - h_t\,) \tag{4}$$

where μ denotes the shadow price of the marine resource in current terms.

The conditions necessary (Kamien & Swartz, 1991) to solve the problem are given by the expressions:

$$\frac{dH\,(X,h,t;\,\mu)}{dh} = \;0 \;==>\; (p - c) - \;\mu = 0 \tag{5}$$

$$\dot{\mu} - \;\delta\mu = - \;\frac{dH\,(X,h,t;\,\mu)}{dX} = \;-\,\mu(\alpha - 2\beta X) \tag{6}$$

$$\frac{dX}{dt} = \;0 \;==>\; \alpha X - \beta X^2 - \gamma T - h = 0 \tag{7}$$

By using expressions (5)-(7) the catch level is obtained $h^*(t)$, which will depend on the level of sea surface temperature, as will stock dynamics (expression (2)):

$$h^* = \alpha\,\left(\frac{\alpha - \delta}{2\beta}\right) - \beta\left(\frac{\alpha - \delta}{2\beta}\right)^2 - \gamma T \tag{8}$$

Once this level is known, we can obtain the losses or profits associated with the new climate scenario in relation with the fishery's present situation through the net profit function for the fishery.

2.3 Results

Declines in the abundance of the most important commercial fish species have often considered as a result of overfishing and occasionally from a combination of environmental effect and fishing pressure (IPCC, 2001). The impacts of climate variations have been shown to have substantial effects on decreases as well as increases in stock abundance, and the success of the future fish stock assessment depends to a large extent on the ability to predict the impacts of climate change on the dynamics of marine ecosystems.

The temperature in the North Atlantic has shown, in general, an increasing trend over the recent three decades. It may be an indication of the climate change caused by emission of different greenhouse gases. However, there is natural variability in the climate in addition to long term climate change induced by anthropogenic activity. And the difficulty in obtain many highly confident outcomes is why the term "climate scenarios" has been adopted in most impact assessment (IPCC, 2001). The climate scenarios should be regarded as internally consistent patterns of plausible future climates, and not predictions based in probabilities. Since most climate models focus on the atmosphere, the climate change scenarios for the ocean are particularly prone to uncertainty (Stenevik & Sundby, 2007). It is, however, concluded that the global warming will affect the ocean through changes in the sea temperature, among other variables (IPCC, 2001). And it has been shown that there has been a general warming of a large part of the world oceans during the past fifty years (Levitus *et al.*, 2000). For the Ibero-Atlantic waters, the sea surface temperature is expected to increase by approximately the same amount as in the last decades (Rosón, 2008), this is 0.027ºC per year ("Current warming" scenario in table 4).

In the table 4, the results obtained in the face of sea surface temperature increases in these fishing grounds are shown for different climate scenarios. For the current warming scenario, we can see that as the sea surface temperature increases, both the catch level as well as the net profits fall for the overall fishery. In the specific case of the net profits, the decrease is estimated to stand at 1.28% using the year 2040 as the time horizon, a medium-term time horizon established in the European Commission's Peseta Report (EEA, 2007).

Current Warming			Higher Warming		
Temperature (°C)	**Catches (tons)**	**Net Benefits (euros)**	**Temperature (°C)**	**Catches (tons)**	**Net Benefits (euros)**
16.6790	13991.89542	41519550.5	16.6979	13849.31678	41096462.6
16.7060	13991.89444	41519547.6	16.7276	13849.31570	41096459.4
16.7330	13991.89346	41519544.7	16.7573	13849.31462	41096456.2
16.7600	13991.89248	41519541.8	16.7870	13849.31355	41096453.0
16.7870	13991.89150	41519538.9	16.8167	13849.31247	41096449.8
16.8140	13991.89053	41519535.9	16.8464	13849.31139	41096446.6
16.8410	13991.88955	41519533.0	16.8761	13849.31032	41096443.4
16.8680	13991.88857	41519530.1	16.9058	13849.30924	41096440.2
16.8950	13991.88759	41519527.2	16.9355	13849.30816	41096437.0
16.9220	13991.88661	41519524.3	16.9652	13849.30709	41096433.8
16.9490	13991.88563	41519521.4	16.9949	13849.30601	41096430.7
16.9760	13991.88465	41519518.5	17.0246	13849.30493	41096427.5
17.0030	13991.88368	41519515.6	17.0543	13849.30386	41096424.3
17.0300	13991.88270	41519512.7	17.0840	13849.30278	41096421.1
17.0570	13991.88172	41519509.8	17.1137	13849.30170	41096417.9
17.0840	13991.88074	41519506.9	17.1434	13849.30063	41096414.7
17.1110	13991.87976	41519504.0	17.1731	13849.29955	41096411.5
17.1380	13991.87878	41519501.1	17.2028	13849.29847	41096408.3
17.1650	13991.87780	41519498.2	17.2325	13849.29740	41096405.1
17.1920	13991.87682	41519495,3	17.2622	13849.29632	41096401.9
17.2190	13991.87585	41519492.4	17.2919	13849.29524	41096398.7
17.2460	13991.87487	41519489.5	17.3216	13849.29417	41096395.5
17.2730	13991.87389	41519486.6	17.3513	13849.29309	41096392.3
17.3000	13991.87291	41519483.7	17.3810	13849.29201	41096389.1
17.3270	13991.87193	41519480.8	17.4107	13849.29094	41096385.9
17.3540	13991.87095	41519477.9	17.4404	13849.28986	41096382.7
17.3810	13991.86997	41519475.0	17.4701	13849.28878	41096379.5
17.4080	13991.86899	41519472.1	17.4998	13849.28771	41096376.3

Table 4. Results of estimations.

Table 4, on the other hand, also shows the results for these variables when faced with an even greater increase in sea surface temperature in these fishing grounds. As was foreseeable, there is an even sharper decrease in both variables. It should be noted that in any of the thermal oscillation scenarios, the level of catches obtained is lower than the average for the period 1987-2008.

3. Effects of climate change on tourism

Given that the aim is to carry out a preliminary estimation of changes in tourism flows to the north-west coast from one of the visitors' main source markets at present, it is necessary to begin by clarifying the basic terminology and, consequently, by delimiting the work done. In this sense, the World Tourism Organisation establishes that if an activity is to be considered a tourist activity, it must involve at least one overnight stay away from the permanent residence. Thus, for example, Evans *et al*. (2000) differentiate between these activities which involve overnight stays and a certain prior planning of recreational activities away from home in general which would be included in the concept of recreation or recreational activities. In the study described below, we will look exclusively at tourism flows according to the internationally-accepted definition, which does not cover recreational activities. This differentiation is also significant for the study's aims, as tourist trips are usually strongly conditioned by climate (when choosing destination and date), while recreation depends more on short-term weather forecasts. In this respect, Limb & Spellman (2001) identify the climatic factors that most influence tourists' decisions and observe that they are temperature, sun and rain. We will take into consideration the direct effect of climate change on tourism demand, and not look at indirect effects (through changes to the landscape, natural resources, etc.). Firstly, we need to identify the tourism destinations and uses of Madrid residents at present and the variables which affect their choice of destination. Secondly, we will reveal how preferences are modified under a climate change scenario, initially in their own region, but then also in different coastal destinations currently preferential for Madrid residents (especially the Mediterranean and the north-west). We will begin by presenting a description of current tourism demand in Galicia. Then we will briefly describe the methodology used to estimate changes in future demand and present the main results obtained.

3.1 Analysis of tourism demand under the baseline scenario

From the data presented in table 5, the relative decisive importance of domestic tourism in comparison with foreign tourism can be observed when we analyse tourist visits to the north-west of Spain (Galicia) 2008. This would explain why a single domestic market (Madrid) makes up half of the total figure for tourism from outside Spain to Galicia. This is also true in terms of the value of increased consumption, although the source used would seem to overestimate the former and underestimate the tourism that comes from the rest of Spain (36% of overnight stays generates only 18% of consumption). This said, it should be underlined that the estimation of tourism consumption received from the rest of Spain (in which Madrid is fundamental) is very similar to the importance of foreign tourism consumption (907 and 1187 million, respectively).

Of the 46 million overnight stays[1] by domestic tourists, 18.3 million (40%) are explicitly identified as summer holidays. To these we should add, among others, visits to family and friends, which can also be highly seasonalised. Per type of accommodation, the distribution of these overnight stays in visitors' own homes and/or those belonging to family and friends (which exceed 53% of the total) will be closely related to the data on access to a second home. It is significant that with regard to Galicia, in 85% of cases the location of this

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[1] The number of overnight stays in hotel accommodation is an "...indicator that in terms of volume it is much more significant than the mere arrival of tourists" (Xunta de Galicia 2005: 13).

	Overnight stays (people)	%	**Consumption (millions of euros)**	%
Domestic total	46,166,152	79.5	3,929	76.8
- Residents	24,889,152	42.7	3,022	59.1
- Rest of Spain	21,277,140	36.5	907	17.7
Madrid[1]	6,497,107	11.2	n.a	n.a
Rest[2]	14,730,033	25.3	n.a	n.a
From outside Spain	11,922,500	20.5	1,187	23.2
Total	58,088,652	100.0	5,187	100.0

[1]Makes up 5% of overnight stays, where the feeder market is Madrid, in the rest of Spain.
[2]Cataluña comes after Madrid, with 3,190,147 visits. Source: www.iet.tourspain.es e www.exceltur.org

Table 5. Analysis of visits and visitors.

second home is in Galicia, whereas with regard to Madrid in 84% of cases the second home is situated outside the region, that is, completely the opposite.

Non-regulated establishments are defined as homes and apartments not legalised as lodgings for business purposes, and therefore reliable statistics in this regard do not exist. For this reason, in order to assess their importance within the tourism sector, we need to resort to indicators that relate to their effective use, such as the overnight stays in non-regulated accommodation by Spanish and foreign tourists. However, we do not have disaggregated data at local level, which obliges us to make *ad hoc* estimations. The data for the three Galician provinces with a coastline is as shown in the Table 6.

NW coastal provinces	**Regulated**	**Non-regulated**	**Total**	**% Non-regulated**	**% prov./GAL**
A Coruña	3,857,573	11,267,254	15,124,827	74.5%	27.8%
Lugo	925,826	10,032,247	10,958,072	91.5%	20.1%
Pontevedra	3,798,427	12,425,654	16,224,081	76.5%	29.8%
Galicia (GAL)	9,191,098	45,099,554	54,290,652	83.0%	*3.4%*
Spain	344,022,030	1,228,798,432	1,572,820,462	78.1%	

Source: Compiled by the authors based on data from *Anuario económico de La Caixa*.

Table 6. Regulated and non-regulated overnight stays in the Galician coastal provinces.

As we can see in the table, overnight stays in non-regulated establishments account for more than three-quarters of the total in Galicia. Such a volume of non-regulated tourism business stands at a slightly higher rate than the average for Spain (5% more), making it especially appropriate to evaluate the real behaviour (under the baseline scenario) or potential behaviour (under a climate change scenario) from the point of view of tourism demand (in our case, the source market of Madrid), as to do so from the point of view of regulated supply[2] would involve only looking at a minor part of tourism uses associated with the use of the coast. On the other hand, overnight stays in coastal areas are especially decisive for

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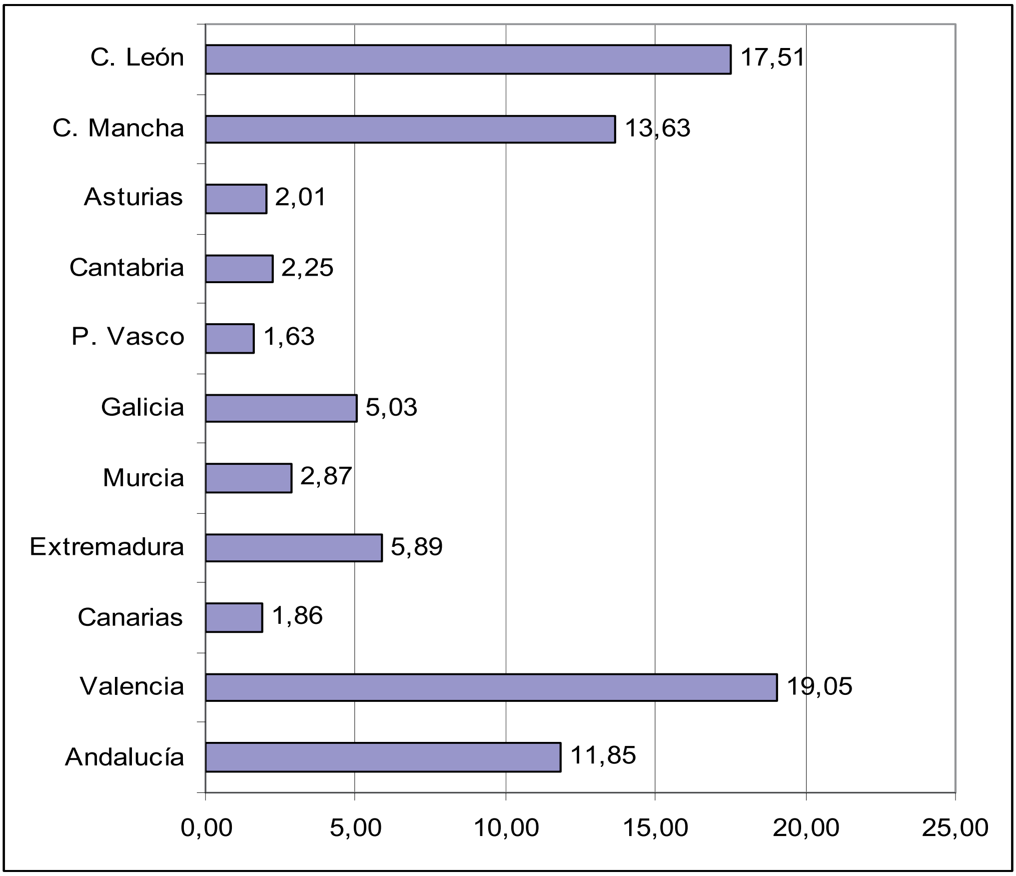
[2] By its very nature, it would be difficult for non-regulated supply to be the subject of a statistical analysis in fieldwork that could be considered rigorous.

the region as a whole, as the main reason for approximately 44% of domestic trips is to visit and enjoy its beaches (Familitur, 2006).



Source: Compiled by the authors based on data from Familitur, 2006.

Fig. 3. Distribution of tourism destinations visited by Madrid residents. Overnight stays with domestic destinations in Spain.

With regard to domestic tourism, the case of Madrid is notable. Therefore, as the main tourism feeder market for Galicia and in relation with the eventual effects of climate change on destination preferences, it is worth noting the following distribution under the baseline scenario (figure 3), in order to contextualise that 5% which translates into 6.5 million overnight stays in Galicia by Madrid residents.

And in the case of foreign tourism, in the minority in the north-west of Spain, it makes up 2.1% of the Spanish total. This fact implies the existence of a potential margin for other currently dominant destinations but concentrated in the south (Andalusia with 14.5%, the Canary Islands with 16.4% or Valencia with 9.2%) to move their preferences towards the north of Spain under a scenario we will evaluate herein. We believe this could be feasible in feeder markets from central and northern Europe, from where tourists mainly travel to spend their holidays (78.8%), usually in the summer.

3.2 Method

The methodology used to analyse changes in tourists' preferences towards coastal destinations under a climate change scenario is based on the economic valuation of stated preferences developed within the scope of environmental economics (Bateman *et al.*, 2002). Economic valuation with stated preference techniques is applied to projects or measures which cause changes to social welfare, and its aim can be to quantify in economic terms the magnitude of such impacts or forecast modifications in the behaviour of individuals in certain simulated scenarios, to quantify such changes and subsequently convert them into economic dimensions. In this study, we will adopt this latter approach within the stated-preference techniques. The method used is a variation of the so-called contingent behaviour analysis. This method, as with the other techniques based on stated preferences, is based on a questionnaire in which a representative sample of the target population takes part. The questionnaire is defined following internationally-accepted protocols and it attempts to place the individual in a hypothetical future situation in which he will have to decide what his behaviour as a consumer would be or, implicitly, how his consumption behaviour would vary in quantity and type in this new situation.

In order to carry out the estimation, we drew up a questionnaire to be completed by Madrid residents who might have visited a Spanish coastal destination in the last year (June 2007-June 2008). The questionnaire was divided up into four sections:

1. The first section aims to find out how many visits were made to the north-west of Spain during the reference period, in order to obtain specific data on each visit: the month in which it took place, the type of accommodation availed of, the approximate number of nights the visit lasted, the means of transport used to go to Galicia and the main reason for the trip. With sole regard to visits to the coast, the respondent was asked to point out the trips he thought were especially agreeable and satisfactory as well as those which did not live up to his expectations, and to specify the reasons why in both cases.
2. In the second section a similar process was undertaken, but relating to visits made to the Spanish coast (excluding Galicia), requesting specific data on each visit and for respondents to point out those that were particularly agreeable and disagreeable, as well as the reasons why.
3. Having completed the analysis of current tourist behaviour, the third section covers the importance of climate variables when deciding a holiday destination. Below we describe the hypothetical future scenario (in a context of climate change) which is accompanied by the corresponding contingent behaviour questions. It begins with a general line of questioning on how the respondent thinks tourist trips to Galicia and the number of overnight stays might change in the new context, if he personally would modify his trips to Galicia and the number of overnight stays on the coast. Finally, a question was posed which began by reminding the respondent of how many overnight stays he had made in the last year on the Galician coast and the rest of the Spanish coast, the aim of which was to quantify the behavioural change. He was then asked to estimate what trips he would make in the future bearing in mind the changes described. Respondents were also asked if they had a second home. Those who did were asked where, and if they would change the location of the second home in the new context. If they did not have a second home, they were asked where they would like to have one in such a future situation.

4. The aim of the fourth and final section of the questionnaire was to find out the socio-economic characteristics of respondents, such as their age, academic background, career situation, income, etc.

The text depicting the hypothetical future scenario described for the respondents to determine their contingent behaviour was as follows:

Access by road to the Spanish coast, including the north-west, has improved considerably, and in the coming years new high-speed rail links will make it possible to travel from Madrid to Galicia in approximately two hours.

Furthermore, experts consider that the following climate changes are already occurring:

- Precipitation will be concentrated in the autumn and will be lower throughout the rest of the year.
- Temperatures will undergo a general increase, especially in spring and summer. Furthermore, in summer and autumn the nights will be warmer.
- The sea temperature will rise.
- The sea level will rise.

With regard to Madrid, as well as the Mediterranean coast and the islands, being inland and further to the south, respectively, these changes will be more intensive than in Galicia".

This scenario was defined on the basis of prior information provided by biologists and other scientists. We chose to show qualitative information in order to facilitate the understanding of the information as well as the simplicity and brevity necessary for a telephone questionnaire.

With this methodology the individual has to choose between two alternatives: acquiring the product (tourism) with the usual characteristics, z_0 (in the current climate scenario); and acquiring the product with an additional attribute (the new climate scenario), at a specific cost for respondents (option z_1). We assume that the researcher does not know the true preferences of the respondents; therefore the social welfare function will be defined by the following expression:

$$V(z_j) = v(z_j) + \varepsilon_j, \qquad j = 0,1$$

where ε is the error term or the part not observed by the researcher, and it is considered to be a identically distributed independent random variable with mean zero. Through the valuation exercise, the researcher offers the respondent the possibility of acquiring products at a price A. The researcher can only assume that the reply is a random variable with a probability function,

$$\begin{aligned} \Pr\ (if\ /\ A) &= \Pr\ \{V(z_1) > V(z_0)\} \\ &= \Pr\ \{v(z_1) + \varepsilon_1 > v(z_0) + \varepsilon_0\} \\ &= \Pr\ \{v(z_1) - v(z_0) > (\varepsilon_0 - \varepsilon_{1i})\} \qquad (9) \\ &= \Pr\{\Delta v > (\varepsilon_0 - \varepsilon_{1i})\} \end{aligned}$$

Where *Pr(if/A)* is the probability the respondent will accept the exchange at the proposed price and *P(not/A)=1- P (if/A).* $\eta = \varepsilon_0 - \varepsilon_1$ and $F\eta$ will be its cumulative distribution function. If this distribution function is specified as logistic, we are facing a logit model,

$$\Pr(if\ /\ A) = F_\eta(\Delta v) = \frac{1}{1+e^{-\Delta v}} \tag{10}$$

whereby, if we also assume that the utility function is linear, the utility differential can be expressed as follows:

$$\Delta v = \alpha + \gamma A, \qquad \alpha = \alpha_0 - \alpha \tag{11}$$

where γ is the coefficient associated with the price attribute. By substituting in the probability expression, the following is obtained:

$$\Pr(if\ /\ A) = F_\eta(\Delta v) = \frac{1}{1+e^{-(\alpha+\gamma A_i)}} \tag{12}$$

the resulting regression equation will be

$$\ln\left(\frac{\Pr(if\ /\ A)}{1-\Pr(if\ /\ A)}\right) = \alpha + \gamma A \tag{13}$$

On the other hand, if the individual is prepared to pay the quantity *A*, then the willingness to pay *(D)* is greater than *A*. Formally,

$$F_\eta(\Delta v) = \Pr(\Delta v > \eta) = \Pr(D > A) = 1 - G_D(A) \tag{14}$$

where $G_D(A)$ is the cumulative distribution of the individual's willingness to pay. That is, the probability that the individual's social welfare will be greater if he accepts the exchange is directly related to the probability that his true willingness to pay is higher than the price.

3.3 Results

The questionnaires designed in order to analyse tourist preferences and their changes under a climate change scenario were carried out by professional pollsters in the month of July 2008 at Madrid City Council. The questionnaires were administered over the telephone and the numbers were dialled at random with quotas in accordance with age. 1495 people were contacted, of which 745 agreed to complete the questionnaire, which is a response rate of 49.8%, usual in this type of study. Of the 745 people who agreed to take part, 131 (17.6%) had visited Galicia in the last year (17.6%). (Therefore, 614 or 82.4% had not visited Galicia). This percentage exceeds to some degree the data provided by Familitur on the source Madrid and destination Galicia put at 5.03% on the baseline scenario. 73 people declared themselves to be visitors to the Galician coast (55.7% of those who had visited Galicia); 38 were inland visitors (29%) and 20 had visited both the coast and an inland region (15.3%). Therefore, 93 people (71% of those who had visited Galicia) had visited the Galician coast. From the initial sample 396 (53.2%) had visited the Spanish coast (excluding the Galician coast) during the last year (349 or 43.8% had not visited it). Considering the initial sample, we can see that 349 people had not visited either the Galician or the Spanish coast (46.84%);

59 had visited both (8%); 34 only the Galician coast (4.5%) and 337 only the Spanish coast (45.23%).

	First trips		**Second trips**	
	Frequency	**Percentage**	**Frequency**	**Percentage**
Work	8	7.0		
To visit family and/or friends	18	15.7	4	33.3
To enjoy the beaches	13	11.3	1	8.3
To go walking or trekking	6	5.2	0	0
Mountain sports	1	0.9	0	0
To visit historical monuments	1	0.9	1	8.3
To visit charming towns and villages	10	8.7	1	8.3
To enjoy the gastronomy	10	8.7	1	8.3
Others	48	41.7	1	33.3
Total	115	100.0	12	100.0

Table 7. Reason for the trip (to the Galician coast).

The sample size finally used for the statistical analysis is obtained after applying a sample filter, and the useful sample is constituted by integrating the visitors to the Spanish or Galician coast in the last year. With the selection, the final sample is made up of 430 people (who visited either the Galician or Spanish coast). We excluded those who visited inland Galicia and did not visit the coast (16 people are not current users of the coast). The end distribution of the sample according to their use of the coast remains as follows: of the 430 visits to the Spanish coast (excluding the Galician coast), 78.37% only visited the Spanish coast, 13.72% visited the Spanish as well as the Galician coast, and 7.9% visited the Galician coast but not the Spanish coast.

Table 7 shows the main reasons for the trips made to Galicia in the last year. 41% did not choose any of the reasons specified and gave a combination of reasons which were equally important for their decisions. It can be seen that visits to family and friends are the principle cause for those who chose some main reason (15.7% of the sample), the second (11.3%) being to enjoy the beaches and the third (8.7%) for its gastronomy.

When the reasons for especially satisfactory trip or trips are analysed, the main reason most of the respondents underlined (table 8) was the green landscape and woodland (46.51%), followed by the agreeable climate (11.63%). Secondary reasons included firstly the gastronomy (39%), followed by the green landscape and woodland (19.4%) and the climate (6%). Of those who state a third reason, 32% specify the amicability of the people and 13% the climate.

As we can see, the climate features in the three most-mentioned reasons, be it in first, second or third place. The people who mentioned more than one reason were asked what they considered the most important to be, and in the distribution of responses 40% replied the green landscape and woodland, 16% the gastronomy, 15% the amicability of the people, 12% the climate and 10% the quiet and non-overcrowding. In the case of trips to Galicia, only five people mentioned a trip that did not meet their expectations, four for reasons relating to the poor quality of the accommodation and one for the unpleasantness of the people.

In relation with trips to the Spanish coast, when the respondents were asked to specify the main reason for their trip (table 9), and in the same way as in the case of trips to Galicia, a significant number pointed to a combination of factors all of which were equally important. Of the individuals who stated a specific reason, beach-based recreation was the most frequent reason (with 28% of first trips and 20% of second ones), followed by visits to family or friends (14% and 18%, respectively).

	Reason 1		**Reason 2**		**Reason 3**	
	Frequency	**%**	**Frequency**	**%**	**Frequency**	**%**
Green landscape and woodland	40	46.51	13	19.40	3	6.38
Gastronomy	7	8.14	26	38.81	5	10.64
Amicability of the people	7	8.14	7	10.45	15	31.91
Pleasant climate	10	11.63	4	5.97	6	12.77
Cultural and historical heritage	2	2.33	3	4.48	2	4.26
Quality and proximity of the beaches	2	2.33	3	4.48	1	2.13
Quiet and non-overcrowding	4	4.65	3	4.48	4	8.51
Other	14	16.28	8	11.94	11	23.40
Total	86	100.00	67	100.00	47	100.00

Table 8. Reasons why the trip (to the Galician coastline) was especially pleasant or satisfactory.

	First trips		**Second trips**	
	Frequency	**Percentage**	**Frequency**	**Percentage**
Work	14	3.5	7	6.7
To visit family and/or friends	56	14.1	19	18.3
To enjoy the beaches	112	28.3	21	20.2
To go walking or trekking	25	6.3	8	7.7
Mountain sports	1	0.3	1	1.0
To visit historical monuments	3	0.8	0	0
To visit charming towns and villages	11	2.8	4	3.8
To enjoy the gastronomy	15	3.8	1	1.0
Others	159	40.2	43	41.3
Total	396	100.0	104	100.0

Table 9. Reason for the trip (to the Spanish coast).

In the total sample, 306 people were of the opinion that their trips were especially satisfactory, 4 that none was satisfactory and 86 mentioned an especially pleasant trip. In total, 392 had at least one especially satisfactory trip to the Spanish coast. Table 10 shows the main reasons for their opinions. Of the reasons they mention in first place, landscape is the most frequent (32.4% of the sample), followed by climate (21%). Of those mentioned in second place, the most important are gastronomy and climate (25% and 12%, respectively), and those who give a third reason point to the amicability of the people (21%) and the climate (14%). As we can see, the climate, in this case, is also quoted as one of the first three reasons relating to the satisfactory nature of the trip.

	Reason 1		**Reason 2**		**Reason 3**	
	Frequency	**%**	**Frequency**	**%**	**Frequency**	**%**
	127	32.4	26	11.02	14	9.59
Gastronomy	15	3.8	60	25.42	13	8.90
Amicability of the people	36	9.2	37	15.68	31	21.23
Pleasant climate	83	21.2	28	11.86	21	14.38
Historical and cultural heritage	4	1.0	9	3.81	5	3.42
Quality and proximity of the beaches	25	6.4	26	11.02	17	11.64
Quiet and non-overcrowding	37	9.4	22	9.32	16	10.96
Others	65	16.6	28	11.86	29	19.86
Total	392	100.0	236	100.00	146	100.00

Table 10. Reasons why the trip (to the Spanish coast) was especially pleasant or satisfactory.

	Positively		**Negatively**	
	Frequency	**Percentage**	**Frequency**	**Percentage**
Mild temperatures	22	61.1%	16	13.8%
Rainfall	7	19.4%	81	69.8%
Wind	1	2.8%	2	1.7%
Cloud/fog	0	0%	3	2.6%
Colder sea temperature	4	11.1%	12	10.3%
Waves	0	0	0	0
Snow	0	0	0	0
Others	2	5.6%	2	1.7%
Total	36	100.0	116	100.0

Table 11. Influence of climate on your decision to visit Galicia.

In relation with the contingent behavior analysis, when questioned whether the climate influenced their decision to visit Galicia or not, 35% of the respondents (152 individuals) answered that it did, 60% (258) that it did not and 4.7% (20) did not reply. Of those who answered in the affirmative, 23.7% (36 replies) indicated that the climate influenced them positively, and 76.3% (116) that it influenced them negatively. The climate variable that has the most positive influence is the mild temperature, mentioned by 61% of respondents. The most important negative climate variable is the risk of rain (table 11).

Once the expected changes for the years to come have been described, both with regard to improvements in infrastructures as well climate (in Galicia and Madrid), the respondents were asked if they thought that under this scenario tourist visits to Galicia would increase or decrease. 67% of those who visited the coast (287 people) considered that the affluence of tourists to Galicia would increase; 18% (79 people) thought that it would not change; and only 3% thought that visits to Galicia would decrease in the new context; 12% pointed out that they could not venture to make such a prediction.

Under the new scenario and when asked whether Galicia would be more attractive to them as a destination, they stated the following. For approximately 50%, Galicia's attractiveness as a destination would increase in the new situation; 36% would not modify their current opinion and, finally, 5% would consider Galicia as a less attractive destination. 9% did not venture an opinion on this point.

When asked whether their overnight stays on the Galician coast would increase or decrease, the replies were distributed in the following manner: 48% stated that under the new scenario they would make more overnight stays on the Galician coast; approximately 35% said that they would maintain their current number of stays; and only 4% said that they would make less overnight stays. 13% stated no opinion on this point.

The respondents were then asked to quantify changes in overnight stays. We will begin by analysing the variation in total overnight stays on the Spanish coast (including the Galician coast) to subsequently describe how future overnight stays are divided up between the Galician coast and the remaining Spanish coast.

We start off from the information obtained from the sample itself which indicates that 430 of the respondents visited the Spanish coast (including the Galician coast) and made 5339 overnight stays. Of the 428 respondents who answered the question on quantifying the changes, 76 (17.76%) would reduce their overnight stays on the coast under the new scenario, 157 (36.68%) would maintain the same number and 195 (or 45.46%) would increase their overnight stays.

Having presented the variations in overnight stays, it is deduced that they would increase by 2384 and drop by 652, with a final positive result in the form of a net increase of 1732 overnight stays (per year). The number of overnight stays would rise to 7071 (as opposed to the current 5339), with an increase in percentage terms of 32.44.

However, these global figures hide a very different situation between the changes observed in demand if we consider the Spanish coast and focus on the Galician coast. Beginning with the Spanish coast, currently 337 of the people polled visited the Spanish coast (excluding Galicia) and made 4421 overnight stays in the last year. In this case, of the 428 people who answered the question on changes, 161 (37.61%) would maintain their overnight stays, 153 (35.74%) would reduce them and 82 (19.16%) would increase them.

When presenting the variation in overnight stays, it can be observed that they would increase by 725 and drop by 1194, with a negative net result of -469 overnight stays in a year. The prediction, therefore, would be that the number of overnight stays per year in the sample on the Spanish coast, excluding the Galician coast, would drop from 4421 to 3952, with an approximate decrease in percentage terms of 11.

Analysing the variations in visits to the Galician coast, the data from the sample shows that in the last year, 93 people visited the Galician coast and made 918 overnight stays. Of the 428 people who answered the question on the quantification of changes, 22 (5.14%) would reduce their overnight stays on the Galician coast in the new situation, 139 (32.48%) would maintain them and 267 (62.38%) would increase the number of overnight stays they make.

Overnight stays would increase by 2226 and fall by 207, with a positive final result in the form of a net increase of 2019 overnight stays (per year). The number of overnight stays would rise to 2937, therefore (as opposed to 918 at present), with an approximate increase of 220%.

We will now describe the changes in preferences associated with a second home in a future climate change context. In the final sample, 146 people (34%) currently have a second home, a figure which closely resembles that obtained in the baseline scenario for Madrid (36.9% according to Familitur). Of these, 1.9% (8 individuals) has a second home in Galicia; 31.6% (136 people) on the Spanish coast and 2 people have a second home in another country. Only 17 people (11.6%) would change their residence under the new scenario, which indicates more rigid tourist behavior associated with second homes. The places to which they would change are presented in table 12, with a greater preference for Andalusia (23.53%), followed by Galicia and the Autonomous Community of Valencia (both with 17.65%).

Of the 284 individuals from the sample who do not currently have a second residence (66% of visitors to the coast), 33% would not know where to buy a second home if they had the opportunity to do so (79 people), 39% (111 people) would prefer to buy it on the Mediterranean, 22.5% in northern Spain (64 people), 4% in inland Spain (12 people) and 4 people (1.4%) chose other places (other countries).

	Frequency	**Percentage**
Asturias	1	5.88
Andalusia	4	23.53
Galicia	3	17.65
Avila	2	11.76
A.C. of Valencia	3	17.65
North	1	5.88
The Coast	1	5.88
Zamora	1	5.88
Ibiza	1	5.88
Total	17	100.00

Table 12. Place to which they would change their second home under the new climate scenario.

Lastly, in relation with the characteristics of the sample, 405 people were in their habitual residence, 94.2% of the sample. 18 was the average number of years that they had been living in that residence. The average age of those polled was 45 (with a minimum of 25 and a maximum of 75), which is representative of the target population. 63% of the sample was women. This percentage is higher than that of the population because in this case quotas per sex were not applied given that the interest lay in the questionnaire being answered by a family member who made the decision on holiday destinations. The average number of family members was 3.13 (median 4). In 65% of the homes that participated in the sample there were no under-19s, in 17% there was one and in 15% there were two. There were more than two in the remaining 10%. In 79% of the homes there were no over-65s, there was one in 14% and two in 6%. Only in 0.9% were there more than two over-65s. Only 4.2% stated they had a family member born in Galicia. 96%had heating in their homes (62% had natural gas) and 61% had air conditioning. 86% of respondents had a car and, of these, 98% had heating-ventilation-air conditioning. 138 personas (32.2% of respondents) had studied to high-school level and 227 people (53%) affirmed that they were the main breadwinner in the family.

4. Conclusions

In this chapter we have analysed the effects of climate change on the anchovy fishery and tourism flows in the north-west of Spain. To do so, we have taken into consideration possible future scenarios involving sea surface temperature increases and possible coastal and climate modifications in the region.

In relation with the effects on the anchovy fishery, we have used a bio-economic model applied to this fishery, which has allowed us to gauge the environmental effects as well as natural and economic factors. Climate change was gauged on the basis of sea surface temperature. The results obtained indicate a reduction both in future fish biomass as well as catch levels. This would be so both if the trend forecast for rises in sea temperatures follows past trends (foreseeable according to oceanographers; Roson, 2008) as well as if an even greater warming occurred as a result of global warming.

Given the poor situation of anchovy biomass as a consequence of low recruitment in recent years, the European Commission implemented a moratorium in the fishery for the period 2005-2009, both inclusive. Consequently, we assumed as a baseline scenario that which corresponded to the last year of fishing activity before the moratorium, that is, 2004. As a summery, table 13 shows the net profits that correspond to the baseline scenario and those that would be obtained on the 2040 time horizon, and for both scenarios with regard to sea surface temperature oscillation (this horizon corresponds to the intermediate period used in the EC Peseta Report).

Scenarios	Value (x10^6 Euros)
Baseline scenario	23,721
Climate scenario (1)	14,947
Climate scenario (2)	14,795
Variation rate for scenario (1)	-1.274 %
Variation rate for scenario (2)	-1.303 %

Table 13. Summary of estimated losses in the anchovy fishery (NW zone).

Therefore, the effects of sea surface temperature increases, assuming that the rest of the parameters remain constant, generate a reduction in net profits of 1.27% and 1.30%, respectively, if the sea temperature increases according to the trend over recent years, or if it increases at a greater rate than that observed to date.

With respect to tourist activity, a questionnaire was drawn up to reveal the tourist behavior, present and future, of the main tourism market in north-western Spain (Madrid). The questionnaire was applied over the telephone and a useful sample (of visitors to the Spanish coast over the previous year) of 430 people was obtained. Of these, 78% had visited the Spanish coast in that period, 8% had visited the Galician coast and 14% had visited both. Of those who had visited Galicia, more than half had made their trips in the summer, at an average of 10 overnight stays per visitor per year. Visitors to Galicia stayed mainly in hotels (42%) and rented apartments or flats (18%). They had travelled mainly in their own car (75%) and the main reason for the trip was to holiday, with a mixture of aims (beach, gastronomy, etc.). In general, they stated they were very satisfied with their trips, mainly motivated by the landscape, climate being among the three main reasons mentioned as agreeable factors.

Visitors to the Spanish coast spent an average of 11 nights per year and also made their trips mainly in the summer (62%). 33% stayed in hotels, followed by 25% who stayed in rented apartments or flats. Once again, their own cars were the main means of travel from Madrid to the coast (72% used their own car to travel) and the reason for the trip was also to holiday, in general. The respondents also affirmed that they were highly satisfied with their trips, the main reasons for this being the landscape and the climate, although 10% stated that one of the trips did not live up to their expectations, the reasons being the quality of the accommodation, the climate or noise and congestion.

It can be observed that the climate appears as a key reason to satisfaction or dissatisfaction with trips throughout the analysis. When asked about the extent to which the climate influences their decisions to visit the north-west, 35% admit that this variable did indeed influence their decisions. For 76% of those who admitted to being influenced by the climate, it was negative or off-putting, mainly due to the risk of rain, low temperatures and the low temperature of the sea.

With regard to the future climate change scenario, both in the north-west as well as the source (Madrid), and in the rest of the Spanish coast, most of the respondents (67%) were of the opinion that the tourism flow to the north-west would increase in the new context. For 50%, the attractiveness of the region would increase, and 48% affirm that they would increase their number of overnight stays in the region. The quantification of this increase in overnight stays indicates that only 5.4% would reduce their current number of stays, 32% would maintain them and 62% would increase them. The net increase would be +2.019 overnight stays (per year), which would involve a 220% increase with regard to the current number of stays in the sample analysed. This increase would occur to the detriment of trips to other areas of the Spanish coast (not the north-west). Thus, 38% of visitors to other parts of the Spanish coast would maintain the number of overnight stays in those destinations, 19% would increase them and 36% would reduce them. The total number of overnight stays would undergo a net reduction of approximately 11% with respect to the situation as it stands at present.

If we assume that tourist demand for the north-west of Spain originating in the rest of Spain adapts to the preferences of the source market of Madrid for the climate change scenario proposed, the consequences could be simulated (table 14) in two alternative scenarios (minimum with a 50% increase; and 100% or duplication maximum). Therefore, we would have the following differential impact on the GDP and in respect of the baseline scenario described in various paragraphs above:

Scenarios	Value (x10^6 Euros)
Baseline scenario	907.00
Minimum scenario (1)	1,360.00
Maximum scenario (2)	1,814.00
Effect on the GDP (1)	+1%
Effect on the GDP (2)	+2%

Table 14. Summary of estimated gains in tourism (NW zone).

To sum up, and considering only these two economic activities, the effect of climate change on the north-west of Spain would generate estimated gains of approximately 1300 million euros on account of the significant importance of the tourist sector in the region and the foreseeably greater number of tourists who would visit it from other regions which would be harmed by the temperature increase forecast (the South and East of Spain).

In summary, in this chapter we assess the possible economic effects of global warming on some of the main economic activities in north-western Spain: the anchovy fishery and tourist activity. With regard to fishing activity, the results showed that if the sea surface temperature trend in the Ibero-Atlantic fishing grounds continues to show warming, both the biomass and the expected profits will drop. With relation to tourist activity, the results showed that the demand for trips and overnight stays would increase in the new climate scenario and the north-west, which would become a more attractive destination for current and potential visitors. The increase in demand would come about as a result of a drop in demand for current destinations as well as a net increase in the number of tourist trips regarding the market analysed.

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2

The CO_2 Equivalent Emissions and Total Economic Output

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1. Introduction

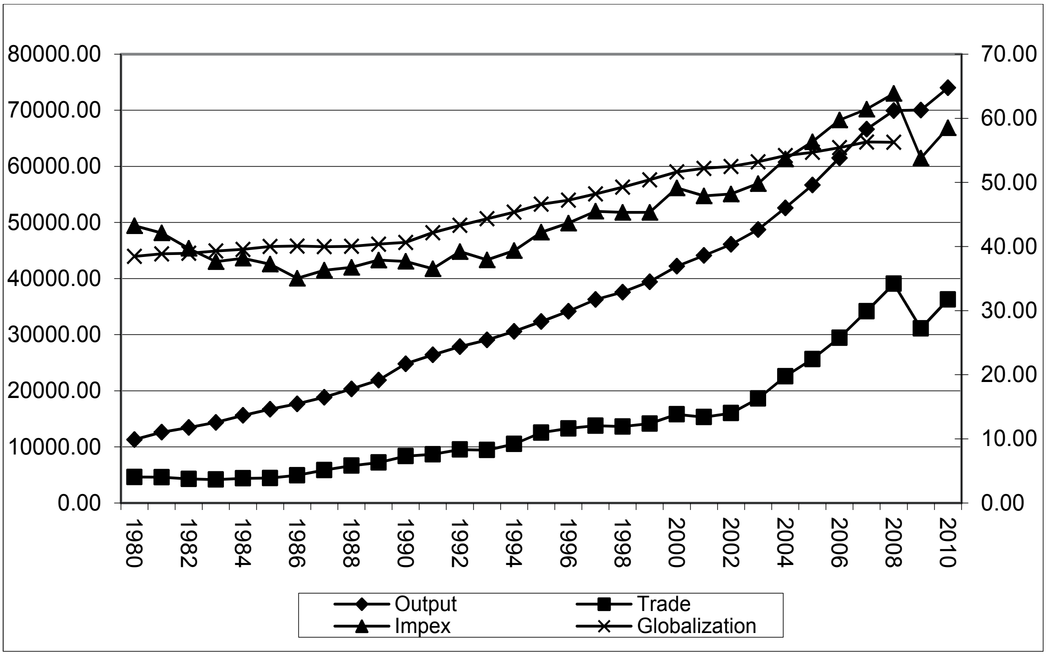
As the process of globalisation rolls on year in and year out, the states of the world become dependent upon each other. The interdependencies between countries – economically, environmentally and culturally – call for common policy-making, i.e. coordination of decision-making. The often heard call for global governance is only credible if it can deliver a theory about effective decision-making. However, often global meetings of governments result in little or nothing except sometimes non-binding recommendations.

This Marxian type contradiction between ONE global economy and environment on the one hand and some 200 states in need of policy coordination in response to the challenges of globalisation is extremely difficult to resolve. On the one hand, the representatives of each and every state will want to have a SAY in global decision-making – the unanimity principle. On the other hand, respecting the will of each of the 200 governments would lead to staggering transaction costs in negotiations. Is there a way out of the veto-transaction cost problematic that can save global reunions from coordination failures like the Copenhagen Summit on Climate Change?

2. Global Economic Interconnectedness: one market economy

The interconnectedness in the global economy has become so large that any major shock hurts almost all economies in the world. The amount of interaction in the global economy is typically measured with the IMPEX indicator, which divides imports plus exports with the GDP. Diagram 1 shows the constantly growing IMPEX scores for the global economy, which follow closely the expansive trend for global output and world trade.

The close match between the trends in Diagram 1 confirms the basic insight in market economics that only free trade can deliver affluence. Global trade and foreign direct investments remain the engine that power global economic expansion. Constantly increasing economic interactions between countries not only cement ONE global economy, but also push the GDP of most countries steadily higher. Growth in aggregate output means that it is easier to fight poverty, but it comes with a most important consequence, namely the increase in CO2 emissions.



Source:
Output = Gross domestic product based on purchasing-power-parity (PPP) valuation of country GDP;
Current international dollar; Billions (left axis)
Trade = Imports and exports of goods and services; Current dollars; Billions (left axis)
Impex = Trade / Gross domestic product, current prices; Current dollars; Billions (right axis)
Globalization = Means for KOF index (Dreher 2006) for 174 constant countries (right axis)
Sources: IMF (2010) World Economic Outlook Database; available via: http://www.imf.org/external/pubs/ft/weo/2010/02/weodata/index.aspx
Dreher, Axel (2006): Does Globalization Affect Growth? Evidence from a new Index of Globalization, Applied Economics 38, 10: 1091-1110;data available via: http://globalization.kof.ethz.ch/

Diagram 1. Interconnectedness: IMPEX scores, trade and global GDP.

3. The three types of pollution

Among the cornucopians, it is believed that affluence reduces pollution. This was the classical policy stance of Julian Simon (2003) and Aaron Wildavsky (1997), rejecting the relevance of environmental policies that reduce CO2 emissions. However, they fail to distinguish between three very different forms of pollution when it comes to the effects of rising affluence, i.e. GDP. One must separate between visible and invisible pollution as well as between direct and indirect pollution. Thus, we have:

1. Littering or petty pollution: it occurs massively in poor third world countries, like e.g. India or Fiji;
2. Toxic waste, metals and sewage: they are to be found on a large scale in the emerging economies where high levels of growth are combined with weak environmental protection;

3. CO2 pollution: it takes place in industrial and post-industrial economies requiring massive input of energy in various forms: transportation, heating, cooling, etc.

Whereas rising affluence would tend to result in lower littering as well as toxic waste, especially if the additional resources that economic growth hand down are used in either public policies or in private efforts to clean up, it is definitely not the case that economic development or quick economic growth decreases CO2 emissions, as we shall see below.

It is absolutely essential to separate between these different forms of pollution. Soumyananda Dinda (2004) has shown in several articles that the relationship between per capita income and different pollutants is complex, varying between different sets of countries depending upon their per capita affluence. Thus, a so-called *environmental Kuznets curve* posits an inverted U-shaped relation between pollutants and country affluence per capita. Here we will only research CO2 equivalent emissions as one kind of pollutant. And we will not look into the nature and complexity of the environmental Kuznets curve, focussing here only upon total economic production or GDP.

Now, a cornucopian like Bjorn Lomborg (2001) argue first like Simon and Wildavsky that the link between CO2 emissions and climate change had not been scientifically established. But he later changed his view (Lomborg, 2007) stating that climate change, when true could not possibly be as dangerous as ecologists warn about. There are two hypotheses involve here in this debate between cornucopians and ecologists:

(H1) C02 emissions are not the major cause of global climate change. Or this assertion has yet to be proven by convincing evidence that is as yet lacking.

(H2) The role of CO2 emissions has been enormously exaggerated. As a matter of fact, this form of pollution is notoriously difficult to both measure and model.

Here, I will concentrate upon H2, as I believe it can be rejected through an analysis of the link between CO2 equivalent emissions and global economic output, as measured by the GDP indicator.

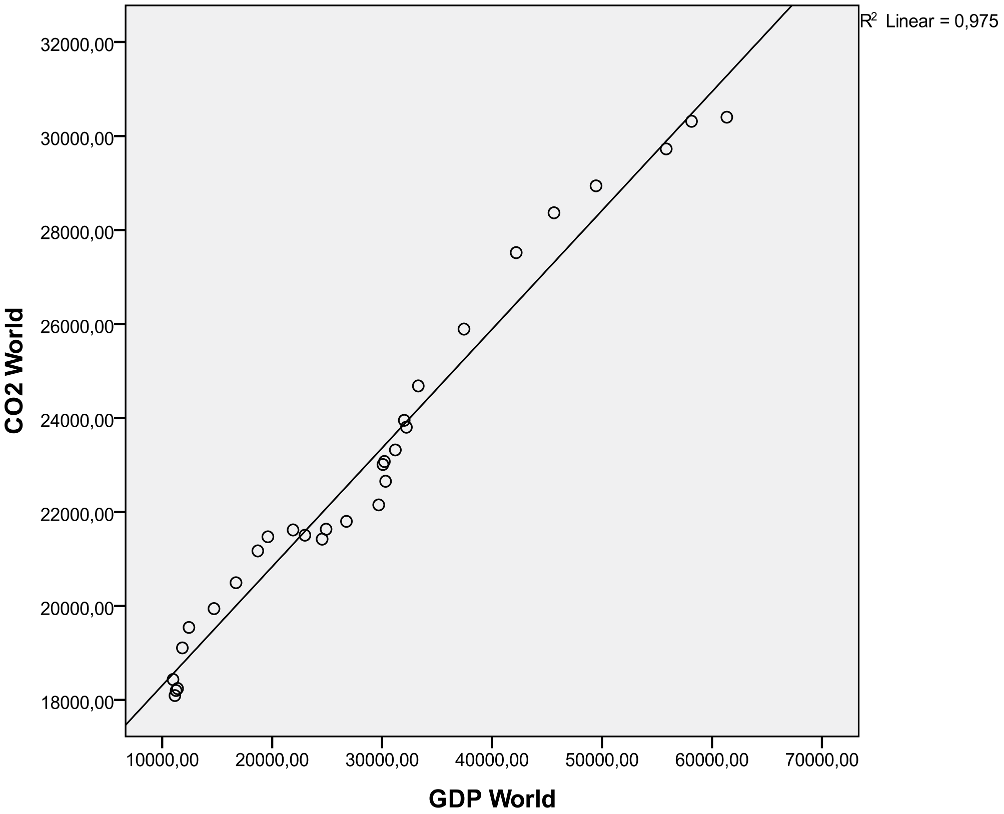
4. The increase in the CO_2 equivalent emissions 1970

The increase in CO2 equivalent emissions appears in Figure 1, where yearly totals are plotted against total output, or GDP. Total emissions per year have doubled over this thirty years period. Since these emissions have a very long life time, they build up in the atmosphere to huge cumulative amounts. As a matter fact, this process has been going on since the start of the industrial period, but typical of recent decades is the sharp yearly increases in emissions.

This type of pollution – CO2 equivalent emissions poisoning the atmosphere – increases as a function of economic activity. Economic output requires huge amounts of energy, which today is mainly coming from the burning of fossil fuels. This in turn results in the CO2 emissions. In Figure 1, the match between GDP increases and growth in emissions is perfect. On the basis of data over time, one may estimate an equation: Emissions = f (GDP) for 1980-2009. It gives the following parameter estimates (Table 1):

	Global emissions 1980-2009
GDP	
Constant	15 780
Coefficient (significance = .000)	.25
R2 = .975	

Table 1. The growth of C02 emissions and global economic output 1980-2008.



Source: CO2 emissions + Population: EIA (2011) International Energy Statistics; data available from: http://www.eia.gov/cfapps/ipdbproject/IEDIndex3.cfm;
GDP data: World Bank (2011) World Development Indicators; data available from http://databank.worldbank.org/ddp/home.do

Fig. 1. Total emissions 1980-2008 against global economic output (Million tons and billions).

This finding implies that a further economic expansion globally at say 6 per cent economic growth during the next decade will lead to roughly a yearly increase of 1,5 per cent in CO2 emissions, i.e. one arrives at a level of pollution of about 40 000 thousand metric tons in 2020.

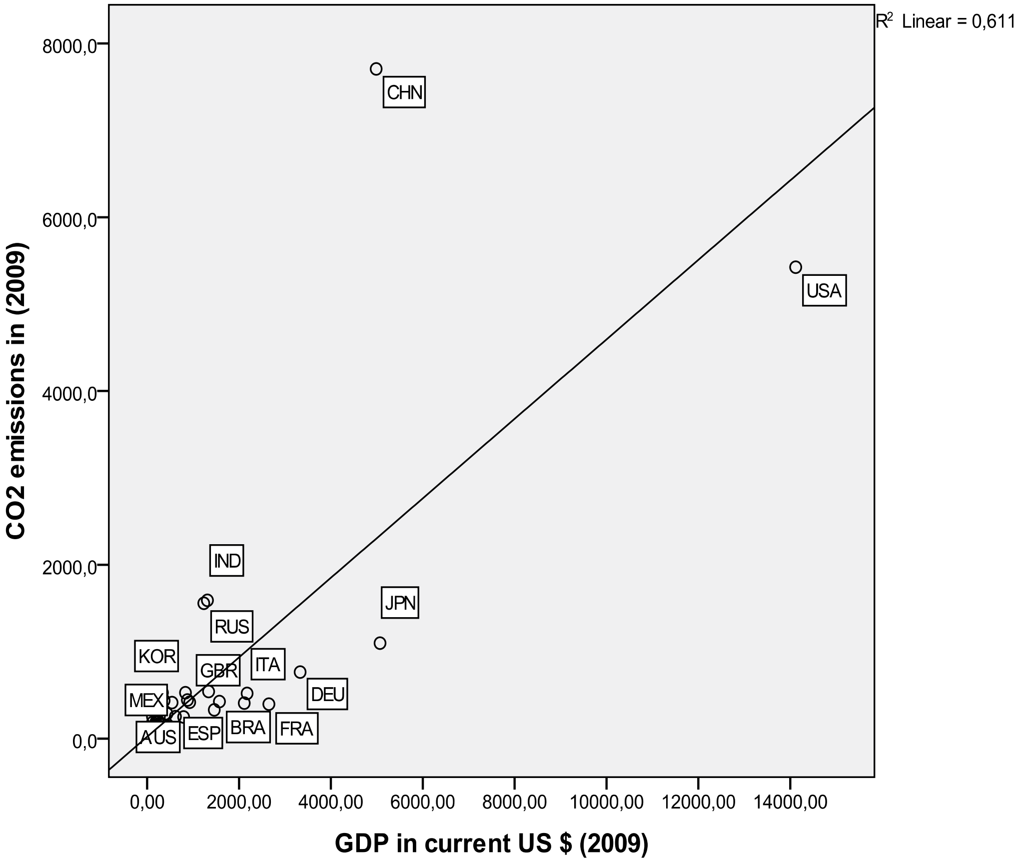
It could be even worse if many emerging countries developing quickly use more coal as substitutes for expensive oil and gas. The Fukushima tragedy makes nuclear power less attractive, again increasing the demand for dirty coal. Thus, the conversion factor between GDP and emissions may rise from 0.25, worsening the pollution of the atmosphere. However, the depletion of oil reserves will stimulate steps towards a green economy, lowering the conversion factor.

When total emissions reach 40 000 thousand metric tons on a yearly basis, then climatologists warn that climate change is not only unavoidable, but it also will be pretty violent. Be that as it may, here the focus is upon the link between economic development and emissions. As mankind is hardly going to settle down for zero growth one may expect that incentives push people to efforts resulting in higher output and thus income, especially when global population is still expected to increase. However, it will lead to huge increases in emissions, unless a green economy is embarked upon somehow, lowering the conversion mechanism between output and emissions.

Now, the global scene with the close link between GDP and emissions harbours considerable country variations, as countries not only differ in terms of output but it is also the case that some countries have much higher transmission factors than others.

5. Variations in the output-CO_2 equivalent emissions connection between economies

Generally speaking, a country economy delivers more CO2 emissions the more affluent it is and the larger its transmission factor between output and pollution. Consider Figure 2 that portrays the large country variations in the GDP-emissions space.



Source: CO2 emissions + Population: EIA (2011) International Energy Statistics; data available from: http://www.eia.gov/cfapps/ipdbproject/IEDIndex3.cfm; GDP data: World Bank (2011) World Development Indicators; data available from http://databank.worldbank.org/ddp/home.do

Fig. 2. Country CO2 emissions against country GDP 2009.

Figure 2 confirms the general connection between economic output and total emissions. It also indicates that China is a so-called outlier, i.e. an exception to the trend because of its high conversion factor between GDP and emissions China is simply the most polluting country in the world although its total economic output is not even half of that of the US. One may employ the regression technique to estimate the same equation (E1) above but this time by means of cross-sectional data. Table 2 has the findings.

	Country emissions 2009
GDP	
Constant	20,632
Coefficient (significance = .000)	.457
R2 = .611	

Table 2. Regression analysis of GDP and CO2 emissions on a country basis in 2009.

Today, the conversion factor between economic output and CO2 emissions stand as high as .45, meaning that one unit of output results in almost 0.5 unit of emission. Since economic growth is unstoppable, one may safely predict that CO2 emissions will rise in the next decade. Economic growth is today strongest among the so-called emerging economies. They differ in how much emissions they have per unit of GDP.

6. Economies of scale in CO$_2$ equivalent emissions?

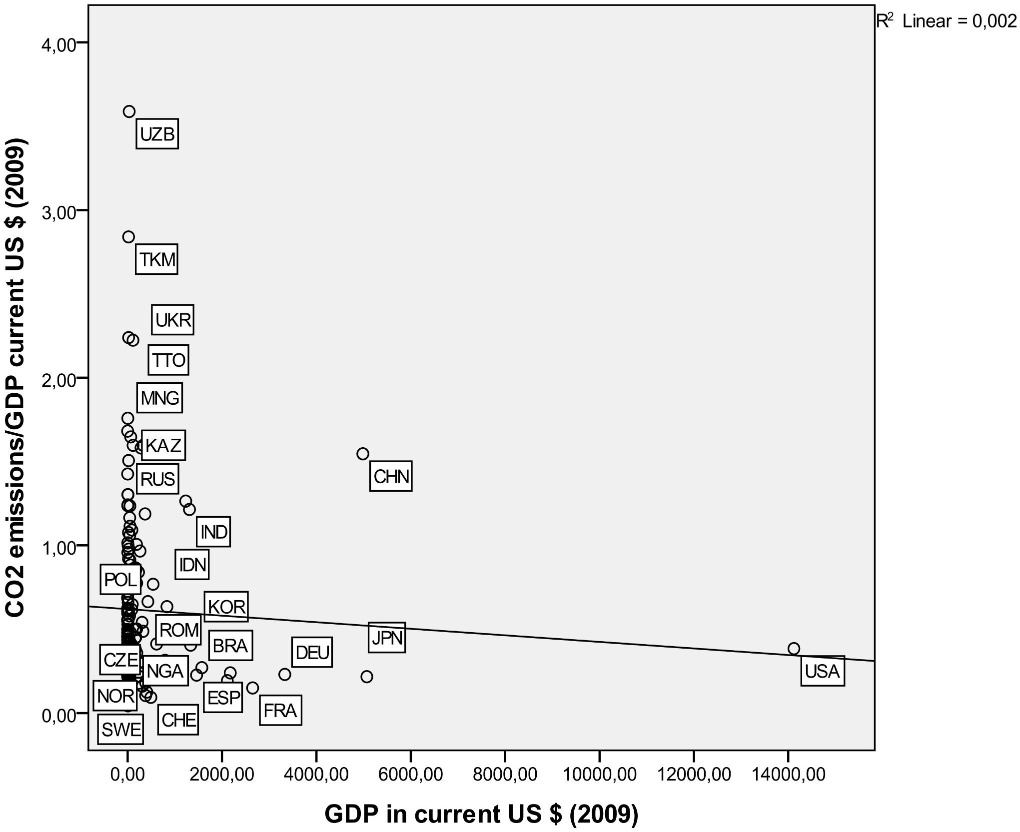
As we have seen, a higher GDP gives more CO2 emissions. But it could be the case that the amount of CO2 emissions per GDP unit decreases at the same time due to economies of scale in energy production and consumption. Figure 3 suggests such a mild tendency, emissions per GP falling the more affluent the county.

This economy of scale is not a strong one, but Figure 3 shows that several countries have emissions per GDP that are much higher than most other countries. It is a matter of not only of China and India, burning massive amounts of coal, but also of countries like Russia and the Khanates. When Chiba declares that it is only committed to holding its emissions per GDP constant until 2020, then this policy would not help reducing emissions increase at all. On the contrary, given the rapid economic development in China, its total emissions would skyrocket.

In general, the increase in emissions from GP growth is not offset by the reduction in emissions per GDP by growing affluence. Thus, total emissions can be predicted to grow to alarming levels, if the climate change hypothesis (H1) is correct, i.e. CO2 emissions drive a greenhouse gases effect.

7. Towards a global CO$_2$ emissions policy?

The most ambitious attempt to come up with a global emissions policy thus far is the Stern Review from 2007. It has been widely debated, receiving both praise and blame. It outlines a policy response to the rising CO2 emissions with a complex mixture of global measures involving price increases upon fossil fuels as well as compensation of Third World countries for these higher energy prises. Also China is suggested to receive compensation, if it lowers its massive use of coal.



Source: CO2 emissions + Population: EIA (2011) International Energy Statistics; data available from: http://www.eia.gov/cfapps/ipdbproject/IEDIndex3.cfm; GDP data: World Bank (2011) World Development Indicators; data available from http://databank.worldbank.org/ddp/home.do

Fig. 3. CO2 emissions per GDP against total economic output (GDP).

We have found that economic development, which is unstoppable, is the main cause of one fo the major global pollutants, namely the CO2 equivalent emissions. There are other contributing factors, like for instance deforestation and desertification. One unit of output today results in almost half a unit of CO2 emission. Over time, economic expansion in the form of a GDP increase has led to a .3 increase in total emissions. Each country economy has its conversion factor, i.e. the link between GDP and CO2 emissions. Some countries have extremely high conversion factors, leading to massive pollution of the atmosphere.

The Stern recommendations do not appear viable, because they are simply too complicated. And they build upon the assumption that global agreements about reductions in emissions, carbon taxes or emissions trading as well as compensation claims can be enforced or even monitored. When one takes opportunism, free riding, ambiguity and myopia into account, then global environmental coordination, as conceived by Stern, is not feasible.

The rise in C02 emissions can only be stabilized when the rate of economic growth comes down in emerging economies or when the conversion factor between economic output and emissions is lowered significantly. This will not be possible through global coordination through the UN schemes where each country has one vote and decisions require unanimity.

Emissions will stabilise when the cost of energy has risen to such a level that the path to a green economy must begin to be trodden. From the perspective of the global environment and its protection, the ongoing sharp rise in energy prises is positive.

8. Conclusions

Total CO2 emissions, being one type of pollutant are closely linked with total economic output, or GDP. To stabilise the CO2 emissions, only two options are available: (a) reducing economic growth, or (b) moving to a green economy where energy consumption does not result in CO2 emissions. Realistically, only the second alternative is feasible, reducing the conversion factor between energy-output-CO2 emissions. It now stands at 0.45, which endangers the atmosphere of Mother Earth. It will go down when new sources of energy replace the fossil fuel dependency. Single countries may engage in various carbon tax schemes or carbon trading mechanisms, but on a global scale this is not feasible, at least not in the complicated formula suggested by the Stern Review, involving massive amounts of compensation and transfers between governments.

Many economists like for instance Bhagwati (2004) welcome the globalisation period that mankind has entered. However, there is a major problem, namely the enormous growth in CO2 equivalent emissions during the last decades. If they drive climate change to drastic levels involving a 4-6 % increase in average temperatures, then mankind will be in dire straits. Given the link between total economic output and CO2 equivalent emissions, global warming and climate change appears unstoppable.

9. Acknowledgements

I am indebted to Svante Ersson (Umea University) for the data analysis.

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Part 2

Global Warming and Human Health: Impacts on the Spread of Infectious Diseases

3

Global Warming and Epidemic Trends of an Emerging Viral Disease in Western-Europe: The Nephropathia Epidemica Case

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1. Introduction

Hantaviruses were first described in Korea in 1978, and are an important group of "new" pathogens, now constituting the most widely distributed zoonotic (i.e. transmitted from vertebrated animals to humans) viruses on earth. Hantaviruses are "emerging" viruses, and are now confirmed as being the only viral haemorrhagic fever agents with a worldwide distribution, including even the temperate Northern hemisphere (Clement et al. 2007a). They are spread by wild rodents (and perhaps also by insectivores), infecting man via their aerosolized but infectious excreta. So far, at least 23 different hantavirus species are officially recognized, each with its own main rodent reservoir, and hence specific geographical spread (Maes et al, 2009). The most important pathogens are *Hantaan* and *Seoul virus* in Asia, *Puumala* and *Dobrava virus* in Europe and West-Russia, and *Sin Nombre* and *Andes virus* in the Americas. American hantaviruses, discovered only in 1993, affect mainly the human lung and cause the "hantavirus cardio- pulmonary syndrome" (HCPS), with a fatality rate of about 35%. By contrast, all Old World hantaviruses are targeted mainly to the human kidney resulting in the "haemorrhagic fever with renal syndrome" (HFRS), an often epidemic form of acute kidney injury (AKI), resulting in a rapidly progressive, but ultimately self-remitting acute renal failure (Clement et al., 2007a, 2007b). Among hantaviral pathogens, the European *Puumala virus* (PUUV) is the least severe. It causes an infection, aptly named "nephropathia epidemica" (NE), which in fact is a mild form of HFRS, with a very low fatality rate of 0.5-0.1 %. However, more severe cases do occur, resulting in multi-organ involvement, necessitating sometimes live-saving acute haemodialysis and/or mechanical lung ventilation in intensive care settings (Clement et al., 1994a, 2007a, 2007b).

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The reservoir and vector for PUUV is a member of the Cricetidae family, the bank vole (*Myodes glareolus,*-formerly named *Clethrionomys glareolus*), one of the most common wild rodents in Europe and W.-Russia.

Since the early '80 s, Belgium has developed a pioneering and long-standing interest for hantaviruses in the country and in its neighbours. The presence of a PUUV-like antigen in Belgian bank voles (Van der Groen et al., 1983a), the earliest clinical description of three NE cases (Van Ypersele de Strihou et al., 1983), and a first sero-epidemiological study (Van der Groen et al., 1983b). were all published in 1983, the same year wherein the first NE cases were also published in France (Méry et al., 1983). From 1983 on, the serodiagnosis of NE was improved by the isolation in Belgium of a PUUV strain, CG 18-20, derived from a bank vole captured in Russia (Tkachenko et al., 1984). It allowed the seroconfirmation of early Belgian NE cases and even of the first "autochthonous" German case in 1985 (Zeier et al., 1986). In fact, the very first serodiagnosis of a human PUUV infection in Germany occurred already in January 1984, in a Belgian military working and living in Germany, and admitted with NE in the (then) Military Hospital in Cologne, Germany (Clement & van der Groen, 1987). CG 13891, the first autochthonous Belgian PUUV strain was isolated in 1985 (Verhagen et al., 1986)(Van der Groen et al., 1987). This local PUUV strain (later by French authors erroneously also called IPH 90-13) appeared more sensitive and more reliable for screening and diagnosing purposes in W.-European NE cases than the former Russian or Scandinavian reference PUUV strains (Saluzzo et al., 1990) (Le Guenno et al., 1994). Thus, the Belgian prototype strain CG 13891 was substantial in the serodiagnosis of the first Dutch NE case in 1986 (Koolen et al., 1989), the first NE outbreak in The Netherlands (1989, around Twente)(Osterhaus et al. 1989), the first NE outbreak in Germany (1990, around Ulm, Baden-Württemberg) (Clement et al., 1996), and the Belgian as well as the French cases in the first joint Franco-Belgian NE outbreak in 1993 (Clement et al., 1994b) (Le Guenno et al., 1994). Native or recombinant versions of CG 13891 were successfully used by the national hantavirus reference laboratory in Belgium, founded by one of us (JC), and form likewise the base for current NE serodiagnosis in France (Le Guenno et al., 1994) (Billecocq et al., 2003)(Clement et al., 2010). These novel screening antigens allowed between 1985-1987 a pioneer study on a total of 21,059 healthy Belgian blood donors, yielding 275 (1.30%) PUUV IgG seropositives, confirming hereby a past (but mostly asymptomatic) NE episode. However, a significantly higher PUUV seroprevalence was found in the densely forested south, versus the sparsely forested north of the country, thus demonstrating statistically and for the first time in W.-Europe an apparently profound impact of a forest biotope on this emerging pathogen (Clement & van der Groen, 1987). Moreover, with the use of these same PUUV screening antigens, we could demonstrate that all early European epidemics of NE were linked indeed to a significantly higher presence of PUUV antibodies in the blood and/or of PUUV antigen in the lungs of bank voles (*Myodes glareolus*), captured locally after such a first outbreak, respectively in Chimay (Belgium), Ulm (Germany) and Twente (The Netherlands) (Clement et al., 1993).

2. The mast hypothesis: of mast, mice and men

As demonstrated in the Introduction, Belgium has a pioneer NE registration history, spanning now well over 28 years (1983-2010), an exceptionally long observation period for an emerging viral illness, virtually unknown before in Europe. During this 28-years registry, a total of 2,790 Belgian and clinically symptomatic NE cases were seroconfirmed. Bearing in mind that probably less than 20% of all PUUV infections are actually registered as such (Brummer-Korvenkontio et al., 1999), the real number of PUUV infections may well have been in fact 5 times higher. Looking at the yearly NE numbers over this long time scale (Fig. 1), the lower results in the first 10 years, i.e. up to 1993, can be ascribed to a lower medical awareness and less performing laboratory capacity to seroconfirm suspected cases. However, these same arguments could not be maintained to explain the cyclic occurrence of ever increasing NE peaks noted since 1993, first with a 3-years, and later even with a 2-years interval (Fig. 1).

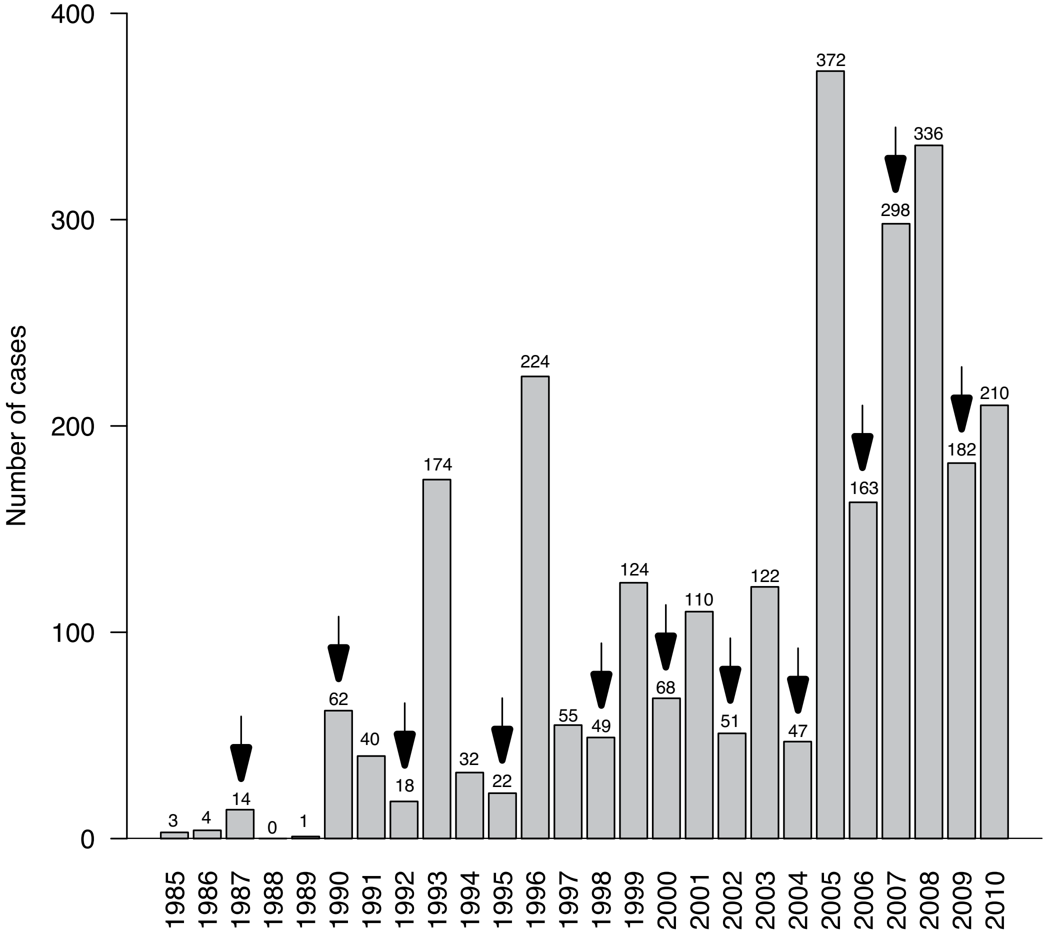

Fig. 1. Evolution of the number of NE cases officially registered in Belgium, 1985-2010. Black arrows indicate a "mast year". Note that from 1992 on, each mast year is followed by a NE peak. Moreover, since 2005, an almost continuous epidemic trend is maintained.

With these elements, an underlying ecologic mechanism related to changing climatological conditions was suspected, formulated in 2005 as the "mast hypothesis" (Clement et al., 2005). "Mast" is the common denomination for the seeds of deciduous broad-leaf trees, in this case mainly beechnuts, and to a lesser degree also acorns. Mast constitutes the main staple food for bank voles, and it was suggested since 1994 (Clement et al., 1994b) that a higher food supply in autumn (called further in the text "heavy masting") might promote a better winter survival and earlier spring breeding in voles, leading to rodent densities up to 20 times the norm starting at the next spring. Thus, after such a heavy "mast year", human population could be confronted from the next spring on with an ensuing "mice year", leading to NE outbreaks, and explaining also the observed NE cyclicity. From the 1992 on, it is striking that each mast year in the subsequent 19 years was followed indeed by a more or less marked NE peak in Belgium (Fig. 1). The difference between the low NE numbers in mast years, and the high NE numbers one year later (i.e. the NE peaks) is highly significant (Clement et al., 2009).

Of note, even under the most favourable conditions, a deciduous broad-leaf tree is biologically not able to produce maximal crop during two subsequent years, as confirmed by the annual registry of beechnuts and acorns by the Walloon Forestry Department in the South of Belgium (Table 1). However, an alternation of heavy beech masting, followed by heavy acorn masting the next year is exceptionally possible, as we witnessed in 2006, respectively in 2007.

Rating		Year
Native oak	Beech	
+++	+++	1995
0	0	1996
0	0	1997
+++	++	1998
0	0	1999
+++	+++	2000
0	0	2001
0	+++	2002
0	0	2003
+++	+++	2004
0	0	2005
+	+++	2006
+++	+	2007
0	0	2008
+	+	2009

+++ = very good year, ++ = good year, + = moderate year, 0 = weak or absent seed production.

Table 1. Rating of beech and native oak mast production 1995-2009 in the Ardennes, forested South of Belgium. Note that maximal seed crop production during two consecutive years by the same tree species is biologically impossible. Source: Le Comptoir Forestier-Région Wallonne (From: Barrios et al., 2010).

3. The rodent reservoir and its biotope: the role of the beech

Overall, NE remains an epidemic (or sporadic) kidney disease prevalent almost exclusively west of the Ural Mountains, i.e. in a part of Europe wherein two entirely different biotopes predominate: the northern coniferous forest or taiga, and the more southern temperate broadleaf forest. A third very bare biotope, the tundra, is much less important and present only in the far-North region of the current Russia. Bank voles prefer a habitat with trees for protection from the air, a thick protective ground layer of fallen coniferous needles or deciduous leaves, and sufficient moisture, the so-called "wet habitat", in which they thrive best (Verhagen et al., 1986). So, the favourite biotope of bank voles are the temperate forests of W.-and C.-Europe, and the boreal forests in Fenno-Scandia. This simple but often overlooked fact explains why NE is virtually absent from most of the South of Europe, whose predominant biotope, the "Mediterranean shrub", is much drier, has less trees, and offers less protective ground layer.

As far as the temperate broadleaf forests are concerned, and from 1992 on, we noted that most NE cases occurred in the Ardennes (forested South of Belgium), on both sides of the Franco-Belgian border around the river Meuse, and particularly in very limited areas wherein beechnuts were abundant, and not so much acorns. That is, areas with a dense coverage of the same deciduous broad-leaf tree species, the European beech (*Fagus sylvatica*) seemed to predispose to an abundance of local bank voles, and consequently to outbreaks of NE (Clement et al., 1994b). Later on, with increased assessment of the spread of NE in temperate Europe, it became clear that the W.-European regions with the highest endemicity of NE, were exactly corresponding to the regions with a dense beech tree coverage, i.e. not only the French and Belgian Ardennes, but also the whole North-East of France, and the South of Germany (Skjøth et al., 2008). Of note, another important European broad-leaf tree, the European native oak (*Quercus robur* and *Q. petraceae*), is clearly present in most of South-Europe, including Portugal and South-& Central- Spain (Skjøth et al., 2008), regions where the bank vole is totally absent, and where, not surprisingly, not a single NE case has hitherto been documented.

Baden-Württemberg in the South of Germany is densely covered with beech trees. More than two thirds of all current German NE cases are localized in Baden-Württemberg, the same region where indeed the first NE outbreak was noted already in 1990 (Clement et al., 1996). Endemic NE in this "Land" is now by far the highest in W.-Europe. Its population (10.7 million) is comparable to that of Belgium (11 million), but the 2007 NE incidence was 3.6 times higher ($10.1/10^5$) than the record 2005 incidence ($2.8/10^5$) for Belgium. (Piechotowski et al., 2008)(Schwarz et al., 2009). It is striking that in Baden-Württemberg, districts with the highest beech forest cover (15% or more) correlate significantly with the highest district NE incidences ($50/10^5$). Moreover, for each 5% increase in beech coverage per district, risk for NE is almost doubled (Schwarz et al., 2009). Thus, the prerequisite for an appropriate biotope for bank voles to generate W.-European NE epidemics can be summarized as the presence of deciduous broad-leaf forests with a predominance of beech trees, and a sufficient degree of humidity.

4. Russia and Fenno-Scandia, two other regions in Europe highly endemic for NE

Of the three regions endemic for NE, being Russia, Fenno-Scandia and W.-Europe, we will discuss in depth only the latter, because the new insights in some ecological mechanisms might be only relevant for W.-Europe, and not applicable in the two former regions. However in Russia alone, 68,612 HFRS cases, most of which NE, were registered (i.e. often hospitalized) between 1978 and 1992, peaking in 1985 with 11,413 cases (WHO, 1993).

Moreover, an even higher total number of 76,000 HFRS cases, the vast majority again being NE, was registered in a subsequent shorter study period of only 9 years (1999-2008). Of these Russian HFRS cases, 87% occurred on the forested foothills of the Ural mountains, or in the steppe-forest regions around Volga river, i.e. in the European part of the country, resulting in a high average annual incidence of $20/10^5$. (Tkachenko et al., 2010). The reasons for this apparent increase of European-Russian NE incidence are not entirely clear, and a possible impact of global warming has not been studied systematically. However, cyclic NE peaks have also been noted during a 1973-2002 study period, linked to cyclic peaks in local bank vole populations every 2-4 years (mostly 3 years). These "mice years" started with higher reproduction of voles under the snow during winter, and were correlated ($R= 0.86$) with abundant linden harvest during previous autumn (Bernshtein et al., 2010).

With around 1,000 NE cases/year, Finland has reported between 1979 and 2010 more than 70% of all cases registered within W.-Europe. Again, an increasing trend was noted in the last decade, with peaks of 2,300 cases in 1999, 2,603 in 2002, 2,526 in 2005 and an all-time high of 3,259 cases in 2008 (National Public Health Institute of Finland, 2011). With its population of 5.2 million, the 2008 Finnish incidence thus reached $62.6/10^5$, the highest in the world. In Sweden, NE has been registered from 1989 on. Incidence averaged between 200-400/year, but peaked suddenly to 2,195 in 2007, and again to 1,483 in 2008 (Olsson et al., 2009). Winter NE peaks are characteristic for Fenno-Scandia, in contrast to the summer peaks in W.-Europe. Global warming during wintertime has been incriminated somewhat paradoxically for an increased contact between humans and voles, since the decreased protective snow cover in Fenno-Scandia is supposed to favour bank voles' entry into human dwellings, in search for food and shelter. Overall, the 3-yearly NE peaks in Fenno-Scandia are ascribed to predator-prey cycles, a mechanism very different from the one operative in temperate Europe (Olsson et al., 2009).

Indeed, the vegetation type that covers most of Norway, Sweden and Finland is another difference, since the boreal forest or taiga consists mainly of pine trees, in contrast to the temperate forest in the rest of Europe, wherein deciduous broad-leaf trees predominate.

5. The role of global warming in the NE surge of four W.-European countries

If our "mast hypothesis" could explain recurrent NE outbreaks in Belgium as showed in chapter 2, it could not explain the noticeable increase of NE cases during last years, nor the smaller interval between subsequent NE peaks, recently every 2 years instead of every 3 years previously (Fig. 1). Indeed, from 2005 on, an epidemic trend of NE in Belgium was heralded, resulting in a record total of 1,554 cases for the last six years (2005-2010) or a robust mean of 259.0 cases/year, versus a mean of only 56.18 cases/year for the previous 22 years, totalling 1,236 cases. This difference between recent and former NE is statistically highly significant ($p<0.001$, $\alpha=0.05$), and again cannot be explained by increased medical awareness alone. As recently noted for other, mostly tropical, infections, an influence of global warming was suspected. It was known that broad-leaf trees reacted with increased bud formation as a survival strategy when confronted with prolonged heat during summertime, particularly if this is enforced by marked drought (Pucek et al., 1993). Moreover, tree flower formation in spring can be stimulated by higher spring temperatures, particularly during the month of April (Piovesan et al., 2001). Higher bud formation in year-1, especially if combined with higher flower formation in the year 0, can result in a (much) higher seed crop harvest in autumn of the same year 0, or "heavy masting" (Bennet et al, 2009). However plausible this approach might appear, it should be supported by hard data and convincing statistics, not available until recently in Europe. For this purpose, a 2009 study was started in Belgium. In a second step, conclusions found for Belgium were matched against NE data registered in its neighbouring countries, France, The Netherlands, and Germany.

5.1 The Belgian study

Base elements for this 1996-2007 study period (Clement et al., 2009) were monthly NE data for Belgium delivered from 1996 on by the Scientific Institute of Public Health (SIPH), Brussels, and the the daily and monthly data of mean temperature (in degrees Celsius) and precipitation (in mm), delivered by the Royal Meteorological Institute (RMI), situated in the centre of the country in Ukkel (Brussels). This station is considered to be representative for the Belgian territory, despite regional variations.

In a first approach, we tried to correlate climatological 1996-2007 data to the seasonal NE data of the same 12 years. Annual average daily temperature in this period was with 11.4C° significantly higher than in the previous decade 1985-1995 with only 10.7°C (p= 0.0001), but annual average daily rainfall was not (2.37 versus 2.30 mm, p=0.5461). Harsh winters with mean monthly temperatures below 0°C were completely absent in the 1996-2007 study period, whereas monthly mean winter temperatures below 0°C were still noted begin 1985 through 1987 (Clement et al., 2009).

As known already before this study, each NE peak was preceded since 1993 by a mast year (Fig. 1), resulting in significantly higher NE case numbers during these peaks (Spearman R = -0.82; P = 0.034). NE peaks were significantly related to warmer autumns the year before (R = 0.51; P < 0.001), hotter summers two years before (R = 0.32; P < 0.001), but also to colder (R = -0.25; P < 0.01) and more moist summers (R = 0.39; P < 0.001) three years before. The correlation improved even when only July was selected as the most representative summer month. Autumn mast production was particularly heavy in 2004 and to a lesser degree in 2007 (Table 1), resulting each time a year later in the two highest NE peaks ever registered to date in Belgium. The summer 2003 had mean temperatures of the months June, July and August consecutively on or above 20°C (mean summer temperature in Belgium 19.7 °C, normal only 17 °C), resulting in what was estimated to be the hottest summer in Europe since 1540. This stimulated flower bud initiation in oaks and even more in beeches, thus paving the way in autumn 2004 for the heaviest masting ever recorded in the country (Table 1), which in turn resulted in 2005 in the most important NE outbreak (372 cases) observed in Belgium to date (Fig. 1).

The next NE peak in 2007, third highest with 293 cases, is less obvious to explain, since it appeared to be a acorn mast year by itself (Fig. 1)(Table 1). However, beech mast production end 2006 was also fairly pronounced (Table 1), and we suppose this food supply for voles was optimized again by very warm autumn temperatures (mean September 18.4 °C, and October 14.2 °C), and one of the mildest winters since decades, allowing early winter breeding in voles and a denser rodent population early 2007, as indicated by the high NE incidence during the first months of 2007 (Clement et al., 2009).

In contrast to winter temperatures or rainfall parameters, showing only very weak or negative correlations, a positive and strong (R = 0.51) highly significant correlation was found for autumn temperatures, the year before NE occurrence, or year-1. Fall climate factors cannot influence any more mast formation of the same year itself, but still can influence favourably other vegetal food sources and the bank vole population itself. Higher staple food availability during increased tree seed production in autumn may allow higher bank vole survival not only during the subsequent winter, but also already in the (late) autumn of the mast year itself, particularly if this is accompanied by milder temperatures as observed during last years (see hereunder). In this hypothesis, human population is already at risk for higher NE incidence during late autumn and early winter of a mast year, as observed indeed in Belgium (Clement et al., 2009). Moreover, "late winter NE peaks" subsequent to heavy autumn masting may ensue the following year, hereby announcing already very early an important NE peak that same year: the record number of 22 Belgian NE cases in February 2005 was heralding the most important summer NE peak ever recorded in Belgium, and an even higher February 2008 record with 28 cases announced the second highest (336 cases) peak that same year (Clement et al., 2009).

A recent similar study, relying on the same Belgian 1995-2007 NE registry, came independently to exactly the same conclusions: NE outbreaks are favoured by hot summers two years before, and warm autumns one year before the facts (Tersago et al., 2009).

5.2 The case of France, Germany and the Netherlands

In a second study, we examined if our "mast hypothesis" was also valid for three neighbouring countries with registered NE data, being France, Germany, and the Netherlands. Mast years are simultaneous in most countries of W.-Europe, including even the British Isles (Bennett et al., 2009), but exceptions can occur due to regional climatological differences. Thus, for the sake of simplicity, we maintained in this international study the same mast years, and even the same mean temperatures for summer and autumn as for Belgium, with the exception however of the years 2006 and 2009, in which beech masting in (South-)Germany appeared to be much stronger than in the three other considered countries (Fig. 2). Indeed, it seems admissible that climatological differences between (South-)Belgium and its direct neighbours (North-East France and The Netherlands) might be less pronounced as to the more distant South-Germany, where the vast amount of NE cases are situated (see chapter 3).

In France, a total of 2,036 cases were reported in 28 years (1983-2010) (Institut National de Veille Sanitaire, France, 2007) with yearly fluctuations surprisingly similar to those in neighbouring Belgium, i.e. often after a mast year (Fig. 4). It is striking that the highest French NE peak (253 cases) so far, was also recorded in 2005, likewise after heavy masting in 2004, itself a consequence of the infamous summer 2003, which in France had been even hotter than in Belgium.

The same phenomenon, but in a much dampened form was observed in the Netherlands, where a total of 121 NE cases was recorded in 16 years (1995-2010) (National Institute for Public Health and the Environment [RIVM], Bilthoven, 2011). (Fig. 4). The mostly very modest numbers of NE cases in this country are probably due to a lack of dense coverage by beech trees. In Germany, official NE registration started only in 2001, but showed a similar cyclic pattern with rising incidences, resulting in a record total of 4,880 cases in 10 years (2001-2010) (Robert Koch Institut, Berlin, 2011). Thus, the four studied countries together passed in 2005 for the first time the mark of more than 1,000 cases (total 1,019) of an until then underdiagnosed and ill-known emerging infection, a rare example of tree ecology having an impact on a human kidney disease. Germany is recently confirming itself as the

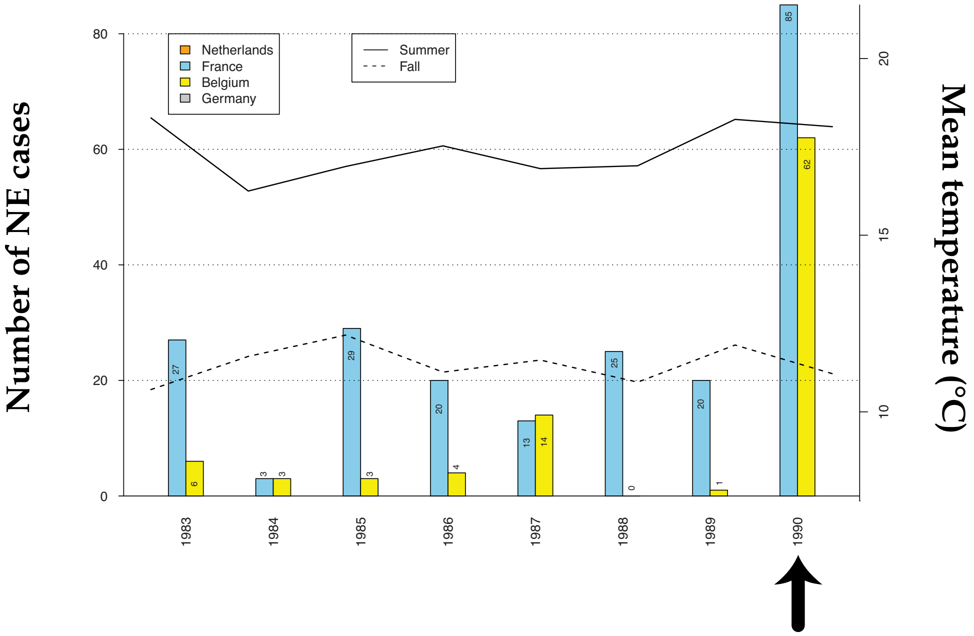

Fig. 2. NE cases 1983-1990 in France and Belgium. The black arrow indicates a possible mast year. Exact 1983-1989 mast data are lacking. Full line indicates mean summer temperatures, dotted line indicates mean autumn temperatures, both in Belgium.

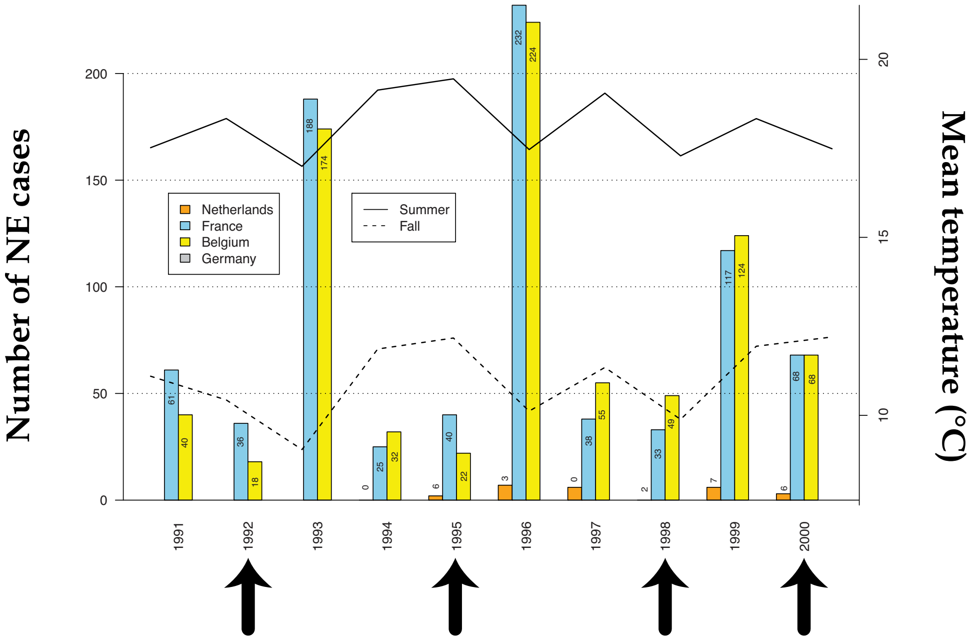

Fig. 3. NE cases 1991-2000 in France, Belgium, and The Netherlands. Black arrows indicate mast years in Belgium. Note that each mast year is followed by NE peaks, the latter often 2 years after warmer summers.

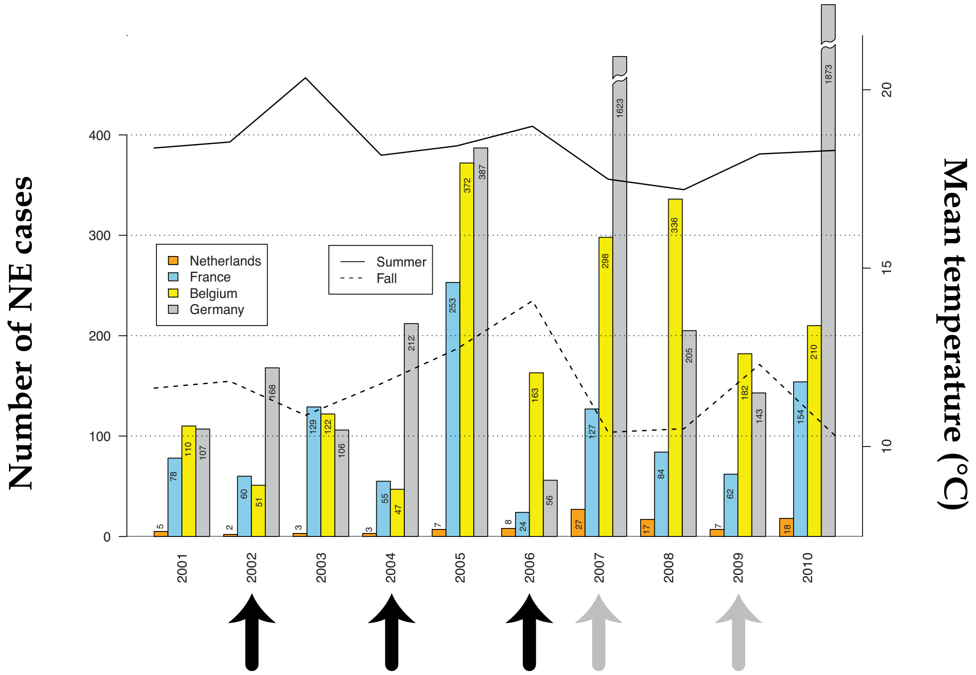

Fig. 4. NE cases in four W.-European countries. Black arrows indicate beech mast years in Belgium. The gray 2007 arrow indicates a heavy oak mast year. The gray 2009 arrow indicates a weak mast year in Belgium, but a heavy beech mast year in (South)-Germany. Note the high 2003 summer temperature, inducing the major joint 2005 NE peak in the four countries.

most endemic country for NE, presenting however some regional aspects different from its neighbours. In contrast to France, and apparently even more pronounced than in Belgium, it witnessed heavy beech masting in autumn 2006, leading to a record 1,623 NE cases in 2007. This record year was preceded by the mildest winter ever recorded in Germany, a very warm spring 2007, and confirmed by a noticeable increase in local bank vole population begin 2007 (Piechotowski et al., 2008). Of note, the Netherlands witnessed in 2007 also their highest NE peak (27 cases). However, the German record 2007 year was surpassed another time in 2010, with an all-time high of 1,873 cases (Fig. 4), again after strong local beech masting in autumn 2009, which in Belgium was much less pronounced (Table 1). It is also noticeable that the two highest German NE peaks were preceded each time by a clear surge in mean autumn temperatures in 2006, respectively in 2009 (Fig. 2), which seems to confirm our statistically significant correlation with warmer autumns found previously in Belgium (chapter 5.1). The role of warmer winters is less clear, although a 7-years (2001-2007) NE risk factor study in Baden-Württemberg concluded that a combination of a mild winter and prior heavy masting constitute the greatest risk for a subsequent NE outbreak (Schwarz et al., 2009). This seems now somewhat in contradiction with the fact that the record 2010 peak was preceded in Germany by a harsh 2009-2010 winter, as in many other European countries. Thus, the impact of low winter temperatures as a separate NE risk factor needs further study, the more so since it is known from Scandinavian countries that a constant winter cover with snow can have a rather protective effect on vole populations (Olsson et al., 2009). All by all, heavy beech masting seems to imply in temperate Europe the greatest risk, since it appeared in the same 2001-2007 NE risk factor study in Baden-Württemberg that an abundant supply of beechnuts conferred by itself already a significant risk ratio of 2.86 (95% confidence interval 1.81-4.50)(Schwarz et al., 2009).

6. Other approaches in the future-and already in the present

Since vegetation characteristics are an important mechanism for understanding and even for predicting NE outbreaks, exhaustive new vegetation monitoring techniques, such as remote sensing by satellite, can now offer valuable techniques and data sources. With the help of a team of bio-engineers, we started satellite monitoring of different vegetation indices and climatological parameters in a series of collaborative studies. A first preliminary finding was that during a 2001-2007 observation period at the same 10 different locations in Belgium and France, a significant increase of the forest "length of the growing season" was observed, most pronounced in the densely forested areas, being also NE hot foci (Barrios et al., 2010). Moreover, a mathematical so-called multiple input-single output (MISO) model was developed, in which the inputs were average measured monthly precipitation and temperature in Belgium, as well as the estimated "vole carrying capacity", expressed as number of voles per hectare, and based mainly on the yearly mast production. The output was the yearly observed number of NE cases in Belgium over the same 12-years study period (1996 – 2007) (Amirpour Haredasht et al., 2011). Since the observed output could be fairly validated by the input calculations, the next step will be to verify if this MISO model will allow us to predict future NE outbreaks in Belgium and in its neighbouring countries.

7. Conclusion

Global warming is the most evident explanation for the epidemic trend of NE, an emerging rodent-borne hantaviral disease, targeting mainly the kidney in humans. The correlation between higher temperatures, mainly during summers and autumns of the last decade, and higher NE peaks was proven to be highly significant in Belgium. Since occurrence and evolution of NE peaks in three adjacent countries, France, Germany and The Netherlands, was very similar to the situation in Belgium, it can be assumed that similar temperature-driven ecological mechanisms were likewise operative in these countries. Consequently, NE is now established as the most frequent infectious cause of acute (but self-remitting) kidney injury (AKI) in W.-Europe, as it was already the case in the two other NE-endemic regions in Europe, W.-Russia and Fenno-Scandia.

In recent medical literature, global warming has been invoked mainly as a driving force behind some (sub)tropical arthropod-borne infections, such as malaria, dengue, and Congo-Crimean haemorrhagic fever (CCHF), via an expansion of the habitat of the responsible vectors, mostly mosquitoes or ticks. This is the first report on the influence of global warming on an "autochthonous" disease, via expansion of the local rodent population. To our knowledge, this study is also the first assessment of a "new" kidney disease by a mathematical formula, or indirectly even by satellite monitoring.

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4

Malaria Transmission in the African Highlands in a Changing Climate Situation: Perspective from Kenyan Highlands

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1. Introduction

Vector-borne diseases are among the diseases that have been linked with climate change (IPCC. 2001). Malaria is probably the deadliest climate sensitive vector-borne disease (Githeko et al. 2000). About 90% of the 300-500 million cases of the reported malaria cases worldwide come from Africa. In the late 80s to the 90s, malaria epidemics occurred frequently in western Kenya highlands, often taking the population by surprise. The epidemics were caused by *Plasmodium falciparum* and transmitted by *Anopheles gambiae* and *Anopheles funestus*. Epidemics were associated with high morbidity and mortality in all age groups, with prevalence of the disease rising from about 20% to about 60%. The case mortality in functional health facilities were estimated at about 7.5% (Githeko and Ndegwa 2001). The malaria transmission system involves a complex interaction between humans, mosquitoes, the plasmodium parasite, climate and the physical environment.

Warming of the climate is expected to lead to latitudinal and altitudinal temperature increase. The temporal and spatial changes in temperature, precipitation and humidity that are expected to occur under different climate change scenarios will affect the biology and ecology of vectors and intermediate hosts and consequently the risk of disease transmission. The risk increases because, although arthropods can regulate their internal temperature by changing their behaviour, they cannot do so physiologically and are thus critically dependent on climate for their survival and development (Lindsay and Birley 1996).

Temperature is inversely related to altitude, thus the high-elevation areas in Africa, or highlands, generally exhibit low ambient temperature, which restricts the development of vectors and parasites. Because malaria transmission rate is temperature-dependent, any factor that alters the temperature in the highland would reduce the duration of parasite development, larval development and increase the mosquito biting rates, and subsequently increase malaria transmission in the highlands.

The greatest effect of climate change on transmission is likely to be observed at the extremes of the range of temperatures at which transmission occurs. For many diseases these lie in the range 14–18 °C at the lower end and 35–40 °C at the upper end. Warming in the lower range has a significant and non-linear impact on the extrinsic incubation period (Watts et al. 1987), and consequently disease transmission, while, at the upper end, transmission could cease. However, at around 30–32 °C, vectorial capacity can increase substantially owing to a reduction in the extrinsic incubation period, despite a reduction in the vector's survival rate (Githeko et al. 2000).

Climatic conditions affect malaria transmission in a number of ways. The development rate of immature mosquitoes is very much temperature dependent. Below 16°C, development of *Anopheles gambiae*, the main malaria vector in most parts of Africa, will completely stop, and the larvae will die in water temperature below 14°C. In low-temperature conditions, mosquito larval development is severely delayed and high mortality incurs. In the adult stage, increase in ambient temperature will accelerate the digestion of blood meals taken by mosquitoes leading to increased human biting frequency and malaria transmission. While female mosquitoes obtain blood meal to develop their eggs, they pick up malaria parasites which they develop and become infectious to the next human host that is subsequently fed upon. Increased biting frequency and faster blood meal digestion also means increased fecundity and better reproductive fitness. Increased temperature also shortens the development time for the malaria parasite in the mosquito (Githeko et al. 2000).

Mosquito species such as the *Anopheles gambiae* complex and *An. funestus* are responsible for transmission of most of the malaria in the continent of Africa and are sensitive to temperature changes as immature stages in the aquatic environment and as adults. If water temperature rises, the larvae take a shorter time to mature (Munga et al. 2007) and consequently there is a greater capacity to produce more offspring during the transmission period. In warmer climates, adult female mosquitoes digest blood faster and feed more frequently (Afrane et al. 2005), thus increasing transmission intensity. Increased biting frequency and faster blood meal digestion also means increased fecundity and better reproductive fitness (Afrane et al. 2006). Similarly, malaria parasites complete extrinsic incubation within the female mosquito in a shorter time as temperature rises (Afrane et al. 2008) thereby increasing the proportion of infective vectors. Warming above 34 °C generally has a negative impact on the survival of vectors and parasites (Rueda et al. 1990).

In addition to the direct influence of temperature on the biology of vectors and parasites, changing precipitation patterns can also have short- and long term effects on vector habitats. Increased precipitation has the potential to increase the number and quality of breeding sites for mosquitoes and the density of vegetation, affecting the availability of resting sites (Githeko and Ndegwa 2001).

In addition to warming of the climate, environmental changes, such as deforestation, could increase local temperatures in the highlands, which in turn accelerates vector and parasite development leading to increased transmission. Deforestation is a common event in many regions of Africa. For example, Malava forest, a tropical rain forest in Kakamega district, has shrunk from 150 km² in 1965 to 86 km² in 1997 (FAO 1993). In the East African highlands, 2.9 million hectares of forest were cleared between 1981 and 1990, representing an 8% reduction in forest cover in one decade (Lindblade 2000). Land use and land cover changes may modify the temperature and relative humidity of malaria vector habitats in the highlands. It was demonstrated that in the southwestern highlands of Uganda, maximum and minimum temperatures were significantly higher in communities bordering cultivated swamps than in those near natural swamps (Lindblade 2000). These changes in regional climate and microclimatic conditions of mosquito habitats causes abundant changes of the existing mosquito species, and may make some areas permissive to the proliferation of new species. For instance, deforestation caused the introduction of *An. gambiae* into a habitat that was previously dominated by *An. moucheti* in Cameroon (Manga et al. 1995). In northern Brazil, *An. marajoara,* a species previously of minor importance, has become the principal malaria vector following changes in land use (Conn et al. 2002).

2. Effect of microclimate changes due to deforestation on malaria transmission

In many parts of the world, including Africa and South America, changes in land use or land cover, especially deforestation, have been linked to changes in the microclimate of the area in question. These changes in microclimate due to changes in land uses and cover has been linked to changes in malaria transmission. The changes in land use affect temperature, humidity and rainfall or precipitation patterns of the area. These also, goes to affect the microhabitat of malaria transmitting mosquitoes and the parasite they transmit, thus affecting malaria transmission in the area. The link between changes in land use and land cover and malaria transmission has been clearly established, which are highlighted and discussed below.

2.1 Deforestation impact on malaria vectors: case studies from western Kenya highlands

We conducted studies in western Kenya to assess the possible effect of deforestation on the microclimate and the subsequent effect on malaria transmission indices in the area. We measured indoor and outdoor temperature and humidity in the forested and deforested areas in the highlands. Entomological parameters such as the duration of gonotrophic cycle and biting frequency, reproductive fitness, survivorship and development of mosquitoes were studied. The sporogonic development of malaria parasites in the mosquito was also studied. Vectorial capacity which measures the potential rate of contact between infectious vectors and susceptible hosts was calculated from these parameters. It is the product of the vector density in relation to man, the proportion that bite man twice, and the expectation of the infective life span of the vector (MacDonald 1957; Garrett-Jones and Shidrawi, 1969).

We found that deforestation increased the indoor mean temperature by 1.8 ^{0}C. Mean maximum and minimum temperatures were increased by 2.3^{0}C and 1.5 ^{0}C respectively. Outdoor temperatures were increased by 0.5^{0}C. The mean indoor relative humidity in the deforested area was about 22.6% lower than in the forest area during the dry season (79.88% vs. 57.29%) (Afrane et al. 2005; Afrane et al. 2006; Afrane et al. 2008; Afrane et al. 2007). Temperature and humidity were measured in houses in study sites that were originally forest but large portions of it have been deforested. Canopy coverage was over 60 % in the forested area and less than 10 % in the deforested area. Temperature and humidity were measured using HOBO® data loggers (Onset Computer Corporation, Bourne, Massachusetts, U.S.A.) which were placed inside all the human-habited experimental houses in the forested and deforested areas of the site. There were five experimental houses in each of the areas.

Since the general body functions of mosquitoes are temperature dependent, these small changes will have a biological significance on their life history characteristics. The mean minimum and maximum temperatures are very crucial for the development of mosquitoes and the parasite they transmit and by extension malaria transmission. Below 16^{o}C, development of many malaria vectors in Africa will completely stop, and the larvae will die in water temperature below 14^{o}C. The parasite in the mosquitoes has an upper and lower threshold of 32^{o} C and 18^{o}C respectively (Boyd 1949; MacDonald 1957).

The changes in the microclimate that were observed as a result of the deforestation caused a decrease in the duration of gonotrophic cycle of mosquitoes by 1.7 days (4.6 vs 2.9 days). The duration of gonotrophic cycle is the the period between the taking of a blood meal by a mosquito through digestion of the blood meal and oviposition or egg laying (Santos et al. 2002). The decreased duration of the gonotrophic cycles implies a decrease in human biting frequency from an average of once every 5 days to once every 3 days (Afrane et al. 2005). Increase in biting frequency means that the *An. gambiae* will feed more frequently on humans and in the process picks up infection, become infective and then transmit the parasite when they next bite another person.

The changes in the microclimate due to deforestation however, did not favour the survival of the adult *An. gambiae*. The effect of deforestation decreased median survival of *An. gambiae* by 5-7 days. The *Anopheles gambiae* mosquito rather prefers areas with high humidity. Since deforestation caused a decrease in the humidity, it rather caused a decrease in the survival of *An. gambiae*. However, despite the decreased survivorship of the mosquitoes due to the effects of deforestation, mosquitoes still had an enhanced reproductive fitness by 40%. Over the course of their life span, mosquitoes in deforested areas laid far more eggs and thus, had better fecundity than mosquitoes in the forested areas by over 65% (Afrane et al. 2006). The reproductive fitness of a mosquito is its ability to reproduce over its entire life span. Fecundity, measured by the number of offspring a female mosquito can produce, is a major fitness trait (Hard et al. 1989.). The implication of these findings is that *An. gambiae* could increase its population within a short time when breeding sites are available. This could potentially lead to an increase in malaria transmission when infected humans are available.

The microclimatic changes also caused the parasite in the *An. gambiae* to have a reduced sporogonic development time from an average of 14 to 12.6 days (Afrane et al. 2008). Both oocyst and sporozoite development times were reduced by 1 and 1.4 days respectively. Reduced parasite development time in mosquitoes implies that the parasite will take a shorter time to become infective inside the mosquito and therefore will be transmitted faster from the mosquito to humans.

Vectorial capacity of the malaria vector was then calculated using the parameters that were measured in the studies described above.

$$\text{Vectorial capacity} = \frac{ma^2p^n}{(-\log_e p)}$$

Where m is the relative density of vectors in relation to human,
a is the average number of humans bitten by one mosquito in one day,
p is the proportion of vectors surviving per day, and
n is the duration of sporogony in days. (MacDonald 1957).

This formula postulates that the length of the sporogonic development of malaria parasites in mosquitoes, biting frequency and vector survivorship are the most important factors for vector-borne malaria transmission

We found that, deforestation substantially facilitated malaria transmission in the highland, as evidenced by two-fold increase in vectorial capacity (Afrane et al. 2008). These are shown in Table 1. Malaria is highly endemic in lowland areas. All the indices for malaria transmission were very much enhanced in the lowland site used for this study. This explains the huge difference between the lowland and two highland sites. In the highland sites, changes in the microclimate due to deforestation explain the changes in vectorial capacity of the two sites.

Site	Land use type	m	a	n	P	Vectorial capacity
Highland	Forested	3.05	0.198	13.9	0.927	0.54
	Deforested	4.64	0.233	12.8	0.917	0.96
Lowland	Deforested	7.85	0.465	11.7	0.923	8.30

Note.- m is the relative density of vectors in relation to human,
P is the proportion of vectors surviving per day,
a is the average number of men bitten by one mosquito in one day, and
n is the duration of sporogony in days.

Table 1. Estimated vectorial capacity of *A. gambiae* in forested and deforested areas in western Kenya highland and lowland.

2.2 Land use and land cover changes and malaria transmission

Land use and land cover changes have the potential to alter the micro-environment of malaria vectors which in turn affects their malaria transmission potential. In the highlands of Uganda, Lindblade and others (2000) compared mosquito density, biting rates, sporozoite rates and entomological inoculation rates between 8 villages located along natural papyrus swamps and 8 villages located along swamps that have been drained and cultivated. Since vegetation changes affect evapotranspiration patterns and, thus, local climate, they also investigated differences in temperature, humidity and saturation deficit between natural and cultivated swamps. They found that on average all malaria indices were higher near cultivated swamps. Maximum and minimum temperatures were significantly higher in communities bordering cultivated swamps. They found that the average minimum temperature of a village was significantly associated with the number of *Anopheles gambiae* s.l. per house. From their studies, it appears that replacement of natural swamp vegetation with agricultural crops led to increased temperatures, which may be responsible for elevated malaria transmission risk in cultivated areas.

To determine the effects of land cover types on mosquito productivity, Munga and others (2007) created semi-natural larval habitats within three land cover types (farmland, forest, and natural swamp) and filled them with *Anopheles gambiae* larvae. The mosquito pupation rate in farmland habitats was significantly greater than in swamp and forest habitats and larval-to pupal development times were significantly shorter. Land cover type may affect larval survivorship and adult productivity through its effects on water temperature and nutrients in the aquatic habitats. They found significantly higher water temperatures in farmland habitats than the other land cover types, which enhanced pupation rates and shortened development times. They also found a significant negative correlation of the occurrence of *An. gambiae* larvae with canopy cover and emergent plants in natural habitats. Their results suggest that deforestation and cultivation of natural swamps in the western Kenyan highland create conditions favorable for the survival of *An. gambiae* larvae, and consequently increase the risks of malaria transmission to the human population.

Other land cover changes such as swamp reclamation have been shown to have similar effects as deforestation on malaria vectors development. In other studies from western Kenya highlands, removal of swamp vegetation reduced shading and increased the breeding habitat water temperature by as much as 5 ^{o}C and whose effect reduced larval development time leading to increased vector productivity and abundance (Wamae et al. 2010). This has the potential to increase the population of mosquitoes and to which could also potentially cause an increase in malaria transmission if infected humans are available.

3. Proliferation of mosquito species to new areas

Deforestation has the potential to also change the microclimate of an area to become suitable to species that previously could not survive in the area. Each mosquito species has their own optimum survival conditions that allow them to survive or not to survive in an area. These survival conditions are mostly climate dependent. For instance, *An. gambiae* and *Anopheles arabiensis,* the most important vectors of human malaria in Africa are sibling species. *An. arabiensis* is either absent or shows a very low abundance in high-elevation areas where temperature is low and relative humidity and the amount of rainfall are high, but it is abundant in dry areas with less humidity which is the preferred habitat (Minakawa et al. 2002; Maharaj 2003). Studies were conducted by Afrane and others (2007) to investigate whether climate conditions in the western Kenya highlands were permissive to the development and survival of *An. arabiensis* and whether deforestation promoted *An. arabiensis* survivorship of immature and adult stages, using life-table analysis.

It was found that *An. arabiensis* larvae were able to survive in the deforested sites compared to the forested areas. Adult *An. arabiensis* placed in houses in the deforested area had an enhanced survival and better reproductive fitness than those in the forested area (Afrane et al. 2007). The implications of these findings are that, if the current trends of deforestation continue in the highlands, there could be a three vector system in the highlands, instead of the current two. This could potentially worsen the malaria transmission system in the highlands and could lead to the return of epidemics in the highlands. We expect that, environmental changes such as deforestation and global warming may facilitate the establishment of *An. arabiensis* populations in the highlands.

In the highland areas west to Mount Kenya which has an elevation of 1,720 – 1,921 m above sea level, malaria has been reported in the last 10 – 15 years. It was not clear whether these cases were introduced from the nearby lowland or resulted from local transmission because of no record of vector mosquitoes on the highlands. Chen and others (2006) reported finding mosquitoes breeding in the highlands. This means that the environment has become conducive for the proliferation of malaria vector species. Environmental changes and global warming could be a factor driving this emergence of malaria vectors to areas in mount Kenya region.

Manga and others (1995), working in an area that has been deforested to build a new airport in Cameroon, observed that deforestation caused the introduction of *An. gambiae* into a habitat that was previously predominated by *An. moucheti*. *An. gambiae* is the most ferocious of all the malaria vectors in Africa. It has been found to be the most efficient vector of *P.*

falciparum in Africa. If the effects of deforestation made it possible for *An. gambiae* to inhabit this new place, the implications are that malaria transmissions in this area will most likely increase.

In northern Brazil, Conn and others (2002) found that *An. marajoara,* a species previously of minor importance, has become the principal malaria vector following changes in land use. Malaria transmission in the area was previously dominated by *An. darlingi*. However, land use and land cover changes made *An. marajoara* to become the most abundant vector and the most infected with malaria parasites, with its anthropophilic behavior. Their discovery highlights one of the challenges of neotropical malaria control, namely that the targeting of specific vectors may be complicated by a changing mosaic of different locally important vectors and their interactions with human populations.

Since 2003, Afrane and others (unpublished) have been studying the spatial and temporal dynamics of adult mosquitoes in the highlands of western Kenya. Each month, mosquitoes are collected from over 40 houses using pyrethrum spray catches. Mosquitoes are collected and brought to the laboratiories of the Kenya Medical Research Institute and identified to species using the morphological keys of Gilles and Demellion (1968). Polymerase Chain Reactions (PCRs) are done to discriminate the sibling species of *An. gambiae* complex.

Species composition reflects a combination of environmental and historical intervention events at a site; hence, changes in species composition can provide a sensitive measure of ecological changes. Figure 1 shows the changes in species composition of the *An. gambiae* s.l. complex from 2003 to 2010 in the study site. Analysis of species composition illustrated that the proportion of *An. arabiensis* in the site was characterized by a significant increase in the proportion of *An. arabiensis* from < 1% in 2003 to 16% in 2010.

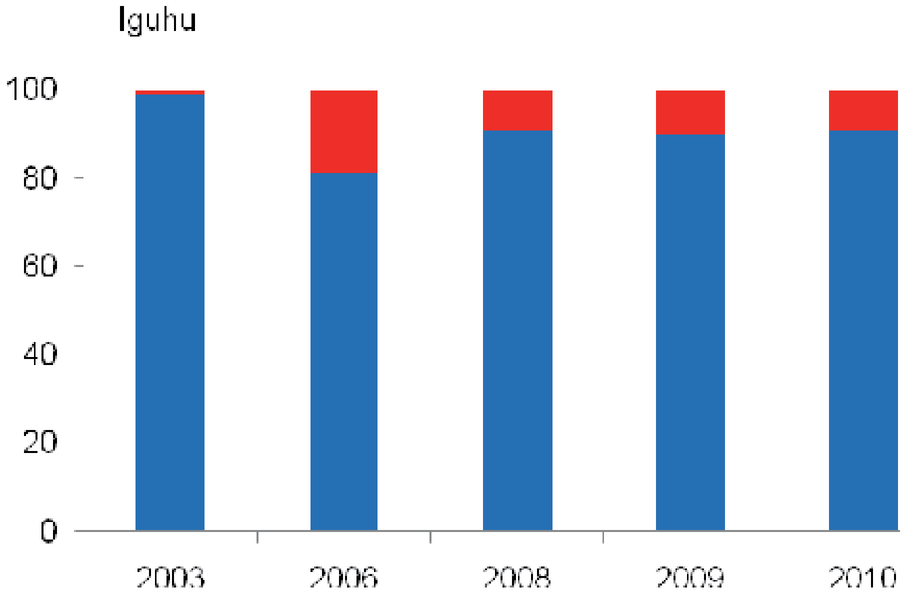

Fig. 1. Species composition of *Anopheles gambiae* (in blue) and *An. arabiensis (in red)* in Iguhu study site, Kakamega district in Kenya from 2003 to 2010.

4. Warming of the climate and malaria incidence in East Africa region

Deforestation in the western Kenya highlands has permitted the gradual colonisation of *An. arabiensis* into these areas that previously did not have this species. The implications are that with a new vector introduced in the area, the malaria transmission situation may worsen leading to resumption of epidemics in the site. The rate of malaria transmission is related to the abundance of malaria vectors while the stability of transmission is related to the diversity of species. Each species tends to dominate in the different seasons when its optimum survival conditions become available (Githeko et al. 2000).

There have been strong debates over the last decade by many authors on whether or not observed increases in malaria incidence in the Kenyan Highlands during the last thirty years are associated with co-varying changes in local temperature, possibly connected to global changes in climate. Studies using differing data sets and methodologies, produced conflicting results regarding the occurrence of temperature trends and their likelihood of being responsible, at least in part, for the increases in malaria incidence in the highlands of western Kenya. Omumbo and others (2011), used over 30 years of quality controlled daily observations of maximum, minimum and mean temperature in the analysis of trends at Kericho meteorological station, sited in Kenya's western highlands.

They found an upward trend of ≈0.2°C/decade in all three temperature variables. Mean temperature variations in the Kericho area were associated with large-scale climate variations including tropical Sea Surface Temperatures (SST). Local rainfall was found to have inverse effects on minimum and maximum temperature. They also used three versions of a spatially interpolated temperature data set, which showed markedly different trends when compared with each other and with their data.

Loevinsohn (1994) conducted a study that assessed the contribution of the climate to a malaria epidemic in Rwanda, focusing on the catchment area of one health centre where diagnosis was consistent and non-climatic variables well monitored. In late 1987 malaria incidence in the area increased by 337% over the 3 previous years. The increase was greatest in groups with little acquired immunity – children under 2 years (564%) and people in high-altitude areas (501%). Case-fatality rose significantly (relative risk = 4.85, $p < 0.001$). The same year also saw record high temperatures and rainfall. An autoregressive equation including lagged effects of these two variables explained 80% of the variance in monthly malaria incidence. Temperature (especially mean minimum) predicted incidence best at higher altitudes where malaria had increased most. Empirically derived relations were consistent with the estimated generation time of the disease and with the known sensitivity of the plasmodium parasite to temperature. These findings are most relevant to regions near the altitude or latitude limits of the disease, where several epidemics have lately been reported.

5. Commentary

Forests have been shown to stabilize local temperatures and this can annul the effects of climate variability that is related to malaria epidemic in the highlands. Deforestation accounts for nearly 20% of global annual carbon emissions. Thus this phenomenon is closely linked to global warming and subsequent increased spread of malaria in the highlands. Forests are carbon sinks as they absorb CO_2 and sequester it. Many policy makers are not familiar with the link between deforestation, climate change and their effect on malaria transmission.

Changes in temperature which are as a result of environmental changes have the potential to affect the vector and their parasites as well as the transmission of many parasite borne diseases including malaria. Environmental changes, either natural phenomenon or through human intervention, alter the ecological balance and context within which vectors and their parasites breed, develop, and transmit disease (Patz et al. 2000). Small increases in temperature affect the mosquitoes and the parasites they transmit (Bruce-Chwatt 1987).

Large-scale conversion of tropical forests for agricultural purposes can significantly change the surface properties, such as soil wetness and surface roughness, of an area and could lead to changes in the local climate. For example, radiation budget and energy balance could be affected (Nobre et al. 1991; (Bounoua 2002). According to Ramakrishna and Running (Ramakrishna and Running 1995), the geometry of the new surface and albedo, which is a measure of the reflectivity of a surface, affect the radiation budget whilst the energy balance is also changed. This leads to a change in the microclimate of the area concerned. Ambient and indoor temperatures as well as humidity are affected by a change in land use (Lindblade 2000). For instance in the Amazon forest of South America, extensive deforestation caused a significant increase in the mean surface temperature (by about 2.5°C) and a decrease in the annual evapo-transpiration (30% reduction) and precipitation (25% reduction) in the region, with the changes being more pronounced in the hot season (Nobre et al. 1991). The deforested area was associated with larger diurnal fluctuations of surface temperature and vapour pressure deficit. Land-cover changes that affect evaporation may also affect both the surface air temperature and the ground surface temperature in surrounding areas to a lesser extent (Skinner and Majorowicz 1999). In the tropics and subtropics, conversion warms canopy temperature by 0.8 ^{o}C all year round (Bounoua 2002.).

The data presented here have implications for understanding the effects of deforestation on an increased malaria transmission in the western Kenya and other African highlands. Malaria transmission force may be measured by the vectorial capacity of the vector. The duration of sporogony of *P. falciparum* in mosquitoes is exponentially related to the vectorial capacity (MacDonald 1957). If the daily survival and biting frequency of a vector are assumed to be constant, decreasing the duration of sporogony will lead to an increase in vectorial capacity. In this study deforestation led to a decrease in the duration of sporogony of *P. falciparum* by 1.1 days. This will translate into an exponential increase in vectorial capacity of *An. gambiae* which will lead to an increase in malaria transmission.

The studies presented here established the relationship between deforestation which is ongoing in the western Kenya highlands and the local climate as well as the effects of this altered local climate on malaria transmission indices in the study area.

The increase in indoor temperature due to land use and land cover changes enhanced digestion of blood meals by the mosquitoes in the deforested area leading to shorter gonotrophic cycles. Shorter gonotrophic cycles made mosquitoes to feed more frequently and thus increased their biting frequency. Frequent feeding by mosquitoes could increase the probability of picking infections from their hosts or infecting their hosts. Biting frequency affects the vectorial capacity and the Entomological Inoculation Rates (EIR), the two indices for measuring malaria transmission force in an area (Garrett-Jones and Shidrawi 1969). The vectorial capacity varies as the square of the daily man biting rates and EIR varies linearly with the daily man biting rates. An increase in the biting frequency of mosquitoes, thus, leads to an increase in vectorial capacity and EIR and hence to an increase in malaria transmission if there are infected individuals in the population.

The present study also showed that land use and land cover changes increased the population of mosquitoes. The increased temperature as well as the decrease in humidity in the deforested site led to a higher reproductive fitness for mosquitoes. The intrinsic rate of growth which is the number of progeny per unit of time and thus more accurately reflects maximal fitness was increased by the effects of deforestation. Generation time for mosquitoes was also decreased in the deforested areas. Increase in the number of mosquitoes has implication for malaria transmission in an area where the effects of deforestation lead to increase in biting frequency. In the case where there are infected individuals in the population, increase in mosquito population and an increase in biting frequency will cause an increase in the EIR leading to an increase in malaria transmission.

In the deforested area *An. arabiensis* had a shorter larva-to-adult development period. *An. gambiae* also exhibited the same phenomenon in a different study in the same area (Tuno et al. 2005). This renders the deforested area particularly vulnerable to mosquito proliferation and colonisation. The adults of *An. arabiensis* had a higher survival and reproductive fitness in the deforested area than in the forested areas. This could lead to proliferation in, and colonisation of the western Kenya highlands by *An. arabiensis*, a particularly crucial event since already *An. gambiae* and *An. funestus* are causing malaria epidemics in the highlands of western Kenya. Even though *An. arabiensis* is considered a zoophilic vector (prefers feeding on animals) rather than an anthropophilic vector (prefers feeding on humans), its efficiency to transmit malaria should not be underestimated. In many places in Africa such as the Kano plains and the lowland areas of western Kenya (White 1974; Githeko et al. 1996), Senegal (Robert et al. 1998) Ethiopia (Taye et al. 2005) and South Africa (Maharaj 2003), it is the main malaria vector. It is possible that it could become another vector in the highlands or it could also replace the current vectors in the highlands.

Deforestation had the effect of shortening the duration of the sporogony of *P. falciparum*. Time for the appearance of oocyst was shortened by 0.9 day and sporozoite appearance was also shortened by 1.1 days. This implies increased malaria transmission. The duration of sporogony of the malaria parasite in mosquitoes has an exponential relationship to the vectorial capacity of the vector. If all transmission variables remain the same, decreasing the duration of sporogony will cause an increase in the vectorial capacity. This translates into an increase in malaria transmission.

Besides their impacts on the duration of the gonotrophic cycle, biting frequency, duration of sporogony and subsequently on malaria transmission, deforestation and swamp reclamation also facilitate the creation of breeding habitats for *An. gambiae.* Those factors further enhance malaria transmission (Minakawa 2005; Munga et al. 2006). Mosquitoes will normally not breed in a natural swamp but will colonise a cultivated swamp (Munga et al. 2005). Deforestation opens up the forest, exposing the breeding habitats to direct sunlight which is a requirement for the maturation of the aquatic life stages of *An. gambiae* (Gilles and De Meillon 1968; Amerasinghe et al. 1997). As human populations increase in the highlands of western Kenya and elsewhere in the highlands of the East African region, deforestation and its subsequent effects on malaria transmission will continue.

The present study has shed some light on the possible impacts of increases in temperature in the highlands during periods of extreme events such as the El Niño events which are associated with anomalous warming and rainfall when they occur (Kovats et al. 2003; Rúa et al. 2005). In general a rise of 0.5^{o}C in temperature in the highlands is equivalent to a decrease in altitude by 77m. This means highland climatic conditions move closer to lowland situations. The implication of this is that malaria transmission which is driven by temperature will also move closer to lowland situations.

Environmental changes such as deforestation and swamp reclamation have been shown to increase microclimate of an area. These changes in the microclimate have been shown to also affect the malaria mosquitoes and malaria transmission indices. Thus, if climate change should lead to altitudinal and latitudinal increases in temperature, this will go to affect malaria transmission especially in highaland areas of Africa.

The highlands of western Kenya are being impacted by three anthropogenic drivers of malaria transmission these being global warming, deforestation and swamp reclamation. Reforestation and swamp restoration can reverse increased local warming while providing, the local populations with ecological goods and services in a sustainable way. With regard to malaria such an intervention could potentially prevent the further spread of malaria to higher altitudes.

6. Acknowledgements

This study was supported by the National Institute of Health (R01 AI094580 , D43 TW01505 and R01 A150243).

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Part 3

Global Warming Impacts on Urban Areas

5

Developing Urban Adaptation Strategies for Global Warming by Using Data Mining Techniques: A Case Study of Major Metropolitan Areas in Japan

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1. Introduction

Modern life and high population density is the main characteristics of cities. Urbanization diffuses all over the world in recent centuries. Metropolitan areas are formed to provide more industrial production as well as business communication. Furthermore, economies of scale arising from spatial concentration of activity within industries in metropolitan area, i.e. industry agglomeration (Rosenthal & Strange, 2001); population, resources, capital concentrate into the cities. Industry agglomeration makes cities more adaptive to uncertainty of business environment (Strange et al., 2006). Hence the most profit seems to be created in metropolitan area in this globalization age. Nonetheless, natural resources are rapidly produced into goods, consumed and transformed into side-products, e.g., solid waste and a variety of pollutants, into the environment. Besides, more and more infrastructures are developed in the progress of civilization, but only a few natural habitats are preserved, leading to the decreases of biodiversity (van Bohemen, 1998; Mcdonald et al, 2008). Though people have convenient life in metropolitan area, however, the urbanization is bringing about a great deal of critical global environmental changes. In particular, the enhanced global warming, due to the urban growth, is threatening the human security and the possibly irreversible changes on ecological systems in a variety of dimensions and scales (Chung et al., 2009; Firman et al., 2011; Kataoka et al., 2009; Khasnis & Nettleman, 2005; Robert & Cory, 2003). Thereby, it is imperative for the municipalities to develop adaptation strategies for metropolitans in the context of human security, urban sustainability and urban growth. In the progress of making urban growth policies, important factors should be taken into consideration from the socio-economic, environmental, cultural, public health and ecological perspectives regarding the potential threats of global warming.

Several types of environmental indicators are developed to diagnose the current situation and formulate adaptation strategies against the global warming and associated issues of urban sustainability. Normally, recent studies argued that the urban sustainability should take the composite system ecology into consideration, implying that the interactions of the stakeholders in the city have to be considered in the evaluation simultaneously (Mistch, 2003; Roseland, 1997). Also, several evaluation bases could be used to examine the performance of the environment system, e.g. the energy, monetary, material bases (Weng & Fujiwara, 2011). A variety of environmental impact assessment tools, e.g., life-cycle assessment (LCA), life-cycle cost (LCC) assessment and cost-benefit analysis (CBA), could serve as efficient evaluation methods in the evaluation of countermeasures against the global warming, given that credible parameters are available (Jeong & Lee, 2009). In fact urban environment is a socio-economic-natural composite ecological system such that public policies should consider all the dimensions simultaneously, reorganizing the urban system into ecological network both for human system and natural system. Some attempts have developed the Environmental Kuznets Curve (EKC) to analyze the relationships between the economic and environmental quality, regarding driving factors of income, consumption and policy interventions (Arrow et al., 1995; Azomahou et al, 2006; Magnani, 2000; Weng et al., 2010). Although more and more evidences showed that the EKCs explain the relationships of several environmental pollutants, including the CO_2 emission, some methodological issues of EKC have to be dealt with from the perspective of statistics (Müller-Fürstenbergera & Wagner, 2007). One reason is that the available socio-economic and environmental data is not sufficient. Meanwhile, as for the conventional environmental evaluation methods, the data availability would lead to the uncertainty of the quantification outcomes, limiting the credibility of the interpretations. Hence, the dimensionless composite environmental indicators could be an alternative tool for environmental evaluation. For this purpose, the pressure-status-response (PSR) framework was established by the Organisation for Economic Co-operation and Development [OECD] in 1993 to serve as an environmental policy evaluation tool (OECD, 1993) and afterward, the driving forces are adopted as driving forces-state-response (DSR) framework in 1996 (OECD, 1996). Also, Kessler and Van Dorp (1998) proposed the adoption of environmental indicators under a strategic environment assessment (SEA) framework, in which socio-economic and environmental variables should be considered simultaneously. Subsequently, a driving forces-pressure-state-impact-response (DPSIR) framework was proposed by European Environmental Agency [EEA] as an extension of the PSR (EEA, 1999). Based on the aforementioned frameworks, Hu and Wang (1998) argued the urban environment should be considered as a socio-economic-natural composite ecological system; they adopted economic, cultural, environmental, and infrastructure variables to simulate the linkages among the functional modules in the evaluation of the performance of eco-reconstructing of eco-villages in China. Button (2002) proposed an analytical indicator framework composed evaluating urban environmental system; the indicators are composed of economic, environmental, social, cultural, and political variables. Jago-on et al. (2009) analyzed the critical urban environmental issues by using the DPSIR framework and proposed countermeasures for Asian cities. Regarding global warming, Omann et al. (2009) conducted a DPSIR analysis discussing the impacts of the climate changes on the biodiversity conservation. The outcomes indicated that the driving forces from the modern human society, e.g., the socio-economic and cultural attributes and the energy demands of transportation, bring about significant negative impacts on the global warming and the related challenges of biodiversity conservation. Also, Rounsevell et al. (2010) proposed a conceptual DPSIR framework qualitatively analyzing the apparent driving factors of socio-ecological indicators and their influences on the eco-services. A normal evaluation scheme is proposed in the study arguing that the attributes and the influencing time-spatial scales of the driving factors should be clarified, and thus possible quantitative impact analyses and efficient countermeasures could be subsequently implemented.

Regarding the quantification of indicator systems, Song et al. (2004) developed a hierarchical indicator system to evaluate the ecological sustainability of inshore cities in China. In their study, many socio-economic and environmental variables are categorized into three functional groups: structure, function, and coordination. Variables were linked as an ecological network, and the sustainability of each city was calculated and compared by a composite evaluating indicator. In addition, Srebotnjak (2007) presented a quantitative indicator system developing an integrated environmental performance index. She also particularly argued the importance of the development and the utilization of credible environmental statistics while the data availability is the main problem in environmental evaluations. Furthermore, Pan & Kao (2009) developed an inter-generation equity indicator (IGEI) to quantify the sustainability among generations in recent decades at a world scale, under a pressure–state–response (PSR) framework.

In fact, local actions are of particular importance in the enhancement of sustainability regarding the urbanization. In this sense, this study aims at developing a precautionary indicator system (PIS), which is in aid of the formation of adaptation strategies of the global warming mitigation. After the World War II, Japan made great economic development in the past six decades. Some regionally nuclear cities have been formed all over Japan. However, the current deficiencies of policies and future adaptation strategies are expected to deal with facing the critical challenges of sustainable development, e.g., the urban growth management and the global warming mitigation. In this study, by evaluating current social, economic, and environmental system of urban area, the precautionary indicators are developed to diagnose the current situation. Finally, strategies for developing a sustainable city are proposed in the final part.

2. Research approach

In order to deal with the information hidden in an enormous amount of statistics, data mining approaches are rapidly developed in recent decades. Mainly, data mining approaches are based on the integration of statistical theories for pattern recognition, causal relationships development, behavior analysis and system control & forecasting. In particular, several methods show superiority for the purpose of data mining, including regression analysis, multivariate analysis, indicator system techniques, artificial neural network, and data envelope analysis (Chen et al., 2010; Ngai et al., 2009). Moreover, the developing information system technologies, e.g., the geographic information systems and the remote sensing technology, provide high quality data and platforms for data analysis and integration.

The aforementioned approaches could be applied to establish the precautionary indicator system of global warming from a variety of perspectives. In developing a precautionary indicator system of global warming, several principles should be taken into consideration in constructing a practicable and informative indicator system (Duke & Aull-Hyde, 2002; Niemeijer, 2002; Solnes, 2003; Valentin & Spangenberg; 2000; Verdoodt & Van Ranst, 2006):

- The indicator system should have sufficient rational theoretical bases;
- The boundary of the indicator system should be identified clearly for the purpose of nature hazard mitigation;
- Credible and consistent databases should be available to support the calculation of the indicator system;

- The interpretations of the indicator system should be direct and informative for all the stakeholders, e.g. policy-makers and citizens.

Some PSR- or DPISR-like indicators have been established in the aforementioned literature. Each indicator system has its specific application purpose and respective data requirement at different scales. Based on the above principles, a modified DPSIR framework is considered in this study to develop a representative precautionary indicator system. Thereby the research flow of this study is represented in Fig. 1.

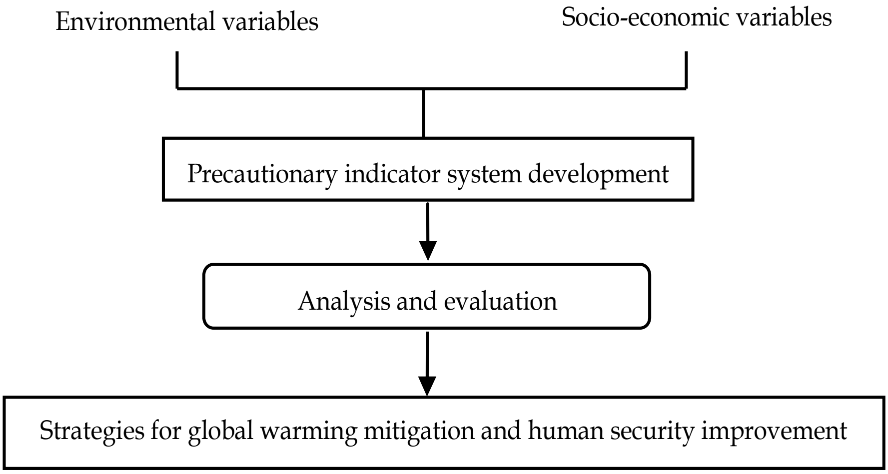

Fig. 1. The research flow diagram of this study.

To meet the goal of reflecting the urban adaptation mechanisms in terms of global warming, a three-layer hierarchical indictor system is induced to develop an evaluating indicator framework. A composite urban system is divided into three levels of indicators, and finally an overall score is estimated. The levels are decided by considering to the urban socio-ecological networks using socio-economic and environmental variables, which serve as the fundmental components of the indicator system. The variables are linked as a composite socio-economic and ecological network, representing the levels of the urban growth and the sustainability. According to the definition of Tanguay et al. (2008), the terms in the statistics are identified as variables, and an indicator means composite information obtained from specific variables.

The PSR analytical framework in this study is composed of three categories- "Pressure and State," "Function" and "Coordination." In addition, the driving factors and the responses are emphasized within the flows among the components. By such manipulation, a composite urban social-economic-natural system could be described by the intrinsic relationships among the components and the flows, on the basis of system ecology, as shown in Fig. 2.

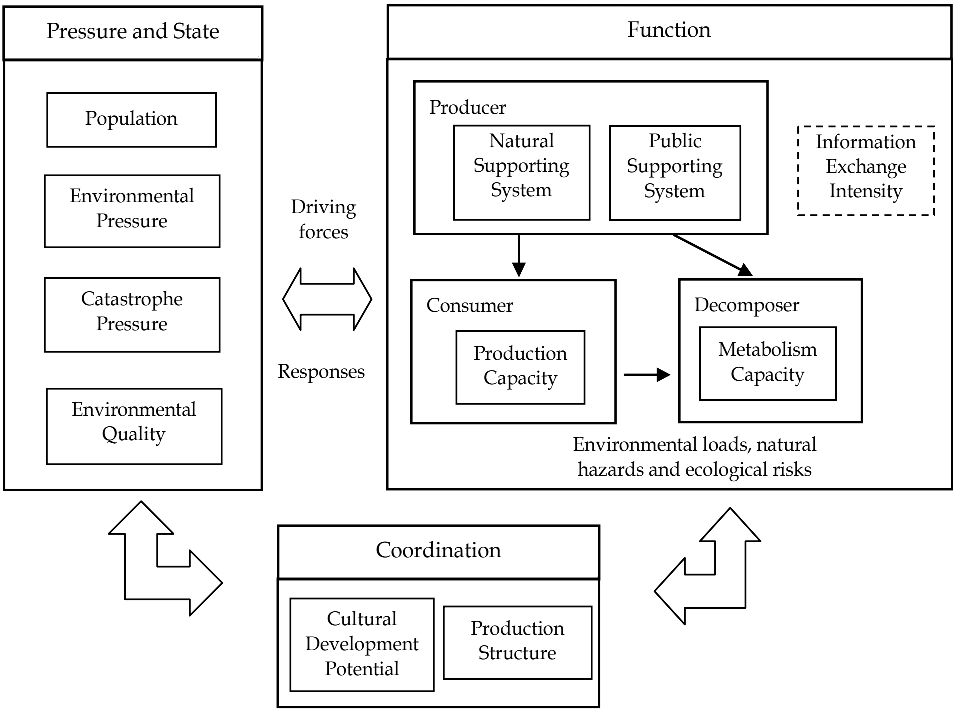

Fig. 2. The conceptual framework of the precautionary indicator system towards a sustainable city.

The characteristics of the intrinsic relationships of the precautionary indicator system are designed on the basis of the system ecology thinking and the research purpose. Some points of view are assumed in the framework as follows:

- The indicator system is to represent the intrinsic interactions of the socio-economic-environment systems, implying that all the sub-systems are integrated by rationally choosing the variables and determining the indicators' weights.
- Each 1st-level indicator is composed of several 2nd-level indicators, which represent the intrinsic properties. Each 2nd -level indicator is composed of some significant 3rd-level indicators, which are specifically selected to represent the characteristics of the upper level indicator, considering the data availability.
- The first 1st-level indicator, "Pressure and State," reflects the current pressure levels on the social, environmental and ecological states. This category reflects the quality and pressures of an urban system. Also, some available natural hazard variables would be highlighted and linked to other common environmental variables.
- The second 1st-level indicator, "Function", denotes the main socio-ecological network in an urban system. Like biological food-web, "Producer" in an urban system is assumed as "Natural Supporting System" and "Public Supporting System". They provide the resource for both social society and biosphere. "Consumer" in an urban system is assumed as "Production Capacity" representing the efficiency of the production sectors. "Decomposer" in an urban system is assumed as the "Metabolism Capacity", which means the efficiency and performance of environmental loads treatment. Finally, the linkages of socio-environmental-ecological networks are

assumed to be highly affected by the "Information Exchange Intensity" in this study. In each 2nd -level indicator, some representative variables are selected as well.

- In principle, the stronger the producer and decomposer are, the more robust an ecological system would be. That is, the production sectors could be transformed into a sustainable manner and the environmental quality could thus be self-regulated at an optimal level through the intrinsic mechanisms. Thereby, a powerful natural supporting sub-system and metabolism sub-system means that the potential of self-resiliency would be large, and the environmental quality and human security can be promoted. In this category, the social security indicators are particularly emphasized regarding the human security.
- The third 1st-level indicator, "Coordination," denotes the future potential indicator of ecologically sustainable city. The importance of the culture and the industrial structure are stressed herein.
- It is assumed that the driving forces are imposed and the responses are exchanged interactively among the main parts.
- Each 3rd-level indicator is given an attribute in the calculation procedure. A larger value of the 3rd-level indicator represents that the city has a better sustainable quality with regard to this indicator, and thus the attribute is positive; otherwise, it is negative. This attribute is determined by the domain knowledge of social and natural science.

In this study, the aggregation procedures of the precautionary indicator system are proposed as follows:

1. Normalize the values of each 3rd-level indicator using the following equations.
    - If the variable is a positive driving indicator (i.e. the larger value of original variable denotes a higher level of the urban sustainability):

$$Q_{i_{3rd-level},j} = \frac{C_{i_{3rd-level},j} - \overline{C}_{i_{3rd-level}}}{S_{C_{i_{3rd-level}}}} \quad \forall i,j \tag{1}$$

where $Q_{i_{3rd-level},j}$ is the normalized score of the *i* item of the 3rd-level variable in *j* region; $C_{i_{3rd-level},j}$, $\overline{C}_{i_{3rd-level}}$ and $S_{C_{i_{3rd-level}}}$ are the original value of the *i* item of the 3rd-level variable in *j* region, its average and its standard error, respectively.

- If the variable is a negative driving indicator (i.e. the larger value of the original variable denotes a lower level of the urban sustainability):

$$Q_{i_{3rd-level},j} = -\left(\frac{C_{i_{3rd-level},j} - \overline{C}_{i_{3rd-level}}}{S_{C_{i_{3rd-level}}}}\right) \quad \forall i,j \tag{2}$$

2. Aggregate the upper level indicator by the weighted aggregation, the formula is:

$$Q_{m,j} = \sum_{i} W_i \times Q_{i,j} \quad \forall m,i,j \tag{3}$$

where W_i is the weight of each lower level indicator; $Q_{m,j}$ denotes the value of the *m* upper-level indicator of in *j* region, and $Q_{i,j}$ is the value of the *i* lower-level indicator in *j* region.

After implementing the normalization transformation, the values of each 3rd-level indicator would obey a standard normal distribution, with a zero average and an unity standard error. Thus, all the indicators could be compared at the same scale. After the articulation, a larger normalized value of the indicator would imply the region is relatively more ecologically sustainable among the regions of interest with respect to the indicator.

The aggregation indicator is calculated by weighted summation. In terms of the determination of the weight of each indicator, expert consultation (i.e., the Delphi Method), analytical hierarchical procedure (AHP), analytical network procedure (ANP) and principal component analysis (PCA), could be considered (Hsu et al., 2010; Solnes, 2003; Song et al., 2004; Srebotnjak, 2007). Moreover, the nonlinear fuzzy theory could be introduced into the aforementioned methods. In this study the weight of each indicator is determined based on the outcomes of Song et al. (2004) and adjusted by the author according to the research purpose. In this sense, some variables associated with the global warming would be highlighted in the precautionary indicator system. In principle, the larger weight means the indicator with the higher degree of global warming.

3. Data and results

Japan has experienced the processes of extensive industrialization and urbanization, and now attempts to construct a sustainable society with particular focuses on the development of low-carbon society, material-cycle society and symbiotic society. In order to achieve the aforementioned objectives and to deal with the potential deficiencies, the adaptation strategies of the metropolitan areas are necessary. For this reason, 18 major cities in Japan are selected as the study areas to prepare required and feasible policy measures from a comprehensive perspective. In this sense, the official statistics of socio-economic and environmental variables in 2008 are utilized to develop the precautionary indicator system (Yokohama City Government, 2011). The structure of the precautionary indicator system is constructed according to the principles discussed in Section 2 and data availability. 30 representive variables are particularly selected in the indicator system, and the detailed definitions and the values of the variables are provided in Table 1 and Table 2, respectively.

In fact, it is difficult and tricky to select appropriate variables. In addition, the measurement bases, such as the measure of area or capita, would have important implications. In this study, normally, per capita variables are often used in constructing the socio-economic relationships while area-specific variables are preferred in establishing the natural-ecological-environmental relationships. Still, some particular considerations are imposed for several variables considering the complex interactions. For instance, this study adopts the spatial density of college students to reflect the degree of the potential on research and regional development. Furthermore, no variables are selected as the adequate industrial structure while the attributes and expectations may vary by regions.

Using the cross-section data in 2008 as shown in the Table 2, the calculation of the indicator system is implemented hierarchically. First, each 3rd-level indicators are calculated using Eq. (1) and Eq. (2), and the results are also shown in Table 2; secondly, the 2nd-level indicators and the 1st-level ones are estimated by Eq. (3), sequentially. Consequently, the overall score of each city can be obtained. A comparative analysis is performed based on the outcomes.

The 1st-level indicator	Weight	The 2nd-level indicator	Weight	The 3rd-level indicator	Description	Primative unit	Weight	Attribute of the original variable
Pressure and State	0.6	Population Scale	0.15	The population density	The indicator is regarded as the driving force of urban resources consumption and environment pollution.	10^3 capita/km^2	0.4	-
				The population natural growth rate	The indicator reflects the population sustainability.	‰	0.3	+
				The household density	The indicator is regarded as the driving force of urban resources consumption and environment pollution.	household/km^2	0.3	-
		Environmental Pressure	0.2	Per capita electricity consumed	The indicator is regarded as the environmental pressure in the urban system.	kWh/day	0.2	-
				Per capita water consumed	The indicator is regarded as the environmental pressure in the urban system.	m^3/yr	0.2	-
				Per capita natural gas consumed	The indicator is regarded as the environmental pressure in the urban system.	10^5 MJ/yr	0.15	-
				Per capita general waste generated	The indicator is regarded as the environmental pressure in the urban system.	kg/day	0.15	-
				The spatial car density	The indicator is regarded as the environmental pressure in the urban system.	number/km^2	0.15	-
				The ratio of road in total area	The indicator is regarded as the heat island effect and ecological habitat fragment in the urban system.	%	0.15	-
		Catastrophe Pressure	0.5	The maximum daily rainfall	The indicator is regarded as the risk indicator for the climate change due to global warming.	mm/day	0.5	-
				The maximum daily temperature	The indicator is regarded as the risk indicator for the climate change due to global warming.	℃	0.15	-
				Crimes incidents intensity	The indicator attempts to reflect the social safety pressure in the urban system.	cases/10^3capita	0.15	-
				Fire accident intensity	The indicator attempts to reflect the social safety pressure in the urban system.	cases/10^3capita	0.2	-
		Environmental Quality	0.15	Ambient Photochemical oxidant concentration	The indicator is regarded as the environmental response to the human activities and the regarded as the current environmental quality.	ppm	0.33	-
				Ambient NOx concentration	The indicator is regarded as the environmental response to the human activities and the regarded as the current environmental quality.	ppm	0.33	
				Ambient PM concentration	The indicator is regarded as the environmental response to the human activities and the regarded as the current environmental quality.	ppm	0.33	-

Table 1. The structure of the precautionary indicator system in this study.
Note: The unit denotes that of the original variable.

The 1st-level indicator	Weight	The 2nd-level indicator	Weight	The 3rd-level indicator	Description	Primative unit	Weight	Attribute of the original variable
Function	0.3	Production Capacity	0.1	Per capita income	The indicator is regarded as the intensity of production and consumption in urban system though only the one year lag data is available.	10^4¥(2008 prices)/yr	1	+
		Natural Supporting System	0.35	The annual rainfall	The indicator is regarded as the resource abundance for the natural ecological system.	mm	0.2	+
				The ratio of natural surfaces within the total area	Natural surfaces denote urban parks, forests, vegetation fields and lakes. The indicator is regarded as the resource abundance for urban environment metabolism, ecological habitats development and natural functions operation.	%	0.8	+
		Public Supporting System	0.15	The spatial availability of hospital bed	The indicator represents the capacity of public health care.	number/km^2	0.15	+
				The spatial availability of doctors	The indicator represents the capacity of public health care.	number/km^2	0.3	+
				Crime clearance rate	The indicator implies the efficiency of social safety system	%	0.25	+
				The spatial availability of disaster assistance	The indicator is regarded as the efficiency of social safety system.	cases/km^2	0.3	+
		Information Exchange Intensity	0.2	The spatial intensity of fixed phone and mobile phone services registered	The indicator is regarded as the efficiency of information exchange flow.	number/km^2	0.5	+
				The spatial intensity of internet service registered	The indicator reflects the efficiency of information exchange flow.	number/km^2	0.5	+
		Metabolism Capacity	0.2	Sewage prevailing rate	The indicator is regarded as the capacity of urban environment metabolism.	%	0.5	+
				The recycling ratio of general waste	The indicator is regarded as the capacity of urban environment metabolism.	%	0.5	+
Coordination	0.1	Civilization Development Potential	1	The ratio in the municipal expenditure on education	The indicator is regarded as the administrative support for civic education and cultural preservation.	%	0.5	+
				The density of college students	The indicator is regarded as the potential for regional development.	number/km^2	0.3	+
				The spatial intensity of museums, libraries, natural and cultural heritage appointed	The indicator is regarded as the resource abundance for cultural development.	number/km^2	0.2	+

Table 1. The structure of the precautionary indicator system in this study. (*conti.*)
Note: The unit denotes that of the original variable.

Variable City	Sapporo	Sendai	Saitama	Chiba	Tokyo (special wards)	Kawasaki	Yokohama	Niigata	Shizuoka	Hamamatsu	Nagoya	Kyoto	Osaka	Sakai	Kobe	Hiroshima	Kitakyushu	Fukuoka
The population density (10^3 capita/km^2)	1. 693 (0.709)	1 .308 (0.803)	5.521 (-0.226)	3 .481 (0.272)	14.046 (-2.310)	9.631 (-1.231)	8.394 (-0.929)	1.118 (0.850)	0.511 (0.998)	0.538 (0.991)	6.886 (-0.560)	1.772 (0.690)	1.193 (-1.793)	5.574 (-0.239)	2. 773 (0.445)	1.289 (0.808)	2.019 (0.629)	4.215 (0.093)
The population natural growth rate (‰)	0.30 (-0.431)	2.50 (0.992)	2.40 (0.928)	2.00 (0.669)	0.40 (-0.367)	4.10 (2.028)	1.90 (0.604)	-0.50 (-0.949)	-1.3 (-1.467)	0.80 (-0.108)	0.90 (-0.043)	- 0.70 (-1.079)	- 0.50 (-0.949)	1.10 (0.086)	- 0.30 (-0.820)	2.30 (0.863)	- 1.00 (-1.273)	3.00 (1.316)
The household density (number/km^2)	783.45 (0.659)	575.14 (0.764)	2,284.94 (-0.095)	1,448.92 (0.325)	7,008.77 (-2.469)	4,438.23 (-1.177)	3,582.28 (-0.747)	421.50 (0.841)	195.82 (0.954)	209.58 (0.947)	3,062.58 (-0.486)	810.80 (0.645)	5,800.22 (-1.862)	2,427.58 (-0.167)	1,207.35 (0.446)	572.92 (0.765)	872.69 (0.614)	2,007.32 (0.044)
Per capita electricity consumed (kWh/day)	4,854.18 (0.520)	6,248.44 (0.114)	6,855.80 (-0.063)	10,603.46 (-1.154)	7,161.74 (-0.152)	6,594.90 (0.013)	6,558.47 (0.024)	5,727.29 (0.266)	7,425.71 (-0.229)	6,725.81 (-0.025)	17,011.74 (-3.020)	2,796.31 (1.119)	2,951.33 (1.074)	2,417.32 (1.230)	2,512.08 (1.202)	5,779.90 (0.251)	8,737.47 (-0.610)	8,574.22 (-0.563)
Per capita water consumed (m^3/yr)	93.03 (1.532)	110.18 (0.328)	106.29 (0.602)	100.50 (1.008)	126.21 (-0.797)	110.11 (0.334)	109.59 (0.370)	125.25 (-0.729)	123.60 (-0.613)	102.62 (0.859)	123.28 (-0.591)	121.28 (-0.451)	155.19 (-2.831)	113.06 (0.126)	118.81 (-0.277)	122.29 (-0.521)	108.99 (0.412)	97.20 (1.240)
Per capita natural gas consumed (10^5 MJ/yr)	69.97 (1.026)	110.26 (0.648)	89.10 (0.847)	455.50 (-2.596)	235.034 (-0.525)	379.868 (-1.886)	138.11 (0.386)	153.46 (0.242)	133.56 (0.429)	55.15 (1.166)	159.84 (0.182)	170.54 (0.081)	259.76 (-0.757)	272.70 (-0.879)	190.24 (-0.104)	138.51 (0.382)	118.55 (0.570)	95.34 (0.788)
Per capita general waste generated (kg/day)	1.08 (-0.096)	1.03 (0.191)	1.03 (0.208)	1.08 (-0.123)	1.11 (-0.326)	0.90 (1.083)	0.83 (1.550)	1.13 (-0.441)	1.08 (-0.096)	0.96 (0.682)	0.91 (1.028)	1.09 (-0.173)	1.43 (-2.434)	1.06 (-0.016)	1.09 (-0.184)	0.88 (1.194)	1.07 (-0.029)	1.37 (-2.018)
The spatial car density (number/km^2)	884.33 (0.769)	757.59 (0.865)	2,549.93 (-0.489)	1,746.95 (0.118)	4,221.22 (-1.752)	3,229.92 (-1.003)	3,337.07 (-1.084)	779.73 (0.849)	339.66 (1.181)	403.52 (1.133)	3,838.11 (-1.462)	728.04 (0.888)	3,850.18 (-1.471)	2,518.65 (-0.465)	1,142.98 (0.574)	710.12 (0.901)	1,175.30 (0.550)	2,037.04 (-0.101)
The ratio of roads in total area (%)	0.0033 (-0.597)	0.0028 (-0.150)	0.0019 (0.541)	0.0025 (0.092)	0.0011 (1.154)	0.0012 (1.112)	0.0015 (0.836)	0.0051 (-2.060)	0.0031 (-0.430)	0.0057 (-2.555)	0.0025 (0.093)	0.0017 (0.715)	0.0015 (0.851)	0.0020 (0.449)	0.0023 (0.201)	0.0026 (0.002)	0.0034 (-0.664)	0.0021 (0.409)
The maximum daily rainfall (mm)	37.5 (1.581)	87.5 (-0.157)	111.5 (-0.992)	83.5 (-0.018)	111.5 (-0.992)	78.5 (0.156)	78.5 (0.156)	65.5 (0.608)	125.5 (-1.479)	103 (-0.697)	133.5 (-1.757)	118 (-1.218)	57 (0.903)	57 (0.903)	47 (1.251)	50.5 (1.129)	65.5 (0.608)	82.5 (0.016)
The maximum daily temperature (℃)	31.4 (2.641)	33.6 (1.277)	37.3 (-1.016)	35.3 (0.224)	35.3 (0.224)	35 (0.410)	35 (0.410)	34.8 (0.534)	36 (-0.210)	36.6 (-0.582)	37.9 (-1.388)	37.7 (-1.264)	36.4 (-0.458)	36.4 (-0.458)	34.7 (0.596)	36.7 (-0.644)	34.5 (0.720)	37.3 (-1.016)
Crimes incidents intensity (cases/10^3capita)	15.34 (0.481)	14.21 (0.689)	17.79 (0.026)	19.59 (-0.305)	17.56 (0.069)	12.69 (0.970)	12.28 (1.046)	13.40 (0.839)	11.94 (1.109)	12.21 (1.058)	26.27 (-1.541)	22.46 (-0.837)	31.14 (-2.441)	21.37 (-0.636)	18.69 (-0.140)	13.17 (0.880)	20.34 (-0.445)	22.39 (-0.823)
Fire accident intensity (cases/10^3capita)	0.38 (-0.179)	0.35 (0.115)	0.34 (0.294)	0.33 (0.395)	0.48 (-1.180)	0.33 (0.366)	0.30 (0.698)	0.19 (1.764)	0.33 (0.385)	0.40 (-0.362)	0.47 (-1.020)	0.13 (2.342)	0.49 (-1.265)	0.40 (-0.323)	0.49 (-1.297)	0.43 (-0.622)	0.44 (-0.762)	0.30 (0.653)
Ambient NOx concentration (ppm)	0.032 (0.488)	0.015 (1.233)	0.029 (-0.853)	0.024 (-0.108)	0.032 (-1.300)	0.032 (-1.300)	0.030 (-1.002)	0.010 (1.979)	0.019 (0.637)	0.015 (1.233)	0.027 (-0.555)	0.021 (0.339)	0.034 (-1.598)	0.026 (-0.406)	0.024 (-0.108)	0.02 (0.488)	0.024 (-0.108)	0.017 (0.935)
Ambient Photochemical oxidant concentration (ppm)	0.030 (0.304)	0.033 (-0.560)	0.030 (0.304)	0.030 (0.304)	0.028 (0.880)	0.028 (0.880)	0.027 (1.168)	0.036 (-1.424)	0.023 (2.320)	0.036 (-1.424)	0.031 (0.016)	0.030 (0.304)	0.031 (0.016)	0.031 (0.016)	0.037 (-1.712)	0.033 (-0.560)	0.031 (0.016)	0.034 (-0.848)
Ambient PM concentration (ppm)	0.013 (2.842)	0.021 (0.806)	0.027 (-0.721)	0.023 (0.297)	0.024 (0.042)	0.025 (-0.212)	0.028 (-0.976)	0.022 (0.551)	0.023 (0.297)	0.022 (0.551)	0.029 (-1.230)	0.020 (1.060)	0.027 (-0.721)	0.026 (-0.467)	0.023 (0.297)	0.028 (-0.976)	0.025 (-0.212)	0.029 (-1.230)

Table 2. The original values of entering variables of the cities of interest.

Note: The number in the parentheses denotes the normalized value of each variable, i.e. the value of the 3rd-level indicator, in a specific category.

Variable / City	Sapporo	Sendai	Saitama	Chiba	Tokyo (special wards)	Kawasaki	Yokohama	Niigata	Shizuoka	Hamamatsu	Nagoya	Kyoto	Osaka	Sakai	Kobe	Hiroshima	Kitakyushu	Fukuoka
Per capita income (10^4¥(2008 prices)/yr)	345.53 (-0.437)	322.62 (-1.147)	381.64 (0.682)	338.35 (-0.659)	400.48 (1.266)	395.05 (1.098)	437.29 (2.407)	372.08 (0.386)	369.29 (0.300)	361.56 (0.060)	345.32 (-0.443)	353.12 (-0.201)	338.79 (-0.646)	323.91 (-1.107)	361.78 (0.067)	379.98 (0.631)	345.08 (-0.450)	301.29 (-1.808)
The annual rainfall(mm)	843.0 (-2.032)	1,349.0 -0.496)	1,392.5 (-0.364)	1,639.0 (0.384)	1,857.5 (1.047)	1,919.0 (1.233)	1,919.0 (1.233)	1,530.0 (0.053)	1,955.5 (1.344)	1,869.5 (1.083)	1,579.5 (0.203)	1,430.5 (-0.249)	1,262.5 (-0.759)	1,262.5 (-0.759)	1,041.0 (-1.431)	1,148.50 (-1.105)	1,447.0 (-0.199)	1,780.5 (0.813)
The ratio of natural surfaces within the total area (%)	61.55 (0.393)	70.27 (0.785)	50.20 (-0.118)	56.09 (0.147)	17.28 (-1.598)	27.50 (-1.139)	32.60 (-0.909)	76.48 (1.064)	85.41 (1.465)	78.11 (1.137)	30.89 (-0.986)	71.18 (0.825)	13.61 (-1.763)	33.80 (-0.855)	68.97 (0.726)	74.07 (0.956)	50.38 (-0.110)	52.38 (-0.020)
The spatial availability of hospital bed (number/km^2)	36.04 (-0.408)	17.46 (-0.850)	39.61 (-0.323)	35.38 (-0.424)	133.95 (1.922)	73.85 (0.492)	66.56 (0.318)	16.07 (-0.883)	6.06 (-1.121)	6.82 (-1.103)	84.18 (0.738)	29.55 (-0.562)	155.47 (2.434)	87.41 (0.814)	35.45 (-0.422)	18.93 (-0.815)	43.16 (-0.239)	71.41 (0.434)
The spatial availability of doctors (number/km^2)	50.73 (-0.535)	30.17 (-0.767)	78.63 (-0.219)	69.02 (-0.328)	316.36 (2.472)	140.24 (0.479)	139.33 (0.468)	26.92 (-0.804)	9.51 (-1.001)	11.78 (-0.976)	152.04 (0.612)	46.87 (-0.578)	297.21 (2.255)	117.45 (0.221)	63.37 (-0.392)	30.98 (-0.758)	61.83 (-0.409)	120.88 (0.259)
Crime crack rate (%)	40.99 (0.729)	33.61 (-0.347)	35.00 (-0.144)	36.13 (0.021)	41.95 (0.870)	43.87 (1.150)	45.51 (1.389)	32.57 (-0.499)	36.75 (0.111)	31.38 (-0.673)	27.98 (-1.168)	27.94 (-1.174)	26.53 (-1.380)	22.91 (-1.909)	35.83 (-0.023)	45.24 (1.350)	40.74 (0.693)	42.88 (1.005)
The spatial availability of disaster assistance (case/km^2)	62.33 (-0.654)	47.60 (-0.713)	224.25 (0.002)	165.18 (-0.237)	783.25 (2.266)	383.32 (0.646)	334.14 (0.447)	39.94 (-0.744)	18.61 (-0.831)	19.60 (-0.827)	294.39 (0.286)	83.57 (-0.568)	869.85 (2.617)	277.70 (0.218)	114.38 (-0.443)	49.88 (-0.704)	92.74 (-0.531)	166.91 (-0.230)
The spatial intensity of fixed phone and mobile phone services registered (number/km^2)	513.06 (-0.583)	432.79 -0.622)	1,508.39 (-0.100)	1,041.03 (-0.327)	8341.10 (3.215)	2,858.91 (0.555)	2,622.62 (0.440)	353.54 (-0.661)	227.08 (-0.722)	181.19 (-0.744)	2,481.46 (0.372)	612.89 (-0.535)	1,955.58 (1.573)	1,405.99 (-0.150)	871.38 (-0.409)	434.04 (-0.622)	559.96 (-0.561)	1,471.64 (-0.118)
The spatial intensity of internet service registered (number/km^2)	3,723.07 (-0.763)	2,425.76 (-0.840)	26,359.83 (0.589)	18,244.63 (0.104)	26,962.28 (0.625)	52,788.36 (2.167)	17,421.92 (0.055)	2,260.09 (-0.850)	2,099.09 (-0.860)	1,961.09 (-0.868)	1,9133.48 (0.157)	2,649.58 (-0.827)	35,864.38 (1.156)	53,154.55 (2.189)	8,122.09 (-0.500)	2,588.69 (-0.831)	8,724.48 (-0.464)	12,478.38 (-0.240)
Sewage prevailing rate (%)	99.70 (0.642)	97.60 (0.422)	85.00 (-0.896)	97.10 (0.370)	100.00 (0.673)	99.30 (0.600)	99.80 (0.652)	73.42 (-2.107)	75.7 (-1.868)	74.1 (-2.036)	98.60 (0.527)	99.20 (0.590)	99.90 (0.663)	93.9 (0.035)	98.60 (0.527)	92.90 (-0.069)	99.80 (0.652)	99.50 (0.621)
The recycling ratio of general waste (%)	9.54 (-0.026)	10.17 (0.062)	22.03 (1.688)	20.85 (1.525)	12.28 (0.350)	6.22 (-0.481)	13.24 (0.483)	25.68 (2.187)	6.94 (-0.381)	10.67 (0.130)	0.60 (-1.251)	5.65 (-0.559)	3.07 (-0.912)	3.15 (-0.901)	4.23 (-0.754)	14.77 (0.692)	3.36 (-0.873)	2.59 (-0.979)
The ratio in the municipal expenditure on education (%)	7.91 (-0.938)	11.27 (0.801)	10.76 (0.540)	10.36 (0.330)	13.11 (1.756)	8.07 (-0.860)	8.37 (-0.700)	10.62 (0.466)	9.27 (-0.234)	12.27 (1.321)	8.44 (-0.668)	7.68 (-1.059)	7.43 (-1.190)	9.62 (-0.054)	9.65 (-0.040)	13.81 (2.120)	8.11 (-0.834)	8.27 (-0.755)
The density of college students (number/km^2)	45.36 (-0.554)	61.71 (-0.459)	91.91 (-0.284)	95.23 (-0.264)	758.28 (3.588)	212.62 (0.418)	181.74 (0.238)	27.12 (-0.660)	10.35 (-0.757)	7.24 (-0.775)	272.31 (0.764)	159.46 (0.109)	125.84 (-0.086)	79.48 (-0.356)	115.48 (-0.147)	33.01 (-0.626)	44.72 (-0.558)	210.95 (0.408)
The spatial intensity of museums, libraries, natural and cultural heritage appointed (number/km^2)	0.074 (-0.491)	0.077 (-0.488)	0.221 (-0.363)	0.107 (-0.463)	4.510 (3.368)	0.277 (-0.314)	0.334 (-0.265)	0.088 (-0.479)	0.055 (-0.508)	0.039 (-0.521)	0.573 (-0.057)	2.578 (1.687)	1.345 (0.615)	0.393 (-0.213)	0.355 (-0.247)	0.064 (-0.500)	0.066 (-0.498)	0.337 (-0.262)

Table 2. The original values of entering variables of the cities of interest. (*conti.*)
Note: The number in the parentheses denotes the normalized value of each variable, i.e. the value of the 3rd-level indicator, in a specific category.

Table 3 shows the points of overall score and the 1st-level indicator of each city. Based on the situation in 2008, Top 3 cities in terms of the global warming adaptation are Sapporo, Hiroshima and Niigata; on the other hand, the last three ones are Fukuoka, Osaka and Nagoya. The overall score and the 1st-level indicators give a comprehensive image of urban system performance. Furthermore, the 2nd-level and the 3rd-level indicators can provide information to make substantial strategy for global warming adaptation on a city level. Table 4 gives the results of the 2nd-level and original indicators for each city.

City	Overall Score	The 1st-level indicator		
		Pressure and State	Function	Coordination
Sapporo	0.452 (1)	0.959 (1)	-0.184 (15)	-0.689 (18)
Sendai	0.196 (4)	0.384 (3)	-0.126 (12)	0.036 (5)
Saitama	-0.129 (6)	-0.277 (15)	0.115 (6)	0.022 (6)
Chiba	0.052 (9)	0.033 (10)	0.135 (5)	-0.086 (8)
Tokyo (special wards)	0.011 (10)	-0.710 (18)	0.528 (1)	2.789 (1)
Kawasaki	0.112 (7)	0.105 (7)	0.266 (3)	-0.313 (14)
Yokohama	0.181 (5)	0.182 (6)	0.336 (2)	-0.288 (13)
Niigata	0.294 (3)	0.471 (2)	0.089 (7)	-0.155 (10)
Shizuoka	-0.073 (14)	-0.067 (14)	0.048 (8)	-0.473 (16)
Hamamatsu	-0.019 (11)	-0.013 (11)	-0.083 (11)	0.139 (3)
Nagoya	-0.732 (18)	-1.055 (17)	-0.312 (17)	-0.055 (7)
Kyoto	-0.033 (12)	-0.050 (12)	-0.048 (9)	0.115 (4)
Osaka	-0.465 (17)	-0.651 (16)	-0.141 (13)	-0.318 (15)
Sakai	-0.068 (13)	0.078 (9)	-0.319 (18)	-0.192 (11)
Kobe	0.093 (8)	0.203 (5)	-0.052 (10)	-0.134 (9)
Hiroshima	0.315 (2)	0.371 (4)	0.137 (4)	0.510 (2)
Kitakyushu	-0.079 (15)	0.094 (8)	-0.236 (16)	-0.651 (17)
Fukuoka	-0.107 (16)	-0.059 (13)	-0.152 (14)	-0.258 (12)

Table 3. The overall score and the 1st-level indicators of the interested city.
Note: The number in the parentheses denotes the rank of each indicator in a specific category.

Indicator / City	Pressure and State				Function					Coordination
	Population Scale	Environmental Pressure	Catastrophe Pressure	Environmental Quality	Production Capacity	Natural Supporting System	Public Supporting System	Information Exchange Intensity	Metabolism Capacity	Civilization Development Potential
Sapporo	0.352(6)	0.576 (1)	1.223 (1)	1.199 (1)	-0.437 (11)	-0.092 (10)	-0.235 (12)	-0.673 (12)	0.308 (6)	-0.689 (18)
Sendai	0.848 (1)	0.322 (4)	0.239 (7)	0.488 (4)	-1.147 (17)	0.529 (6)	-0.658 (14)	-0.731 (15)	0.242 (7)	0.036 (5)
Saitama	0.159 (9)	0.274 (6)	-0.586 (16)	-0.419 (15)	0.682 (4)	-0.167 (12)	-0.150 (8)	0.244 (7)	0.396 (4)	0.022 (6)
Chiba	0.407 (5)	-0.406 (15)	0.058 (10)	0.163 (6)	-0.659 (15)	0.194 (8)	-0.228 (11)	-0.111 (8)	0.948 (1)	-0.086 (8)
Tokyo (Special Wards)	-1.775 (18)	-0.407 (16)	-0.688 (17)	-0.124 (9)	1.266 (2)	-1.069 (17)	1.927 (1)	1.920 (1)	0.512 (3)	2.789 (1)
Kawasaki	-0.237 (14)	-0.035 (13)	0.358 (6)	-0.208 (10)	1.098 (3)	-0.664 (14)	0.699 (3)	1.361 (3)	0.060 (8)	-0.313 (14)
Yokohama	-0.414 (16)	0.332 (3)	0.436 (4)	-0.267 (11)	2.407 (1)	-0.481 (13)	0.670 (4)	0.248 (6)	0.567 (2)	-0.288 (13)
Niigata	0.307 (7)	-0.304 (14)	0.863 (2)	0.365 (5)	0.386 (6)	0.862 (3)	-0.722 (16)	-0.755 (16)	0.040 (9)	-0.155 (10)
Shizuoka	0.245 (8)	-0.006 (12)	-0.528 (15)	1.074 (2)	0.300 (7)	1.441 (1)	-0.690 (15)	-0.791 (17)	-1.125 (18)	-0.473 (16)
Hamamatsu	0.648 (3)	0.231 (8)	-0.349 (13)	0.119 (7)	0.060 (8)	1.126 (2)	-0.875 (18)	-0.806 (18)	-0.953 (17)	0.139 (3)
Nagoya	-0.383 (15)	-0.746 (17)	-1.522 (18)	-0.584 (17)	-0.443 (12)	-0.748 (15)	0.088 (6)	0.265 (5)	-0.362 (16)	-0.055 (7)
Kyoto	0.146 (10)	0.360 (2)	-0.456 (14)	0.562 (3)	-0.201 (10)	0.611 (4)	-0.722 (16)	-0.681 (13)	0.015 (10)	0.115 (4)
Osaka	-1.560 (17)	-0.923 (18)	-0.236 (12)	-0.760 (18)	-0.646 (14)	-1.562 (18)	1.482 (2)	1.364 (2)	-0.125 (13)	-0.318 (15)
Sakai	-0.120 (13)	0.135 (9)	0.223 (8)	-0.283 (12)	-1.107 (16)	-0.836 (16)	-0.223 (9)	1.019 (4)	-0.433 (15)	-0.192 (11)
Kobe	0.066 (11)	0.258 (7)	0.434 (5)	-0.503 (16)	0.067 (9)	0.295 (7)	-0.319 (13)	-0.455 (10)	-0.113 (12)	-0.134 (9)
Hiroshima	0.811 (2)	0.318 (5)	0.476 (3)	-0.346 (13)	0.631 (5)	0.544 (5)	-0.223 (9)	-0.726 (14)	0.311 (5)	0.510 (2)
Kitakyushu	0.054 (12)	0.024 (10)	0.193 (9)	-0.100 (8)	-0.450 (13)	-0.128 (11)	-0.145 (7)	-0.512 (11)	-0.110 (11)	-0.651 (17)
Fukuoka	0.445 (4)	-0.003 (11)	-0.137 (11)	-0.377 (14)	-1.808 (18)	0.147 (9)	0.325 (5)	-0.179 (9)	-0.179 (14)	-0.258 (12)

Table 4. The 2nd-level indicators of the interested cities.

Note: The number in the parentheses is the rank of each 2nd-level indicator in a specific category.

From Table 2-4 the comparative advantages and disadvantages of each city in 2008, in terms of global warming adaptation and human security, could be observed under the assumed intrinsic relationships of the precautionary indicator system. The upper-level cities in the overall ranking primarily obtain high scores on "Pressure and State" while this perspective is highlighted for the precautionary purpose in this study. Even the top 1 city, Sapporo, has low rankings in the other two 1st-level indicators, the differences compared with other cities are not too large. This is also one reason that the cities with high 1st-level scores would occupy high rankings. Still, some important policy implications for the development of adaptation strategies could be found by examining the scoring structure in Table 2-4. In principle, some implications could be observed as the following:

Pressure and State

Sapporo, Niigata and Sendai obtain the highest scores in this category, implying that the current pressures on global warming and human security are less than other cities in 2008. Regarding global warming, cities in north areas, e.g., Sapporo, Sandai and Niigata, might face less threatens of heat waves and the extreme weather than the sourth cities. Such outcome implies the geological condition would be an influencing factor on the regional climate stability. In view of the catastrophe pressures and climate change adaptation, meteorologically, the adequate latitude condition of a city might shift to a higher level than that of most current major cities in Japan. However, variables related to some sorts of natural hazards, e.g., earthquakes and tsunami, are not included herein while it is difficult to obtain appropriate quantitative precautionary variables in the existing statistics. On the other hand, Nagoya, Tokyo (special wards) and Osaka get relatively low scores while the current megacity scale is not suitable to relieve the pressures on global warming and human security.

Regarding the "Population Scale" indicator, for lower-scoring cities, the control of high population and household densities could be considered, while the later term seems to be a characteristic of modern society (Weng et al., 2009). As for the "Environmental Pressure" indicator, countermeasures on eliminating the resources and energy consumption and controlling the heat island effect could be taken into consideration. Also, incentives for using public transportation could be further designed. In fact, the public environmental education should be promoted as well so as to change the unsustainable lifestyle. In terms of the estimates of the "Catastrophe Pressure" and "Environmental Quality" indicators, as mentioned earlier, the urban heat island effect should be noticed and controlled by increasing green area inside the city while this argument is also highlighted in the "Natural Supporting System" indicator. In addition, the promotion of the green roof at buildings could be a multi-functional measure on pollution mitigation, stormwater runoff control, energy saving and heat island effect mitigation (Cartera & Keeler, 2008). Meanwhile, the restriction of private cars, incentives for using public transportation and the effective management on the pollution sources would reduce the air pollutant emissions associated with global warming and improve the urban environmental quality. In particular, the spatial car density data shows a strong positive relation to the ambient NOx concentration (the correlation coefficient is 0.84 for the original series). Economic instruments, e.g., car taxes and pollutant emission credits, would be potentially effective policy measures. Some strict emission standards of greenhouse gas could be suggested as well. Regarding the human security in urban area, municipal governors should eliminate the occurrence of crime and fire acccidents by launching strict regulations and frequent inspections.

Function

In fact, except for the "Natural Supporting System" indicator, the cities with high population density may have sufficient financial supports to enhance the capacities on this part. Therefore, Tokyo (special wards), Yokohama and Kawasaki have high scores on the "Function" indicator. On the other hand, Kitakyushu, Nagoya and Sakai obtain relatively low scores, implying that the natural service and the public governances should be promoted to cope with essential tasks of adapting global warming and improving human security.

In terms of the "Production Capacity," this study chooses per capita income only as a reference index. Some additional influencing factors might exist in this category, e.g., the technology innovation towards global warming mitigation. However, some quantitative variables might be difficult to be obtained. In addition, since the main purpose of this study is to developing the precautionary indicator for global warming, the weight of this category is not significant. In this sense, a moderate representative index might be sufficient. However, the representativeness of this index might be biased sine many employees are not inhabitants in the area where they work. As for the "Natural Supporting System" indicator, mainly, an open natural space inside the city is expected to enhance the potential of the service of natural systems. In addition, there is high potential to implement a variety of ecological engineering approaches in urban area to increase the natural supporting capacity (Chapman & Blockley, 2009). In addition, as aforementioned in the interpretation of the "Pressure and State" indicator, constructing new urban parks and green roof (or roof gardening) are effective measures. Regarding the "Public Supporting System" indicator, concerning about the human security capacity, the development of the public health service and the social security enhancement should be improved although the tasks might be low priority in conventional urban governances. In order to distribute in-time emergent alarms and implement reaction plans, the enhancement of the information change systems is required. In addition, the practice of the emergency reaction plans should be performed routinely. Though not strongly related, the metabolism capacity in large cities should be promoted considering the improvement of all the perspectives of urban sustainability.

Coordination

In this category, Tokyo (special wards), Hiroshima and Kobe have high scores while Shizuoka, Kitakyushu and Sapporo get relatively low scores on the "Civilization Development Potential" indicator. Examining the detailed scoring structure in Table 1, the low ratio of the public expenditure on education seems to be a main reason for this result. Meanwhile, more public education facilities are expected in the low-score cities to provide more opportunities for adult education. The public education facilities indeed could serve as platforms for promoting the education for sustainable development (ESD), which highlights issues covering global warming mitigation and human security improvement (UNESCO, 2011). Still, some additional indicators are required to take the sustainable industrial structure into consideration in this part.

Although the evaluation outcomes come out only by using the data in 2008, the results are informative for the decision-makers and citizens. The related stakeholders could find potential directions to improve upon the current situation in the comparative analysis. Based on the previous observations, concrete adaptation strategies of global warming mitigation and human security improvement for each city are proposed in Table 5.

City	Proposal	
Sapporo	Pressure and State	Improve the greening of roads
	Function	Build water storage facilities and facilitate the water resources management against potential droughts; Improve the spatial homogeneity of the resources of public health;
	Coordination	Improve the public investment on education; Improve the regional research capacity
Sendai	Pressure and State	Improve the greening of roads and promote the utilization of public transportation systems
	Function	Increase the resource (doctors and facilities) of public health care; Improve the capacity of crime crack by increasing the manpower; Establish efficient alarm networks for natural hazards and human security
	Coordination	Improve the regional research capacity; Improve the resources and infrastructures of public education
Saitama	Pressure and State	Manage the utilization of car by imposing a higher car tax for instance; Promote roof gardening, improve the drainage systems, and establish detention ponds to prevent from potential stormwater; Create natural surfaces to eliminate potential heat waves, by roof gardening for example
	Function	Increase the natural surfaces and promote green roof or green buildings by revising built environment regulations; Create urban parks; Increase the resource of public health care; Improve the capacity of crime crack and hazard security, by increasing the manpower for instance
	Coordination	Improve the regional research capacity; Improve the resources and infrastructures of public education
Chiba	Pressure and State	Encourage energy/natural gas saving by using economic incentives and adjusting the prices for instance
	Function	Improve the regional research capacity
	Coordination	Improve the regional research capacity; Improve the resources and infrastructures of public education

Table 5. Proposals towards sustainable city for interested cities.

City	Proposal	
Tokyo (special wards)	Pressure and State	Control the population/household density; Encourage water/natural gas saving by using economic incentives and adjusting the price levels for instance; Promote roof gardening, improve the drainage systems, and establish detention ponds to prevent from potential stormwater; Control NOx pollution: implement more strict pollution countermeasures such as making more strict emission standards and eliminating pollutant emission sources.
	Function	Increase the natural surfaces and promote green roof or green buildings by revising built environment regulations; Create urban parks;
	Coordination	Under stable development
Yokohama	Pressure and State	Manage the utilization of car by imposing a higher car tax for instance
	Function	Increase the natural surfaces and promote green roof or green buildings by revising built environment regulations; Create urban parks
	Coordination	At an appropriate level
Niigata	Pressure and State	Improve the greening of roads and promote the utilization of public transportation systems; Encourage the water saving by using economic incentives and adjusting the price levels for instance; Improve the greening of roads
	Function	Establish efficient alarm networks for natural hazards and human security
	Coordination	At an appropriate level;
Shizuoka	Pressure and State	Encourage the increase of newborn babies; Promote roof gardening, improve the drainage systems, and establish detention ponds to prevent from potential stormwater
	Function	Increase the resource (doctors and facilities) of public health care; Improve the capacity of hazard security by increasing the manpower; Improve the prevailing of sewage services; Establish efficient alarm networks for natural hazards and human security
	Coordination	Improve the regional research capacity; Improve the resources and infrastructures of public education

Table 5. Proposals towards sustainable city for interested cities. (*conti.*)

City	Proposal	
Hamamatsu	Pressure and State	Improve the greening of roads and promote the utilization of public transportation systems; Prevent from Oxidant pollution: survey the possible precursors' emission and eliminate the sources.
	Function	Increase the resource (doctors and facilities) of public health care; Improve the capacity of crime crack and hazard security, by increasing the manpower for instance; Improve the capacity of hazard security by increasing the manpower; Improve the prevailing of sewage services; Establish efficient alarm networks for natural hazards and human security
	Coordination	Improve the regional research capacity; Improve the resources and infrastructures of public education
Nagoya	Pressure and State	Encourage energy saving by using economic incentives and adjusting the price levels for instance; Manage the utilization of car, e.g. by imposing a higher car tax; Create natural surfaces to eliminate potential heat waves, by roof gardening for example; Prevent crime and fire accidents
	Function	Increase the natural surfaces and promote green roof or green buildings by revising built environment regulations; Create urban parks; Improve the capacity of crime crack and hazard security, by increasing the manpower for instance; Improve the recycling and reuse of general waste (the original data might be questionable due to the natural hazard occurred in the year)
	Coordination	At an appropriate level
Kyoto	Pressure and State	Encourage the increase of newborn babies; Promote roof gardening, improve the drainage systems, and establish detention ponds to prevent from potential stormwater; Create natural surfaces to eliminate potential heat waves, by roof gardening for example
	Function	Improve the capacity of crime crack and hazard security, by increasing the manpower for instance; Establish efficient alarm networks for natural hazards and human security
	Coordination	Improve the public investment on education

Table 5. Proposals towards sustainable city for interested cities. (*conti.*)

City	Proposal	
Osaka	Pressure and State	Control the population/household density; Encourage water/natural gas saving by using economic incentives and adjusting the price levels for instance; Promote the reduction of general waste generation; Manage the utilization of car, e.g. by imposing a higher car tax; Prevent crime; Control NOx pollution: implement more strict pollution countermeasures such as making more strict emission standards and eliminating pollutant emission sources.
	Function	Increase the natural surfaces and promote green roof or green buildings by revising built environment regulations; Create urban parks; Improve the capacity of crime crack and hazard security, by increasing the manpower for instance; Improve the recycling and reuse of general waste
	Coordination	Improve the public investment on education
Sakai	Pressure and State	Encourage natural gas saving by using economic incentives and adjusting the price levels for instance; Manage the utilization of car, e.g. by imposing a higher car tax
	Function	Improve the capacity of crime crack and hazard security, by increasing the manpower for instance; Improve the recycling and reuse of general waste
	Coordination	At an appropriate level
Kobe	Pressure and State	Prevent crime and fire accidents; Prevent from Oxidant pollution: survey the possible precursors' emission and eliminate the sources.
	Function	Improve the recycling and reuse of general waste
	Coordination	At an appropriate level
Hiroshima	Pressure and State	Create natural surfaces to eliminate potential heat waves, by roof gardening for example
	Function	Increase the resource (doctors and facilities) of public health care; Establish efficient alarm networks for natural hazards and human security
	Coordination	At an appropriate level
Kitakyushu	Pressure and State	Encourage the increase of newborn babies; Improve the greening of roads and promote the utilization of public transportation systems
	Function	At an appropriate level
	Coordination	At an appropriate level
Fukuoka	Pressure and State	Create natural surfaces to eliminate potential heat waves, by roof gardening for example
	Function	Improve the recycling and reuse of general waste
	Coordination	At an appropriate level

Table 5. Proposals towards sustainable city for interested cities. (*conti.*)

In addition, applying the ideas of the EKC, a quadratic equation is preliminarily established to fit the possible relationship between the overall scores and the area of the regions. The ordinary least squares (OLS) method is used to estimate the parameters, and the results are statistically diagnosed to confirm the statistic credibility of the model. As shown in Fig.3, the results of the F test and the t test denote that most of the parameter estimators are significant; the Durbin-Watson (DW) statistic shows that no significant serial correlation problem exist in the error term. However, only about 17% of the model variances are explained by the current one; one reason is that the equation only considers the influencing factor of area, on the basis of the concept of EKC. Still, the developed equation could provide a preliminary estimation for the optimal area of a sustainable city for the research purpose. In Fig. 3, the results imply that 987.26 km^2 would be the optimal area according to the methodological assumptions and data in 2008. Besides, the area of the top 2 cities in the ranking is close to this optimal value, supporting the current outcome. On the other hand, satisfactory results are not obtained in developing the function of the overall scores and the population scales of the interested regions. Given that more rational weights of the indicators, the result suggests that the coupling of the indicator system and the EKC could be an informative tool to analyse the optimal development scale from a variety of perspectives with the current available statistics, and thus this methodology could aid future urban design towards sustainable development.

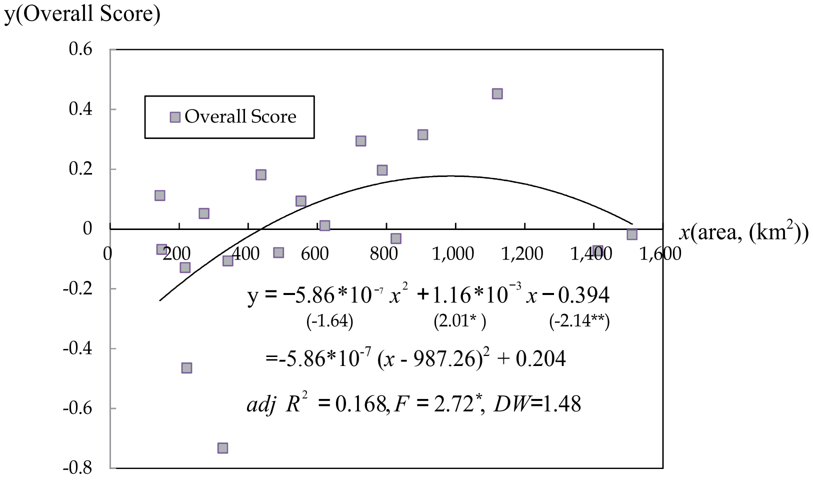

Fig. 3. The relationship between the overall scores and areas for the study regions. Note: Values in the parentheses are t statistics for the parameter estimator; * and ** denote significance at the 10% and 5% levels, respectively.

In fact, some deficiencies in this study are expected to be improved at the next step. First, an additional analysis on the weights in the current precautionary indicator system is required. Second, the aggregation process in the precautionary indicator system actually assumes that the intrinsic relationships among the variables are linearly. In this sense, the weights of the indicators serve as the coefficients in a linear equation in each category. Therefore, the potential collinearity among the indicators in the current indicator system has to be further examined given that a more credible spatial-temporal panel data. Third, regarding the cooperation and competition among the cities, some neighboring cities may have strong interactions to form a regional economy. For example, in the eastern Japan, several major cities comprise of the informal Kando regional economy. In this sense, the current methodology of the development of indicator systems should take the interactions among stakeholders into consideration by adopting import/export flows. Still, the current methodology could provide adaptation strategies to a certain extent with a small data requirement.

4. Conclusion and future prospect

Considering the composite socio-economic-environmental relationships, this study makes an attempt to develop a precautionary indicator system to quantify the degree of the risks with regard to global warming and human security in urban areas. An normalization procedure considering the attributs of impacts is proposed to develop the indicator system. Regarding the improvement of the current methodology, two parts could be further studied. Firstly, considering the manipulability of the calculation, the behaviors of the variables are assumed to obey the standard normal distribution in this study while some might not. Further distribution tests could be implemented for the recognition of the behaviour of each index. Secondly, the weights within the hierarchies could be re-structured by using the AHP or ANP-like methods, e.g., AHP, fuzzy-AHP, or ANP methods, so that all the stakeholders' view points could be taken into consideration.

Using the official data in 2008, the preliminary empirical results provide concrete adaptation strategies for the major cities in Japan. Furthermore, every city could find some solutions to improve their capacity regarding the global warming and human security. In addition, concerning the catastrophe pressures and the climate change adaptation, the adequate latitude condition of a city might shift to a higher level than that of most major cities in Japan. Furthermore, using the overall scores of the precautionary indicator systems, a preliminary EKC is established to discover the optimal size of a city, showing that a city in the area of around 987.26 km^2 would be adequate for the purpose of global warming adaptation and human security improvement with regard to city governances. Consequently, as shown in the demonstrated EMC example, more attributes on the city scales could be exploited based on the established indicator sytem using a comprehensive data. Based on the outcomes of this study, the precautionary indicator system and the proposed adaptation strategies regarding the global warming mitigation and human security improvement would contribute to the facilitation of the current urban planning for sustainable development.

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6

Urban and Peri-Urban Tree Cover in European Cities: Current Distribution and Future Vulnerability Under Climate Change Scenarios

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1. Introduction

Scientific data collections and databases are exponentially growing. Modeling techniques and data analysis procedures have also been evolving rapidly in the lasts decades. Specific scientific domains such as medical and biological sciences have adopted a routine of scientific dissemination where datasets and analytical methods are visible and usable for the researchers.

This means publishing results and giving access to data and algorithms in order to allows the reproducibility (i.e. reproduce the same techniques by applying different input data) and repeatability (i.e. same technique and input data) of scientific experiments. The accessibility and possibility of sharing algorithms and programming routines is getting more important, because of the complexity of experiments. As a matter of fact, even if a methodology is explained in a very precise and detailed scientific text, the reproducibility of an experiment is highly challenging for scientists that try to implement the same method without the access to data and codes.

The global warming and climate change issues are approached by different scientific domains (climatologist, ecologists, economists as an example). This book illustrates such differentiation. The research areas of spatial ecology and ecological modeling are strongly linked to climate change applications and are continuously producing a huge amount of scientific publications and results in this domain. In comparison to biomedical studies, access to data and source codes are most of the time not available in the field of spatial ecological modelling. Recent works have been changing this routine and scientific papers in ecology are starting to include sample data and open source programming codes (Elith et al., 2008).

This chapter approaches the impact of global worming on urban greening in European cities. At the FBK foundation we highlight the importance of the accessibility of data and codes, and on the reproducibility and repeatability of our methods. The uncertainties related to predictions of global warming can be minimized or quantified only by a complete scientific transparency. Transparency is also important for the transfer of scientific knowledge to the policy macking process. The main objective of this study is to focus next to the results on the visibility and reproducibility of the method. Transparency allows further studies to improve data processing routines and produce more accurate and precise informations.

In this book chapter are analysed the impacts of global warming in urban greening. There is a wide interest in urban greening because urban greening and peri-urban forests have a strong positive effect on the physical environment of urban areas and in people life quality.

Urban greening comprises recreational and social value (Tarrant & Cordell, 2002), affect the economic value of housing (Kong et al., 2007), preserves biodiversity and wildlife corridors between urban and non-urban habitat islands (Blair, 1996; Zipper et al., 1997), reduces noise (Fang & Ling, 2003), sequester CO_2 and produce O_2 (McHale et al., 2007; Nowak & Crane, 2002; Nowak et al., 2007), reduces air pollution (Cavanagh et al., 2009; Escobedo & Nowak, 2009; McDonald et al., 2007; Yang et al., 2005), regulates the micro-climate and reduces effects of heat island in cities (Akbari et al., 2001; Shin & Lee, 2005).

Due to climate change, a degradation of air quality is expected to occurs predominantly in urban-industrial areas as well as an urban climate warming (McCarthy et al., 2010). With a proactive management strategy, vegetation greening and belts of peri-urban forests have strong potentials to mitigate the impact of global warming such as extreme heat waves. Besides the mitigation potentials of urban greening, climate change will possibly increase the vulnerability of urban vegetation. For this reason proactive planning of urban greening is important to mitigate the impact of climate change on humans and to prevent urban vegetation vulnerability.

Proactive planning of forested urban areas require an integration of ecological information such as output of niche models in a general landscape and urban sprawl planning framework. Because of the high uncertainty of ecological changes in the future and our potential choice of development strategies, the analysis of various scenarios and the possibility to compare different mitigation strategies are interesting for scientists, decision makers and informed citizens.

In the last decades scientists have proposed several ecological niche models (ECONM) (Bolliger et al., 2000; Elith et al., 2006) and developed related habitat distribution maps. Such models are empirical statistical models relating climatic conditions to the distribution of living organisms. ECONM relate current climatic conditions to the distribution of plants and predicts vegetation vulnerability under changing climatic conditions.The output prediction maps do not provide information on a certain extinction of a specie under climate change (CC), but they will rather inform us on it's suitability. We assume the more a species grows in its fitted climate the more the ecosystem will be homeostatic. This means that the ecosystem will be more stable, resistant and resilient despite natural disturbances. In the last years, ECONM have been mainly applied to the analysis of natural reserved areas for proactive planning of landscape management, biodiversity conservation and risk assessment of species extinction. There is a lack of applied studies in the context of ECONM and vulnerability of urban and peri-urban greening (UPUG). Results of such applications could help to highlight the potential impact of CC on UPUG and to provide feed- back on effects of greening to urban micro-climate, human health and well-being. Additionally, the findings could help landscape planners to select those tree species which are best adapted to specific urban areas coinciding to current and future expected climate conditions and limit UPUG management costs.

Before analysing the potential future trends of changes for UPUG, the current distribution traits need to be defined in order to be able to interpret and evaluate scenarios of future changes. This chapter presents an automatic open access and open source procedure for the analysis of 15 urban areas in Europe. Key aspects are:

1) the visualization of the current urban greening and estimations on the extent of tree cover in urban and peri-urban areas.

2) The analysis of climate change impact on two common tree species: The Mediterranean

evergreen Holm Oak *Quercus ilex* (L.) and the Scots pine *Pinus Sylvestris*. An example analysis is applied in two different city.

2. Method

For this study the available data needs to be selected as well as the urban and peri-urban areas that will be used for the case studies. Further, the method for the data processing and its computational implementation needs to be defined.

2.1 Input data selection

At present a large variety of data on European forests, urban greening and urban development exists but frequently difficulties occur with the harmonization of input data for comparability of local scale analysis. The main source of harmonized data on European forest is provided by the Eurostat forestry statistics. However, Eurostat does not include a forest mapping survey.
Remotely sensed data provide an useful information on the estimate of tree cover in European cites. Currently existing forest maps on a European extent (derived by remote sensing data) range from 1 km resolution based on Advance Very High Resolution Radiometer (Häme et al., 2001) and Spot-vegetation (Bartholome & Belward, 2005) to 180 m resolution Wide Field Sensor data (GAF, 2001), and 25 ha minimum mapping unit of CORINE Land Cover (CLC) database (Perdigao & Annoni, 1997) where forest and urbanized area data can be retrieved. Using this data will lead to a strong generalization of results including errors in the estimate. In fact, none of these data have the possibility to detect tree cover of objects smaller of 25 ha of surface. One alternative solution is the forest non forest pan European map 2000 (FNFMAP) (Pekkarinen et al., 2008). This harmonized data on a European extent is available for studying tree cover distribution of minimum of 25 m mapping units. The forest non forest map was not conceived for urban greening study purposes but it includes urban tree cover. For this study the latter dataset was chosen because its scale and extent is appropriate as well as the fact that it is an open access product and harmonized for the whole European extent. Such data peculiarity allows potential reproducibility of our method on other potential European urban zones and to eventually produce urban cover changes using the 2006 map now available at the Joint Research Centre of the European Commission web site [1].
Beside the greening component of our study we selected the Urban Morphological Zones (UMZ) (Milego, 2007; Simon et al., 2010) map as definition and geographical determination of urban areas. The UMZ are defined as a *set of urban areas laying less than 200 m apart* (Simon et al., 2010). Those urban areas are drawn by CLC land cover classes contributing to the urban topology and function: continuous urban fabric; discontinuous urban fabric; industrial or commercial units; green urban areas, port areas, airports, sport and leisure facilities. Besides the previously mentioned "core" classes, road and rail networks are also considered if they are neighbors to the core set of classes. Water courses, forests and scrub classes are also considered if they are completely within the core classes. As a result, the administrative boundary of a specific city is different and not directly comparable to what we define as city using the UMZ. The exercise of harmonizing and extracting green urban areas in Europe was already carried out by using a mosaic map derived from remotely sensed data [2]. Two resulting maps were achieved: the Green Urban Areas within Urban Morphological Zones 2000 map (GUA, 2006) and the Percentage of Green Urban Areas in Core Cities (GUA, 2011). Both results derive

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[1] http://forest.jrc.ec.europa.eu/forestmap-download

[2] Image2000: Joint Research Centre of the European Commission http://image2000.jrc.ec.europa.eu/ - The Spatial Reference for Europe, based on Landsat 7 ETM+ data

urban zones from CLC data. The latter focuses on cities with more 100.000 inhabitants (see GMES Urban Atlas GMES) while the first is not restricted to any city size. Both data are also not open access data therefore, only a low resolution map or low resolution statistics for percentage green cover can be visualized This is the main reason to use the UMZ and FNFMAP maps for this research project.

Once defined the urban tree cover distribution (refer to sub-chapter "spatial analysis and computational implementation"), the ECONM can help to understand vegetation vulnerability under climate change scenarios (Casalegno et al., 2010). ECONM are based on field data locally sampled. The harmonization of such data at continental scale is technically difficult and implies the use of rigorous scientific methodology to limit inaccuracy and imprecision. An example of integrated efforts to collect harmonized data in the forest sector on the European scale is the *forest Focus* regulation (EC, 2003). The Forest focus database was implemented in 1994 for a better understanding of the impact of air pollution and other biotic factors concerning European forest ecosystems. It is a Pan European Programme for Intensive and Continuous Monitoring of Forest Ecosystems. Results of the programme and datasets contribute to the assessment of criteria and indicators for sustainable forest management. Other results from the forest Focus regulation are ECONM models of main dominant European tree species and forest categories, which is on-line available (Casalegno et al., 2011; 2010; EFDAC, 2011).

In this application, ECONM map derived from forest focus datasets are used as the only open access prediction maps at high resolution of 1 km and continental extent for European tree species. Summarized, the CC impact assessment is build on urban and peri-urban European areas using the forest non-forest Pan European map, the Urban Morphological Zones map and the ecological niche models of tree species available at JRC - EFDAC website.

2.2 Selection of the urban study area

From the UMZ 15 city capitals in Europe were selected (Fig. 1) including : Amsterdam, Athens, Berlin, Bruxelles, Budapest, Copenhagen, Helsinki, Lisbon, London, Madrid, Paris, Rome, Stockholm, Warsaw, Vienna.

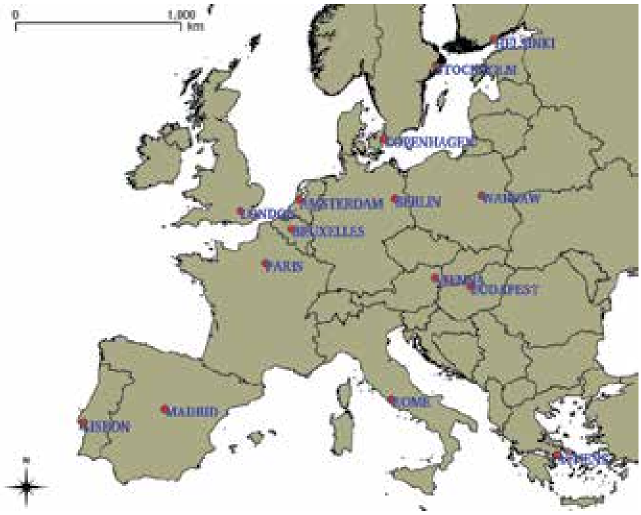

Fig. 1. Selected European capitals for the analysis

2.3 Spatial analysis and computational implementation

The spatial analysis and data processing include following steps:
(1) Defining the extent of the study areas. For each urban study area a squared bounding box was defined including the core UMZ corresponding to each city. The squared area is larger than the core UMZ. The selected areas contain urban zones and not urbanized areas according to the UMZ classification scheme.
(2) Downloading and importing forest cover data with the same projection into a Geographic Information System project.
(3) Mapping current UPUG: The intersection between UMZ and FNFMAP produces maps of UPUG cover.
(4) Estimate for each city the proportion of the tree cover / non-tree cover within the UMZ and outside (the peri-urban area). The size of the bounding box determines the quantity of urban greening that is analyzed. Here a percentage cover is used as measure unit to allow comparisons between different cities. A table summarizing results and a figure plotting the percentage urban green cover versus the percentage peri-urban green cover are automatically produced by executing the script. This allows easy data interpretation. Since the pixel resolution of the analysis is set to 100 meters, the original output statistics are in hectares (ha). In order to simplify the data visualization the map units in ha were converted into km.
(5) Downloading and importing the ECONM habitat suitability maps of Scots pine and Holm oak into the Geographic Information System. The maps are binary classified in suitability / non-suitability of the specie. (6) Plotting the maps of current and future trends of suitability under climate change projections. For both specie the difference maps between the year 2000 and the three future projections maps (2020-2000, 2050-2000 and 2080-2000) are computed.
Difference maps contain information categorized in four classes representing suitability changes in time: Class 1: Stable suitability with no changes between the input maps. During the years the species maintain their suitability. Class 2: Gain of suitability. Pixels classified as not-suitable will be suitable. There is a climatic fitness of the species to the changing climate.
Class 3: Loss of suitability. Pixels classified as suitable will be not-suitable. The climate is not suitable anymore for the growth and reproduction of the tree specie. The population is now displaced out of the optimum climatic ecological niche of the species. In these areas plants become potentially vulnerable, because the particular specie does not grow anymore under it's appropriate climate. This leads to a potentially declining resilience capacity, inability to regenerate and lower resistance to external biotic and abiotic events. An increasing vulnerability to pathogens, extreme climatic events and competition is to be expected. Class 4: Unsuitable. Pixels are classified as not-suitable in both maps. The area is not within the optimal condition in neither past nor under future climate conditions.
Data processing is carried out in Linux Ubuntu environment using the GIS software: Geographic Resources Analysis Support System (GRASS Development Team, 2010) and R software and environment for statistical computing and graphics (R Development Core Team, 2011). Both software are used in text mode allowing the scripting routines to be processed in the Linux bash shell terminal.

3. Results

After downloading all required input data, the overall computational time on a 2CPU computer and 4GB memory is relatively fast (30min). This allows the reproducibility of the research project using the selection of different city or the city extent bounding box. The analysis of other tree species is also feasible changing the ECONM suitability maps imported within the scripting routine.

3.1 Current tree cover distribution

Maps on urban and peri-urban greening within each European capital is displayed in figure 2, 3, 4. The maps visualise the extent of the urbanized areas against the peri-urban areas as well as the tree cover within both classes.

The extent of the study area for each city is available in table 1 as well as the extent of the urban and peri-urban spatial extension. The exact location of each city study area is available on-line together with the scripting codes [3].

In figure 5 are visualized the data found in table 1 to facilitate the analysis and allow immediate understanding and comparison of urban greening distribution trends.

	Total sq km	Urban sq km	Peri-urban sq km	% UPUG	% UG	% PUG
Amsterdam	1370	422	948	4.1	4.1	4.0
Athens	1583	454	1129	9.7	0.9	13.2
Berlin	2487	1002	1485	43.8	42.0	45.0
Bruxelles	1783	857	927	16.0	12.0	19.7
Budapest	2704	718	1986	20.8	2.5	27.3
Copenhagen	1352	547	806	21.0	28.5	16.0
Helsinki	1360	498	862	57.0	49.1	61.6
Lisbon	2063	491	1572	23.7	8.7	28.4
London	3521	1897	1623	9.9	4.9	15.8
Madrid	1903	524	1379	6.4	6.8	6.2
Paris	3549	1777	1771	20.8	10.8	30.8
Rome	1654	446	1208	8.4	3.5	10.2
Stockholm	2541	720	1820	70.5	57.3	75.7
Warsaw	3782	646	3135	32.8	36.5	32.0
Vienna	1685	457	1228	28.9	4.9	37.8

Table 1. Synthetic overview of urban and peri-urban tree cover estimated using The pan-European Forest non forest map (Pekkarinen et al., 2008) and the European Urban Morphological Zones (Milego, 2007; Simon et al., 2010). The resolution of the analysis is 100m. UPUG: urban and peri-urban greening; UG: urban greening; PUG: peri-urban greening.

3.2 Tree species vulnerability under climate change

Tree species suitability maps from the ECONM are generated by the *Random Forest* software package in R (Liaw & Wiener, 2002) as described in (Casalegno et al., 2010). Input of the ECONM maps is the *Worldclim* climatic database (Hijmans et al., 2005) for simulating current and future plant-climate suitability. The total number of predictions available in the ECONM maps per specie is 25. One of them correspond to the predictive model plotted for the year 2000. The other 24 ECONM maps per specie correspond to future climate scenarios: three different global circulation models and their averaged model simulating three years (2020, 2050 and 2080) under two different future development trends (A2a and B2a). A2a and B2a scenarios are detailed in the Intergovernmental Pannel on Climate Change (IPCC, 2001) Special Report on Emissions Scenarios story-line (SRES).

The three different Global Climate Models used in the *Worldclim* dataset simulations are: HADCM3 (Hadley Centre Coupled Model version 3) (Collins et al., 2001), CCCMA (Canadian Centre for Climate Modelling and Analysis) (Kim et al., 2003), CSIRO (Commonwealth

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[3] http://www.spatial-ecology.net/doku.php?id=wiki:urbanmod

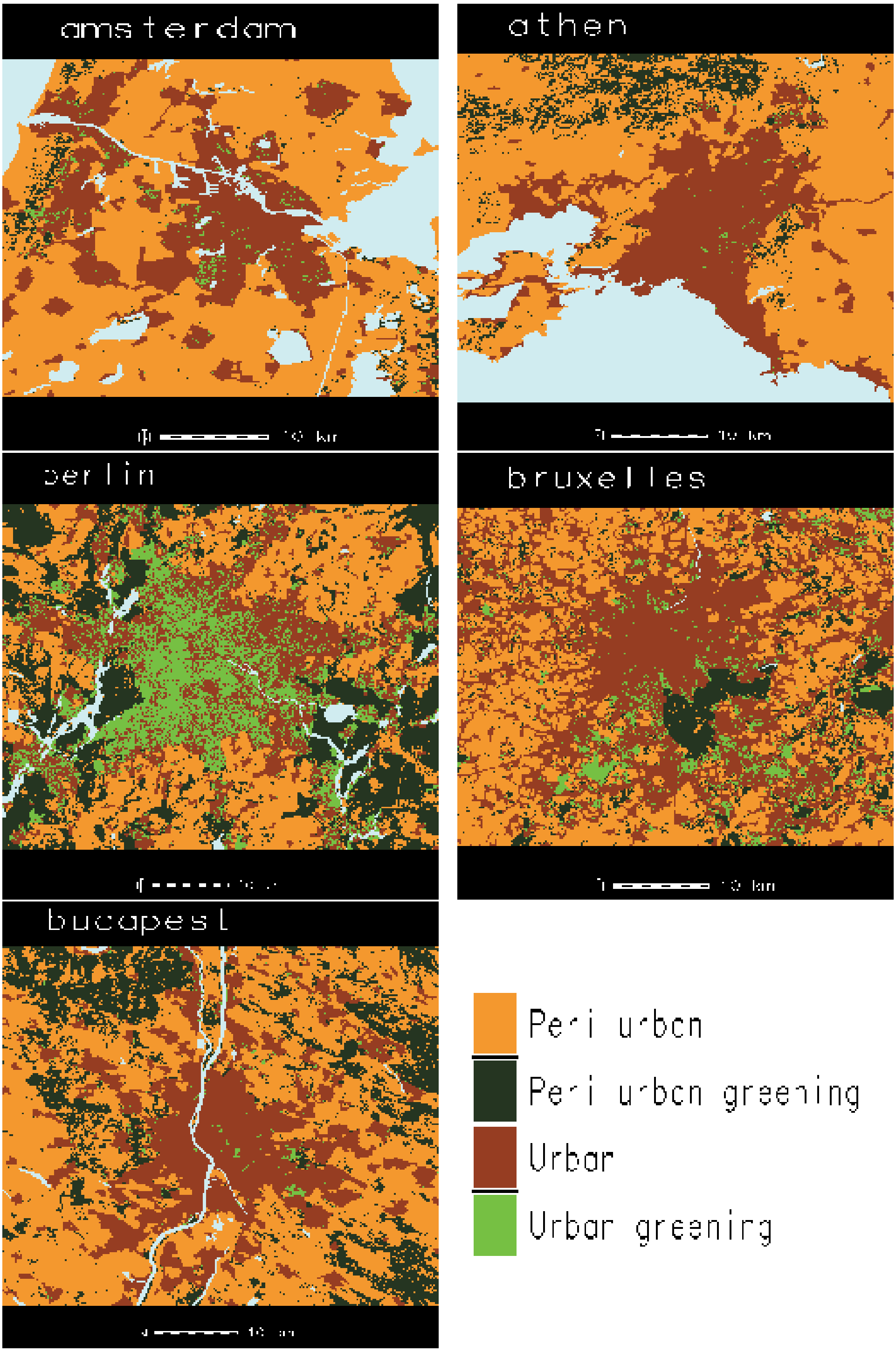

Fig. 2. Urban and peri-urban tree cover distribution in European Capitals

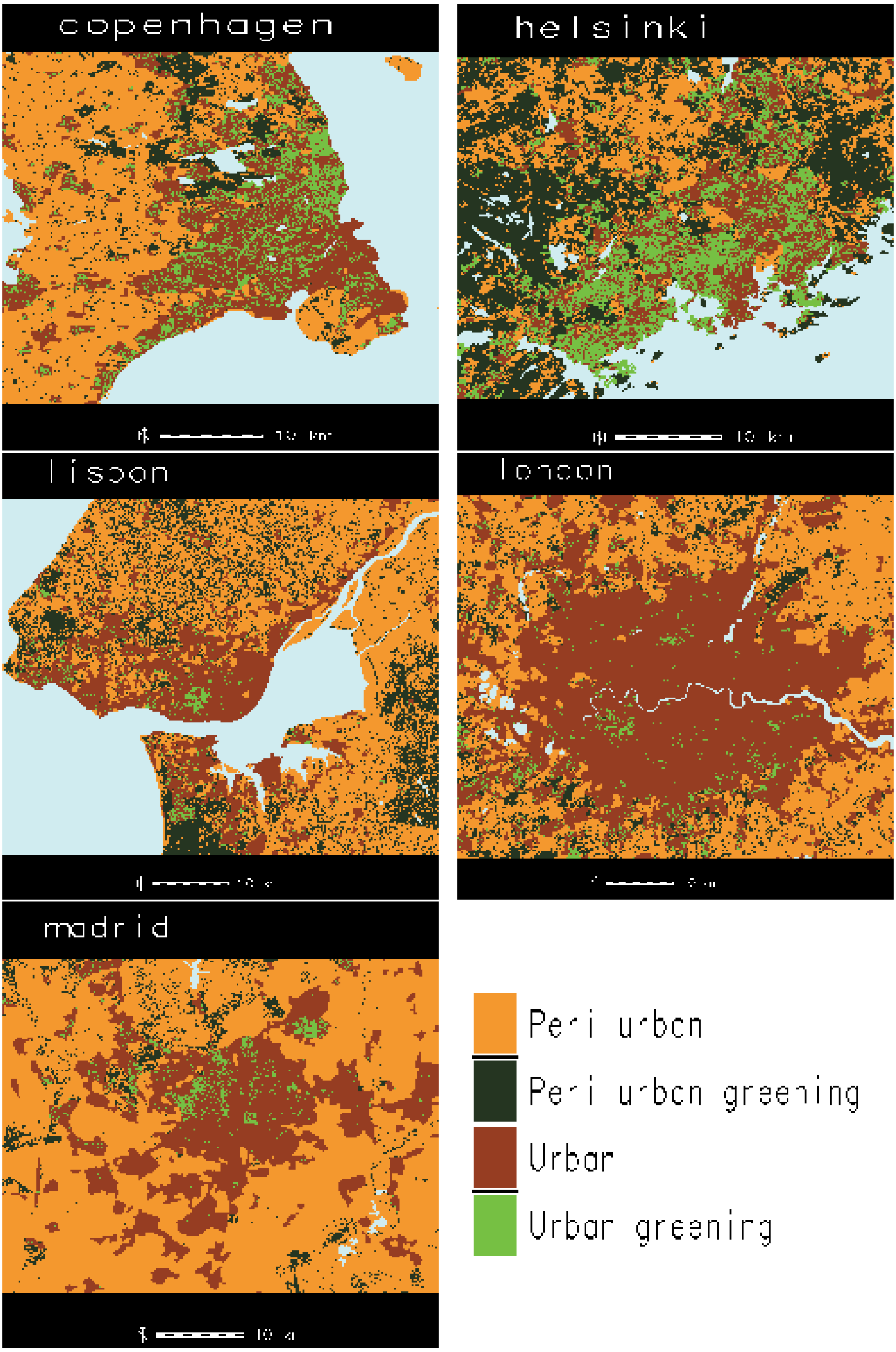

Fig. 3. Urban and peri-urban tree cover distribution in European Capitals

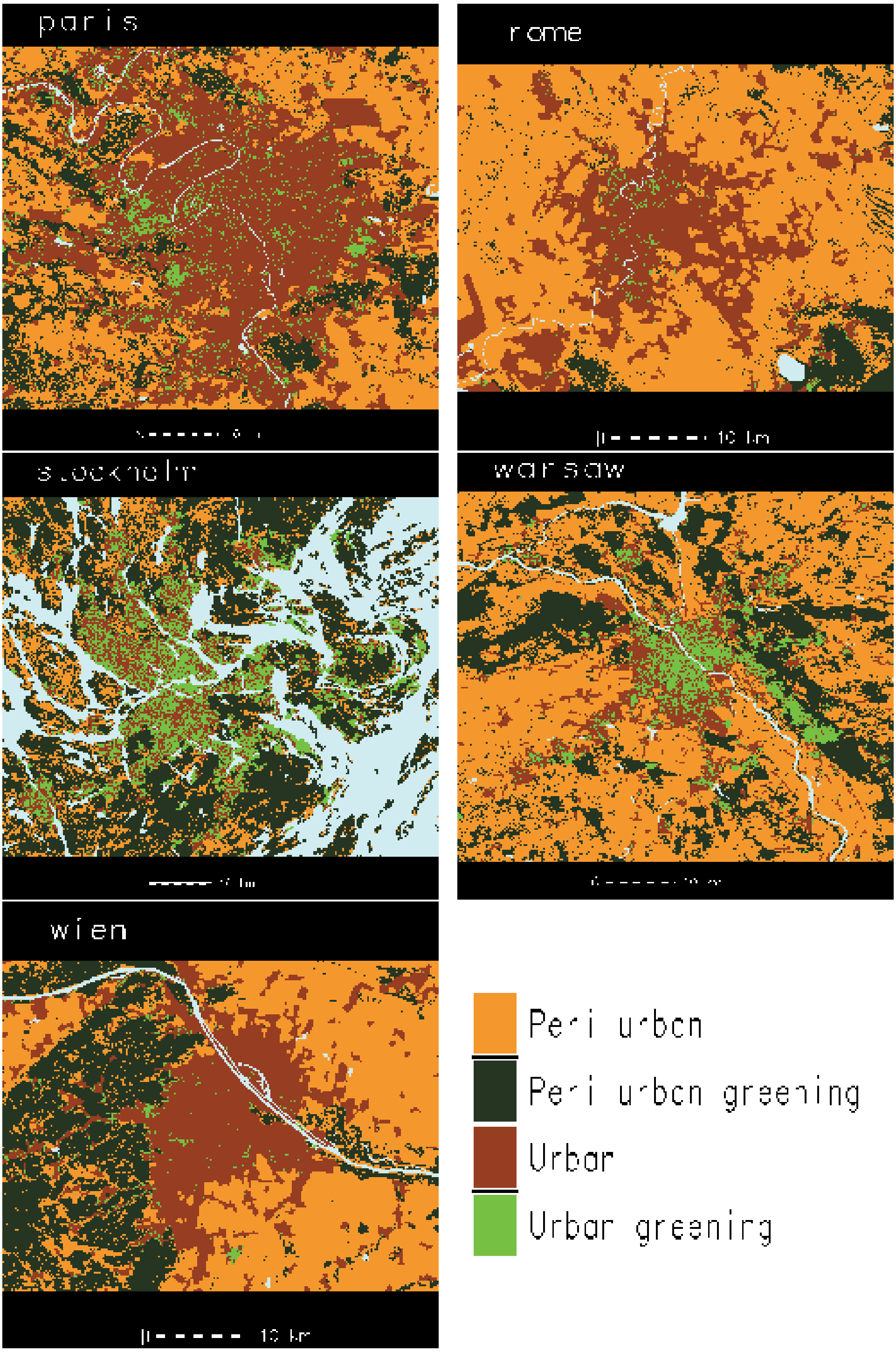

Fig. 4. Urban and peri-urban tree cover distribution in European Capitals

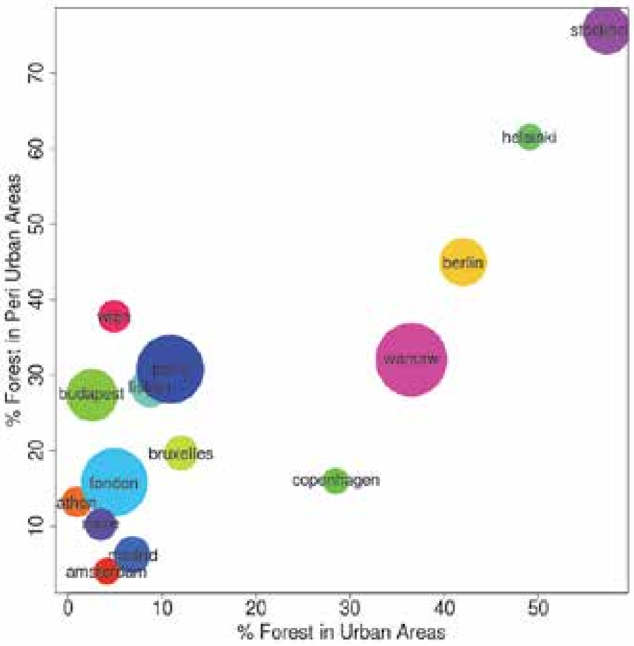

Fig. 5. Urban and peri-urban tree cover proportions in 15 selected European City capitals. The size of circles is proportional to the study area considered for the analysis.

Scientific and Industrial Research Organisation) (Gordon & O'Farrell, 1997).

The two SRES story-line (A2a B2a) included in the *Worldclim* scenarios describe the relationships between the forces driving greenhouse gas and aerosol emissions and their evolution during the 21st century. Each storyline represents different demographic, social, economic, technological, and environmental developments that diverge in increasingly irreversible ways: A2a describe a highly heterogeneous future world with regionally oriented economies. The main driving forces are a high rate of population growth, an increase in energy use, land use changes and slow technological change. The B2a storyline produce a minor increase in the temperature for the future, it is also regionally oriented but with a general evolution towards environmental protection and social equity.

The amount of maps produced for one specie is equal to 375 (24 prediction maps x 15 Urban areas). The potential applications of such maps can be multiple. Governmental and intergovernmental pannels or biodiversity conservation centres can be interested in the analysis of the overall vulnerability of a species in UPUG environments. Local managers and decision makers could use the suitability trends of a particular species for proactive landscape planning.

Here, few maps were chosen from the large variety of maps produced: the current and future distribution of Scots Pine in Helsinki and Holm oaks in Paris, which were simulated according to the SRES A2a scenario, using the averaged global circulation climatic model.

Figure 6 and 7 shows the trends of suitability changes for the next century in Paris and Helsinki. According to the ECONM output suitability maps, Scots Pine is adapted to the climate of Helsinki in year 2000 but will lose most of its climatic habitat suitability during the next century. On the contrary, the Mediterranean specie Holm Oak is gaining suitability in the warming climate of Paris. The major increase in suitability is visible between 2000 and

2020 ECONM maps. Difference maps between year 2000-2050 and 2000-2080 also predict an increased suitability but in different areas.

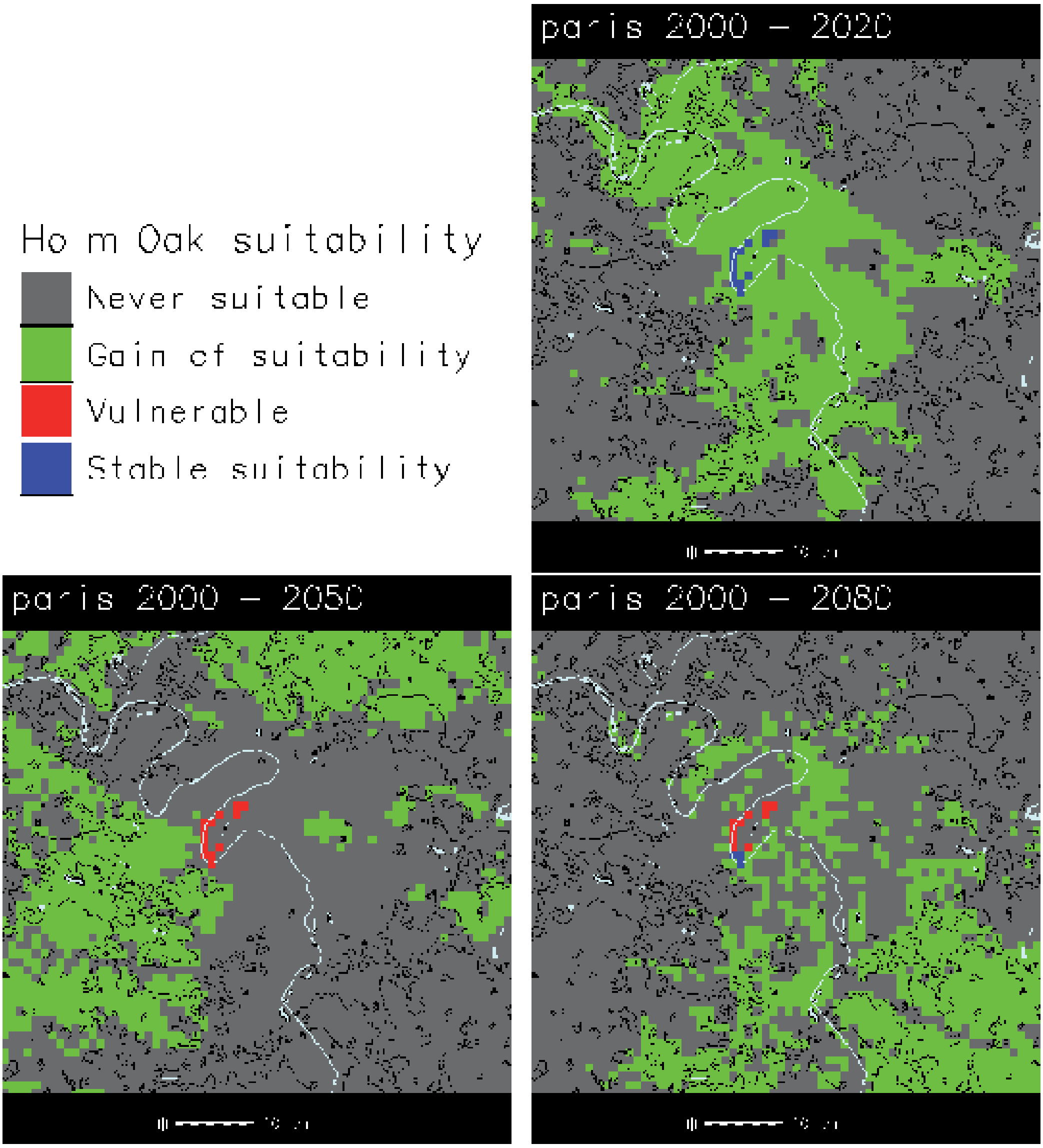

Fig. 6. Urban and peri-urban tree cover distribution in European Capitals

4. Discussion

Global change studies and analysis of climate change impact need transparency of data processing routines and their methodology. This study proposes a spatial ecological analysis of UPUG zones using open source codes and open access data. The main objective is the reproducibility and repeatability to target and improve the understanding of high uncertainties of studies on future projections and predictive model. This is important for

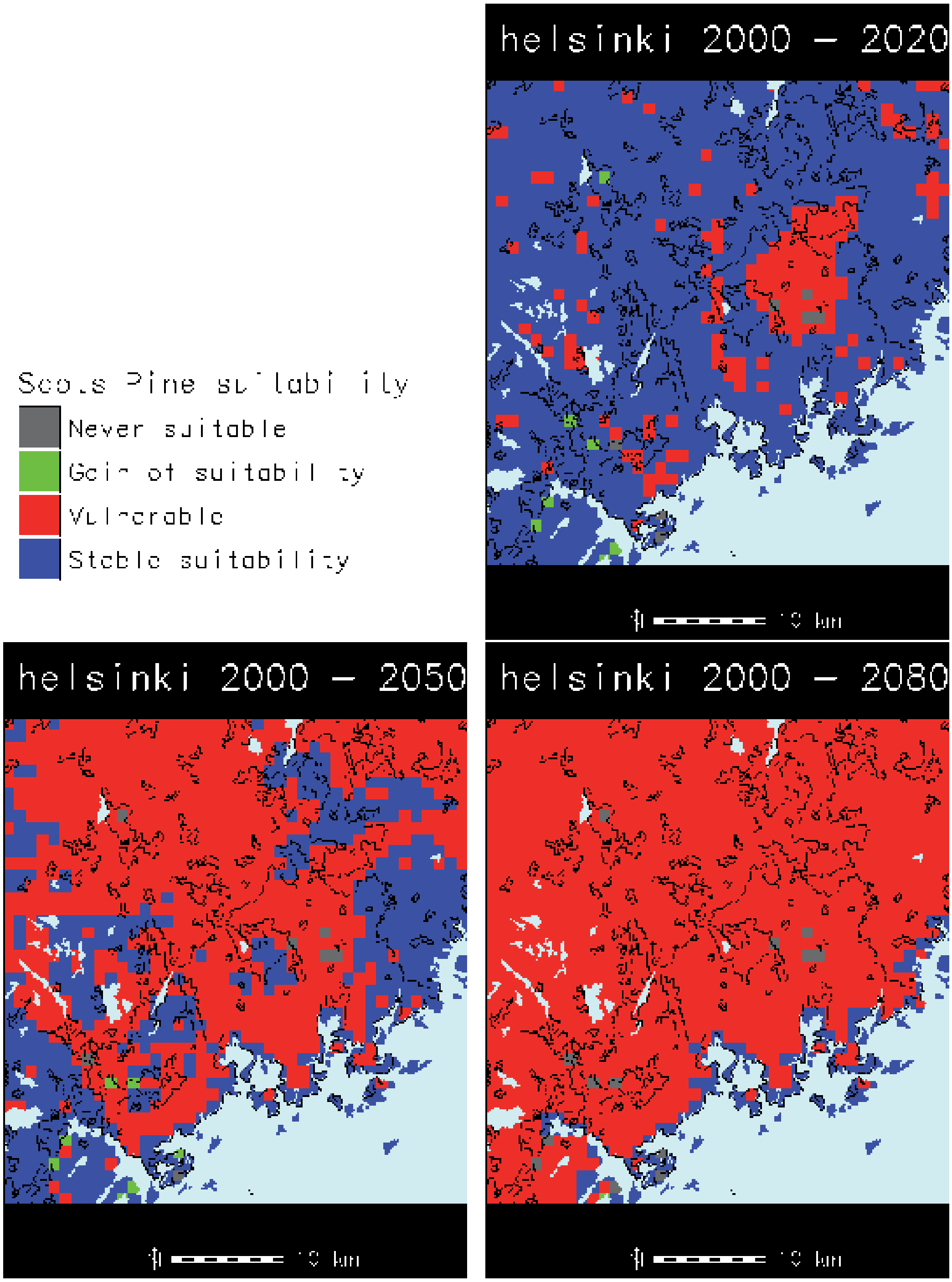

Fig. 7. Urban and peri-urban tree cover distribution in European Capitals

improving our knowledge on the impact of climate change and the capacity to react and eventually mitigate the consequences.

Regional data may be more accurate and of higher resolution compared to the data applied in this project. However, the local data is facing the problem that level of accuracy and detail is varying for different regions. Local data are frequently not freely available and divers sources of information are used to produce them standing upon different definitions. In this study the UPUG maps are based on the same tree cover definition allowing inter and intra-city comparison. Therefore, local data are not appropriate in applications like the one which is proposed here targeting international comparison for policy and reporting purposes.

Besides the subject matter of data accuracy, harmonization and accessibility the major proposal of the present data analysis study is to share the underlying scripting routines. We believe open source codes should be compulsory in spatial ecological science and in climate change applications. The scripting routines produced for this application are available to be used, improved and reused. Whichever future climate data or improved vegetation map will be available in future, the script can be changed and adapted for reproducing the analysis. Tables and figures are directly produced by the coding routines, changing parameters such as the number of cities or the extent of the bounding box area will directly modify graphs and reproduce maps and tables. Another benefit of the scripting routine is the potential to use them in virtual machines for cloud computing or in stand alone computation for cluster processing when computational time is a limiting factor in research.

One drawback of this application is the "black box" represented by the ECONM and their input data used for modelling and mapping species suitability, due to the fact that the *forest Focus* database is not open access yet. In order to open the "black box" for more transparency and shared knowledge, we strongly recommend to rebuilt a set of ecological niche models for tree species using as inputs open access database such as the Global Biodiversity Information Facility [4].

This study demonstrates two examples of future trends projections: the increased vulnerability of Scots pine in Helsinki and the increased suitability area of the Mediterranean oak in Paris. In many cases the trends of changes are not so pronounced as in the described example. More details such as probability maps instead of or in addition to the binary suitability maps would help to interpret the results and to understand model limits. As an example we could be able to clarify the discrepancy of future projections found for the Holm oak in Paris. Instead of the different trends of suitability changes in time according to sub-areas of Paris (figure 6), probability map could eventually highlight a common trend of suitability increase with different probability of increase according to city sub-areas.

5. Conclusion

Due to the negative future prospects for the urban environment caused by global warming, there is a need to monitor and manage pro-actively urban greening and peri-urban forests. They have strong potential in mitigating the impact of climate change. Vegetation is necessary for urban environmental sustainability, human health and well-being.

When investigating complex systems such as the urban ecosystem, predictive modeling and spatial ecological analysis like the one presented in this chapter are some elements of many that are required to simulate the dynamics of urban ecosystems in space and time. This knowledge is prior and can be used for promoting urban sustainability and managing urban greening.

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[4] http://www.gbif.org

The exponential increase in data availability concerning urban areas, urban greening, climate and human health has to be followed by an improved ability to make full usage of those data. We believe this can be done by increasing the transparency of scientific applications and by the use of open access data and open source codes as proposed in this application. This will exponentially improve quality and accuracy of scientific applications allowing a better transfer from knowledge to policy and implementation.

6. Acknowledgments

I warmly thank the whole MPBA unit at Bruno Kessler foundation and in particular Cesare Furlanello, Riccardo De Filippi, Claudia Dolci, Shamar Droghetti, Gabriele Franc and Giuseppe Jurman. I am also very gratefull to the forest action at JRC, to Victoria O'Brien, Anssi Pekkarinen at FAO and Giuseppe Amatulli at *www.spatial-ecology.net*. This study was carried out in the frame of the project ENVIROCHANGE, funded by the Autonomous Province of Trento.

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Part 4

Global Warming and Agriculture: Impacts on Crop Production

7

The Influence of Climate Change on Rice in China from 1961 to 2009

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1. Introduction

At present, 40% of the Earth's land surface is managed for cropland and pasture (Foley et al., 2005). In developing countries, nearly 70% of people live in rural areas where agriculture is the largest supporter of livelihoods. For China, as such large developing country, the total population accounted to 13 billion with 73% of them pursuing agriculture, and the cropland was 1.3 billion ha in 2006 (CAY, 2007). About 20% of the global population lives in China supported only by 7% of the world's cultivated land. Although Chinese agriculture has undergone tremendous structural changes over the last decades, the average staple crop productivity has doubled in 25 years while the population increased by 25 % (CSY, 2003), until now, agriculture is still the most important industry for China which can affect food supplies of 13 billion populations.

Rice is one of China's most important staple food crops, and it's planting area amounted to 27.4% of all food crop area, and it's production was 37.1% of total food production in China (CAY, 2007). Meanwhile, the production of rice was influenced strongly by climate (Olesen, 2002), so it's confirmed that the agriculture will be affected greatly by climate change.

2. Indexes

2.1 Rice planting regions

The triple-cropping rice can be planted in southern China when the accumulated temperature amounted to 7000 ºC (daily temperature >10 ºC), while when the accumulated temperature changed during 5300 – 7000 ºC accumulated temperature amounted to, the double-cropping rice can growth (Cheng and Li, 2007).

2.2 The growing season length

Cheng and Li (2007) gave the indexes of the growing length of rice in southern China, the start of growing length was defied by the daily temperature more than 10 ºC stably, and the end of growing season was defied by the daily temperature more than 20 ºC.

2.3 High temperature

The production of rice was influenced strongly when the daily temperature was more than 35 ºC in southern China, so 35 ºC was defied as high temperature.

3. Results

3.1 Air temperature and precipitation variation in China, 1961-2009

The high quality data collected by 511 weather stations (selected from 748 CMA baseline or basic stations in line with the criteria of continuity and integrity) were employed to analyze and understand the temperature and precipitation variation trends in China during the period of 1961-2009. Anomalies were calculated based on the benchmark values of meteorological elements. Meanwhile, temperature and precipitation anomalies were calculated in grids (5 ° × 5 °, longitude × latitude). The averaged nationwide series were obtained through an area-weighted process. The benchmark values of meteorological elements were derived from the averages of 1971-2000.

3.1.1 Temperature variation trends, 1961-2009

Fig. 1 depicts the averaged temperature anomalies in China during the period of 1961-2009. It is apparent that in a period of 49 years, China has witnessed an ascending mean temperature trend across the country, or 1.5°C up for the period of 1961-2009. The mean temperature in most years has registered a positive anomaly since the 1990s, with 2007 being the warmest.

Most parts of China enjoyed an ascending trend of air temperature, as shown by the spatial distribution of air temperature variation in Fig. 2, with the northern part sitting in a noticeably warming range between 0.3-0.6 °C/10a. The northeast part of the northeast region, the central part of Inner Mongolia, and the east part of Xinjiang also saw a temperature rise up to 0.6-0.9 °C/10a. Most part of the Yellow River in the south came up with a universal small rise of temperature, basically under 0.3 °C/10a.

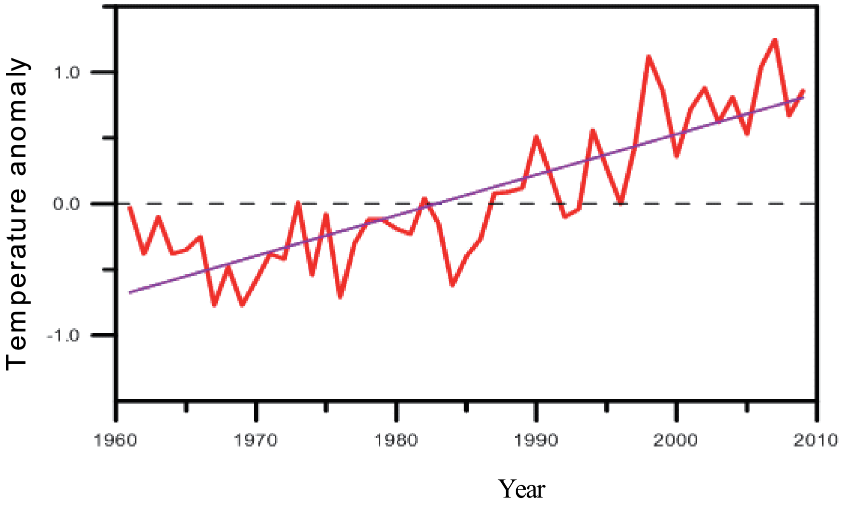


Fig. 1. Averaged temperature anomalies, 1961-2009 (°C).

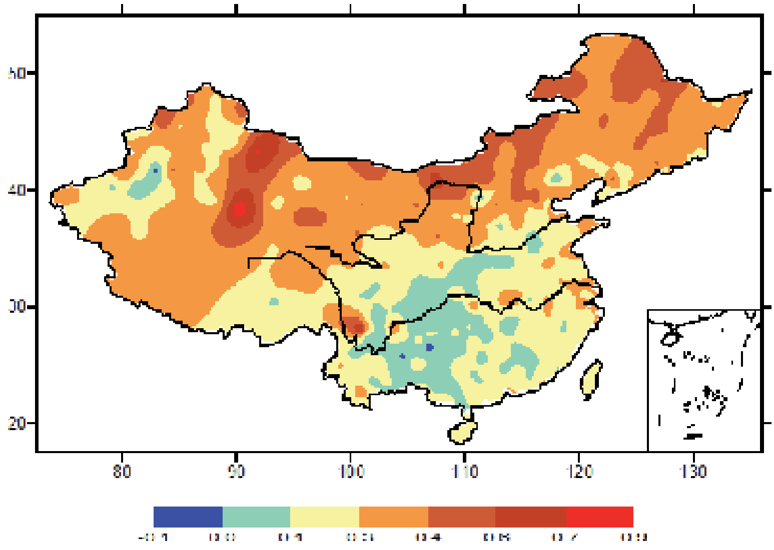


Fig. 2. Spatial distribution of temperature variation across the country, 1961-2009 (°C/10a).

3.1.2 Precipitation variation, 1961-2009

China had not registered a noticeable trendy variation of averaged precipitation during the period of 1961-2009, with a slight increase of 12.86mm (Fig. 3), though the curve went down in the latest 10 years. Fig. 4 shows the spatial distribution of precipitation trends across the country, suggesting a decline in most parts of East China, noticeably in most parts of North China, the Pan-Bohai Sea region, and the central and east part of the southwest region. During the same period of time, the lower and middle streams of the Yangtze River, the southeast coastal areas, and Hainan saw increased rainfall. On the other hand, most parts of China west of 105 °E tended to have an increased precipitation, noticeably in the southeast part of Tibet.

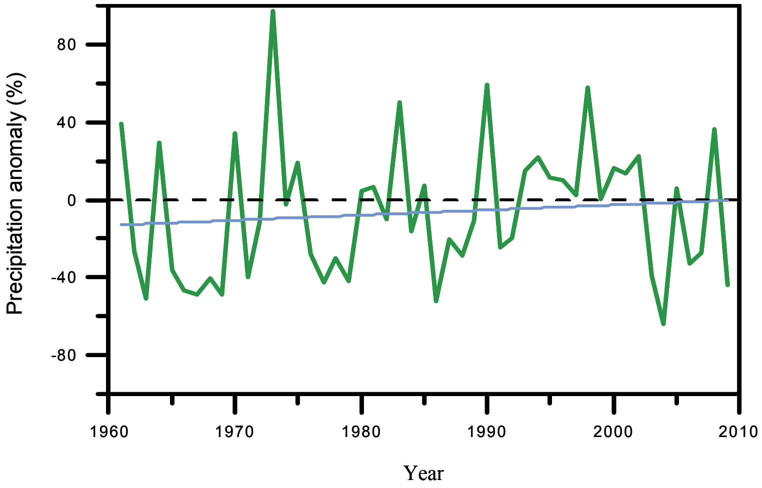


Fig. 3. Averaged precipitation anomalies, 1961-2009 (mm).

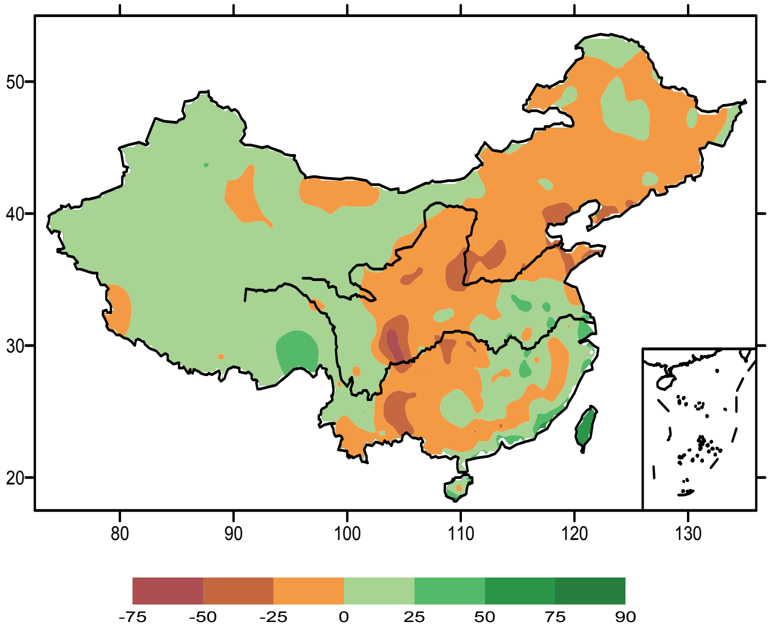


Fig. 4. Spatial distribution of precipitation variation, 1961-2009 (mm/10a).

3.2. Climate change impact on the northward shift of double rice cropping in South China

3.2.1 Active accumulated temperature variation across the southern rice growing areas

Paddy rice is a short-day plant which needs the warm and wet environment. Rice growing activities have to be defined in line with a range of ecological and environmental elements, including heat, growing season, water, sunshine, elevation, soil, production condition, and cropping system (Cheng, 2007). Heat resource makes a pivotal element in defining the distribution of rice growing areas. Theoretically, the heat resource defined for paddy rice is technically expressed in an active accumulated temperature≥10°C. Active accumulated temperature is the sum total of the temperatures that are above the lowest biological temperature a plant has had during the entire growth season in a year, or the sum total of the averaged daily temperatures that are above a given threshold value. In southern China, triple cropping rice can be planted when the active accumulated temperature was more than 7000°C, and double cropping rice can grow when the active accumulated temperature was more than 5300°C (Cheng, 2007).

Previous studies show that most parts of China have registered an increased heat resource against the background of global warming, which extends crops' growing season and allows thermophilic crops to move further north, changing the pattern of cropping systems. During the period of 1961-2009, the southern rice growing areas witnessed a noticeably increased active accumulated temperature (≥ 10 °C), with an averaged active accumulated temperature at 5712.8 °C in the 60's, and 5686.3 °C and 5677.0 °C in the 70's and 80's, respectively. The same indicator rose to 5809.8 °C in the 1990's, or 97.0 °C up compared with the 60's. During the period of 2001-2009, the averaged active accumulated temperature hit 5980.8°C, or 268.0 °C higher compared with the 60's, or 303.8 °C up against the 80's. During the 19 years running from 1991 to 2009, 16 years reported an active accumulated temperature that was higher than it from 1971 to2000, with 1998 being the warmest at 6144.9 °C, or 420.6 °C higher than what would have been in a normal year. The same indicator appeared at 6011.1 °C in 2009, or 286.8 °C higher compared with a normal year (Fig. 5).

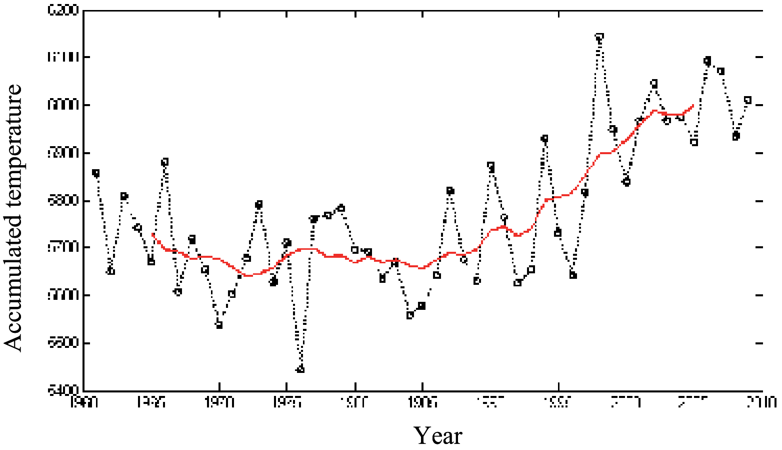


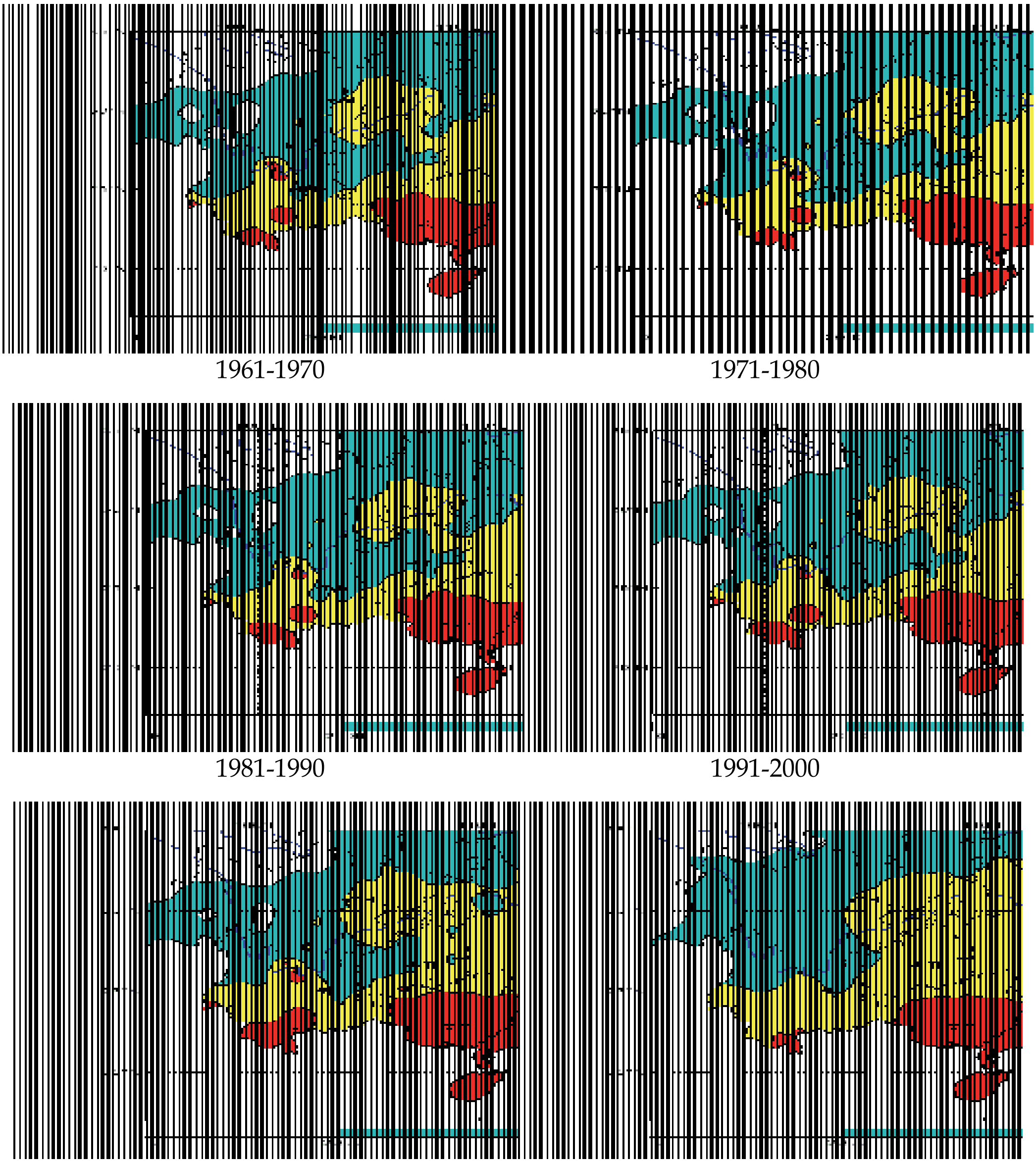
Fig. 5. Active accumulated temperature variation in the southern rice growing areas, 1961-2009 (°C).

Rice is a staple food crop in China. In 2000, the rice sown area reached 29.962 million hectares, accounting for 27.6% of the grain sown area in the country, with a yield of 187.91 million tons, or 40.7% of the total food crop yield in the country (CSY, 2001). Heat resource defines the distribution and cropping of rice growing. For example, an area having an accumulated temperature at 2000-5300°C (≥ 10 °C) is desirable for the one-cropping system, while the one at 5300-7000°C may enjoy a double cropping practice. An area with an accumulated temperature at 7000°C or above is allowed to grow three cropping.

During the period of the 1960's-1980's, China saw limited variations in heat distribution. The areas having an annual active accumulated temperature (≥ 10 °C) at 7000°C or above sat mostly in the central and southern part of South China, practicing a three cropping system. The areas with an annual active accumulated temperature (≥ 10 °C) between 5300°C and 7000°C have included most parts of Hunan, Jiangxi, the central and southern part of Zhejiang, most parts of Fujian, the southeast part of Hubei, some parts of Sichuan and Chongqing, and the southern part of Yunnan (Figs. 6).

During the period from the 1990s to 2009, the safe threshold for double cropping (5300°C) and triple cropping (7000°C) moved further north. For example, the northern boundary of double cropping moved up for more than 2 degrees, or some 300 km (Figs. 6). As a result, a range of areas, including the east part of Sichuan, most parts of Chongqing, the east part of Guizhou, most parts of Hubei, most parts of Anhui, and the southern part of Jiangsu, became desirable for double cropping.

China National Climate Center predicts that China will see a further warming climate during the period of 2011-2020 (Ding et al., 2007). Most parts of the country will have a sustained rise of active accumulated temperature. The trend may further increase the heat resource for the newly added double cropping areas. As a result, the northern boundary of double cropping may move further north (Fig.6). These areas apparently need to readjust the cropping system in a scientific manner, in line with the local conditions, adapting to the changed climate resource and environment, and enhancing the utilization of climate resources.



1961-1970 1971-1980

1981-1990 1991-2000

2001-2009 2011-2020

(the data during 1961-2009 from observed meteorological stations, and the data during 2011-2020 projected by RegCM3)

Fig. 6. Distribution of active accumulated temperature (≥ 10 °C) in the southern rice growing areas. Note: the red color represents the areas desirable for triple cropping, and the yellow one for double cropping.

3.2.2 Changed duration of the growing season

The growing season duration is also an element that defines the distribution of rice growing areas. For example, early rice is sown in the late February in the southern part of China, with late rice being harvested in the early November. The sowing could be later, starting from the mid-March in the south of the Yangtze River, with late rice becoming ripened in the mid-October. In southern China, triple cropping rice can be planted when the growing season length was longer than 270 days, and double cropping rice can grow when the growing season length was longer than 200 days (Cheng, 2007).

During the period of 1961-2009, the duration of rice growing season (the days with an averaged temperature passing the threshold of ≥ 10 °C in the beginning of the growing season and ≥ 20 °C at the end of it) in the southern part of the country was noticeably prolonged (Fig. 7). For example, the duration of rice growing season lasted for 214.9 days in the 60's, with 221.9 days and 211.7 days in the 1970's and 1980's, respectively. In the 90's, an averaged rice growing season would last for 220.3 days, a bit longer compared with the 60's and 80's, though slightly shorter against the 70's. During the period of 2000-2009, the rice growing season rose to 231.4 days in the southern rice growing areas, or 16.5 days longer compared with the 60's, or 19.7 days longer against the 80's. Apparently, the duration of rice growing season has become noticeably longer in the southern part of China since the 21st century.

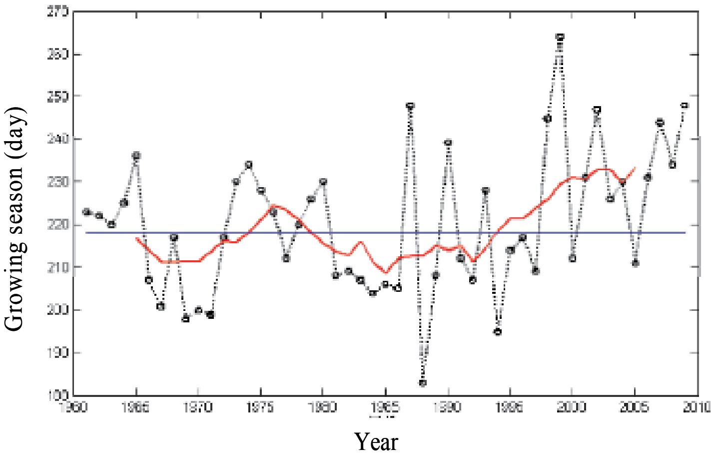
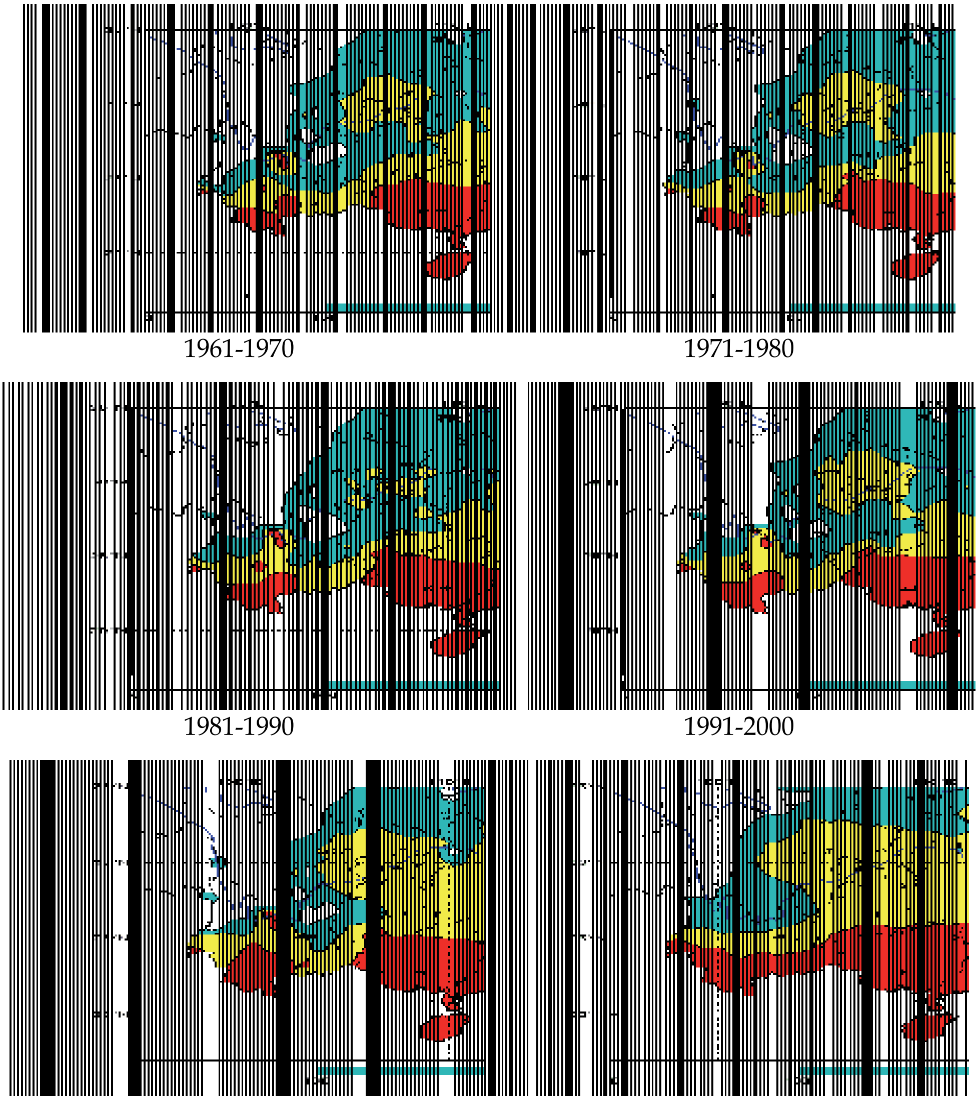


Fig. 7. Changed duration of rice growing season in the southern rice growing areas, 1961-2009 (day).

In China, the safe rice growing season would last for some 270 days under a triple cropping system, or some 200 days for a double cropping system. In other words, the 270-day growing season is desirable for triple cropping, and the 200-day for double cropping.

Figs. 8 show that as far as the safe rice growing season is concerned, climate warming has imposed no significant impacts on the scope of the areas desirable for triple cropping. However, climate warming have noticeably pushed the northern boundary of double cropping further north. Such northward shift has become increasingly noticeable since the 21st century. In the period from the 60s to the 90s, the double cropping system was mainly practiced in the south of the Yangtze River Valley. However, the northern boundary of double cropping has gone further to the north of the Yangtze River since the 21st century, including the northeast part of Sichuan, the east part of Guizhou, Chongqing, most parts of Hubei, the central and southern part of Anhui, and the southern part of Jiangsu. Apparently, the northern boundary of double cropping has gone further north, compared with the 90's.

According to the analysis and prediction made by China National Climate Center, the period of 2011-2020 will see a further intensified climate warming trend in China, with a prolonged rice growing season in the southern part of the country, and a further northward shift of the double cropping boundary. The conclusion agrees with the northward shift of the double cropping boundary depicted by the results of active accumulated temperature calculation.


1961-1970 1971-1980

1981-1990 1991-2000

2001-2009 2011-2020

(the data during 1961-2009 from observed meteorological stations, and the data during 2011-2020 projected by RegCM3)

Fig. 8. Changed duration of rice growing season in the southern rice growing areas (day). Note: the red color represents the areas desirable for triple cropping, and the yellow one for double cropping.

3.2.3 Annual precipitation variation

Precipitation is also in a position to affect the distribution of rice growing areas. In China, both double and triple cropping need an annual rainfall no less than 1,000 mm. Fig. 19 shows that climate warming has produced limited impacts on the rainfall in the southern part of China. In the 60's, the southern part of the country where paddy rice was grown registered an averaged annual precipitation of 1379mm. The 1970's, 1980's, and 1990's recorded a sustained increase of precipitation at 1412 mm, 1435mm, and 1491 mm respectively (Fig. 9) . China, however, has seen a slightly decreased precipitation to 1431 mm starting from the 21st century.

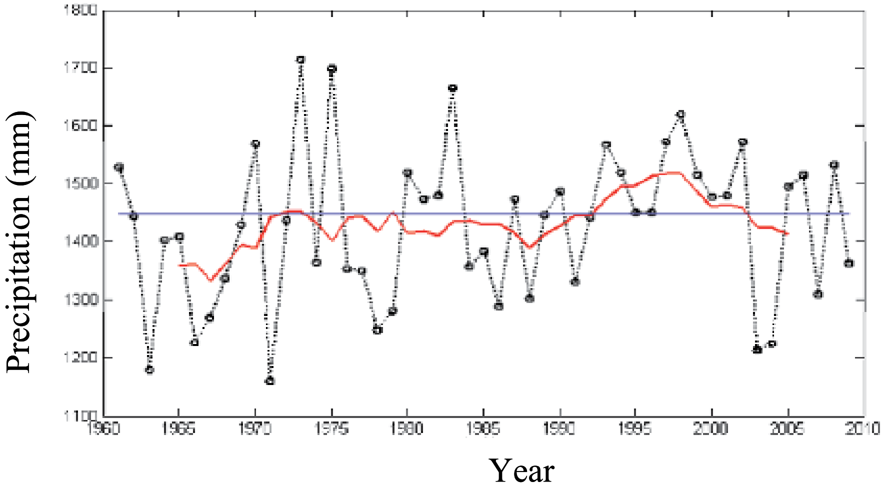
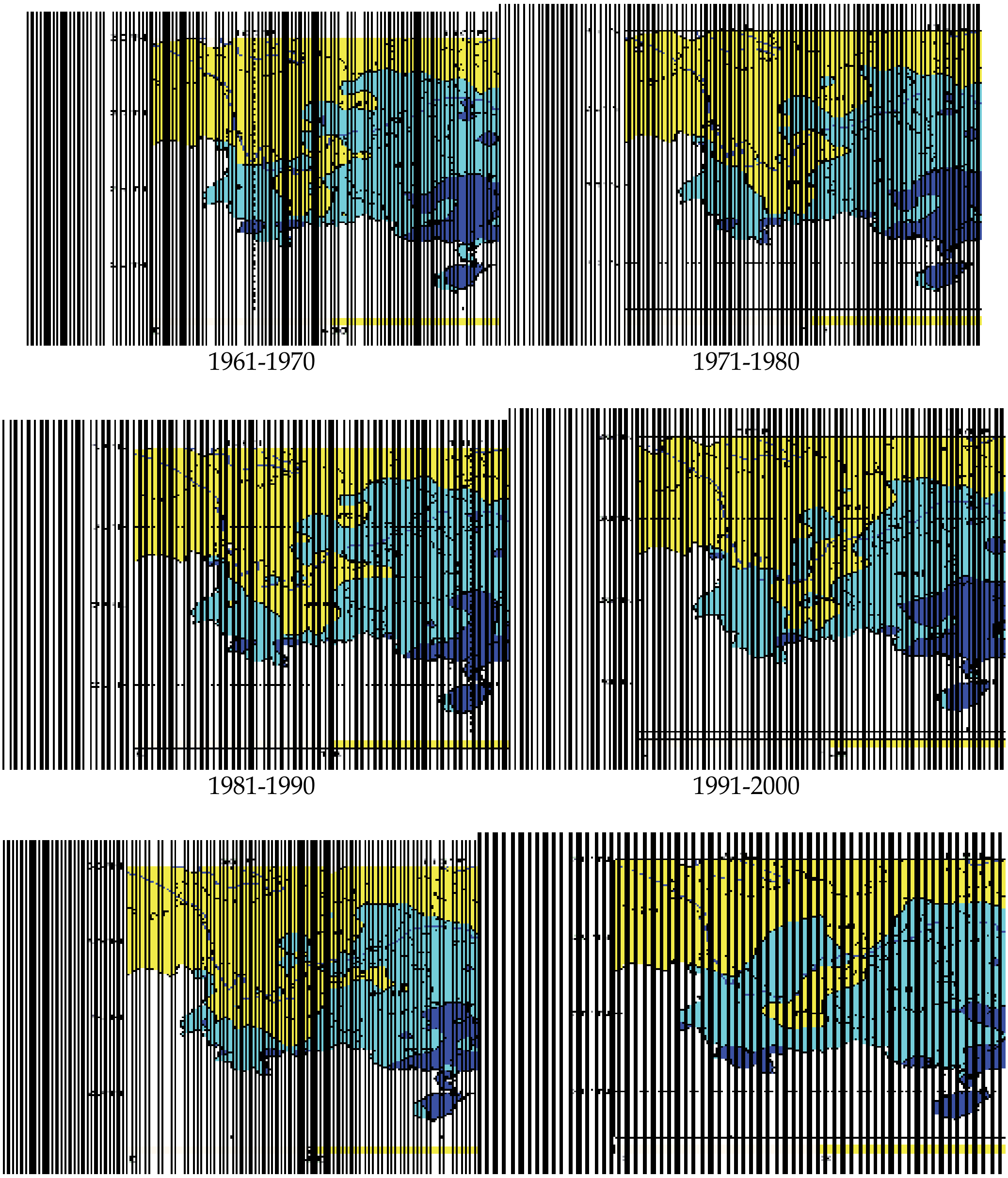


Fig. 9. Annual precipitation variation in the southern rice growing areas, 1961-2009 (mm).

In addition, most parts of Hainan Province, the east part of Guangxi, Guangdong, Fujian, and Jiangxi reported an annual precipitation of 1,500 mm or above in the 60's, with the rest of rice growing areas in the south sitting between 1,000mm and 1,500 mm (Fig. 10). In the 70's, the areas enjoying an annual precipitation of 1,500 mm or above did not see much change in number, though the areas sitting between 1,000mm and 1,500 mm in both Sichuan and Jiangsu reported a slight drop in number. In the 80's, the areas having an annual precipitation of 1,500 mm or above in Guangxi saw a slight drop in number, with little change of the areas sitting between ,1000mm and 1,500 mm. In the 90's, the areas having an annual precipitation of 1,500 mm or above in Guangxi reported some increase in number, though the areas sitting between 1,000mm and 1,500 mm in Sichuan suffered a noticeable drop in number. Zhejiang, Anhui, and Jiangxi have reported a noticeably declined number of the areas having an annual precipitation of 1,500 mm or above since the 21st century, with a slight drop of the areas sitting between 1,000mm and 1,500 mm in both Sichuan and Yunnan.

Overall speaking, the southern paddy rice growing areas in China didn't see much change in precipitation during the period of 1961-2009, though a number of provinces, including Jiangsu, Hubei, and Sichuan, had reported a declined number of the areas sitting between 1,000mm and 1,500 mm since the 21st century, which deserves further attention.

China National Climate Center predicts that the southern part of China will not see a large variation in precipitation during the period of 2011-2020 (Ding et al., 2007). As a result, precipitation will produce no significant impacts on the southern rice growing areas in the coming decade if the precipitation change slightly.



1961-1970

1971-1980

1981-1990

1991-2000

2001-2009

2011-2020

(the data during 1961-2009 from observed meteorological stations, and the data during 2011-2020 projected by RegCM3)

Fig. 10. Distribution of annual precipitation in the southern rice growing areas (mm).

3.2.4 High temperature day trends in the southern rice growing areas

The Jiangnan region

In the most part of the Jiangnan of China, rice would enter the heading, flowering, and filling stages in June and July. In the Jiangnan, the first cropping rice enters the heading and flowering stage in August. This period of time is featured with the positive dominance of subtropical highs, claiming more high temperature days. The abnormal frequency of hot days would result in a shortened period for heading, flowering, and filling, reducing the leaf assimilation on the one hand, and causing the surge of blighted rice and a reduced yield and quality on the other (Zhang and Wang, 1998).

In June, hot weather (≥ 35 °C) starts to affect the lower and middle reaches of the Yangtze River. In the early June, this part of the Jiangnan would have 0.3 hot days in a normal year, with 0.5 hot days for the period of 2001-2009. In the mid-June, 0.4 hot days would appear in a normal year, with 0.8 days in the period of 2001-2009. In the late June, 0.6 hot days is a common place, with 1.7 days for the period of 2001-2009. It is noteworthy that the lower and middle reaches of the Jiangnan has witnessed a noticeably raised number of hot days at 2.1 days during the period of 2005-2009 since 2005 (Table 1).

July is a month featured with a noticeably raised number of hot days in the lower and middle reaches of the Yangtze River. In the early July, hot days would reach 1.9 in number in a normal year, with 2.6 days for the years since 2000. The mid-July would produce 2.7 hot days, though 3.5 days since 2000. In the late July, high temperature days would go up to 3.2 days on an average, with 4.5 days for the period of 2000-2009. Technically, the late July claims the most hot days in the lower and middle reaches of the Jiangnan with a noticeably raised number of hot days in the past 20 years (Table 1).

August starts to see a declined number of hot days in the Jiangnan. In the early August, high temperature days reach 2.9 on an average, though with a slightly descending trend in the past 10 or 20 years. The mid-August would have 1.5 hot days, expecting no ascending trend. In the late August, high temperature days are averaged at 1.2 days. Technically, the early August would have a slightly increased number of high temperature days, and the mid-August a steadily decreased number of hot days since that time on.

Overall, the Jiangnan would have 14.7 hot days for the summer (June-August). The number of high temperature days has witnessed a noticeable rise, especially in the late June and late July, since 2000.

South China

The South China starts to have hot days (≥ 35 °C) in June. In the early June, this part of the country would have 0.5 hot days on an average (Table 1), with 0.6 days for the mid-June, and 0.8 days for the late part of the month. This part of the country has registered a noticeably increased number of hot days in the late June since 2000.

July is featured with a noticeably raised number of hot days, with 1.5 hot days for the early July (Table 1). The mid-July would have 1.9 hot days on an average, though 2-5 days for the years since 2000. The late July has registered a pattern similar to the mid-July, with 2.2 hot days on an average, and a noticeably increased number of hot days to 2-5 days since 2000.

In August, the lower and middle reaches of the Yangtze River start to see fewer hot days. The early August is averaged with 1.7 hot days, witnessed a noticeably increased number of hot days in a 10-year period. The mid-August would have 1.4 hot days, and the late August 1.2 hot days. Overall speaking, the early August has slightly more high temperature days, with an ascending trend in the past decade. The number of hot days steadily declines starting from the mid-August (Table 1).

		1961-1970	1971-1980	1981-1990	1991-2000	2001-2009
Jiangnan	Jun 1-10	0.3	0.2	0.4	0.3	0.3
	Jun 11-20	0.5	0.6	0.4	0.3	0.8
	Jun 21-30	0.8	0.7	0.6	0.7	1.7
	July 1-10	1.4	2.5	1.8	1.4	2.8
	July 11-20	3.6	2.1	3.3	2.8	3.4
	July 21-31	4.3	3.1	2.5	3.8	4.5
	Aug 1-10	3.1	3.3	2.6	2.8	2.9
	Aug 11-20	2.6	1.4	1.8	1.4	1.8
	Aug 21-31	2.7	1.4	1.0	1.1	2.1
South China	Jun 1-10	0.3	0.2	0.3	0.9	0.4
	Jun 11-20	0.4	0.7	0.6	0.5	0.5
	Jun 21-30	0.8	0.7	1.0	0.7	1.5
	July 1-10	1.1	1.7	1.5	1.2	2.1
	July 11-20	1.8	1.9	2.2	1.6	3.0
	July 21-31	2.5	1.9	2.1	2.4	3.1
	Aug 1-10	1.4	1.2	2.1	1.9	2.7
	Aug 11-20	1.4	0.9	1.9	1.4	1.8
	Aug 21-31	1.7	0.8	1.2	1.5	1.8

Table 1. The high temperature days(≥35 °C)for every 10days over Jiangnan and South China regions during 1961-2009.

In summary, the South China has, on an average, 11.8 hot days in the summer, though with a noticeably raised number of hot days since 2000, especially from the late June to the early August. In the past decade, the southern rice growing areas have witnessed a noticeably increased number of hot days in the summer, which may cause heat injury to the rice plants in their filling stage, compromising both the yield and quality of rice. In this context, one has to breed heat resistant rice varieties and develop technical measures to ease the damages caused by high temperature.

4. Conclusion

Rice is one of China's most important staple food crops, and the climate change have already influenced the growth of rice in China. All the above studies showed that the climate change were influenced the rice planting in southern China. For recent two decades, as the active accumulated temperature increases in the southern China, the rice growth period extended, with the double-cropping rice growing boundaries being apparently pushed northward, even showing a slight northward shit of triple-cropping rice boundaries. From 1960s to 1980s, the double-cropping rice only grew in the areas to the south of the Yangtze River. However, for the recent 10 years, its growth areas had shifted to those to the north of the Yangtze, with their northern boundaries having been pushed approximately 300 km to the north, extending to northeastern part of the Sichuan, eastern Guizhou, Chongqing, most Hubei, central and southern Anhui, as well as southern Jiangsu (Fig.11). Although climate warming increased the thermal resources for rice growth areas over the region, creating favorable conditions for making use the thermal resources, and for increasing the multi-cropping index, farmers may face challenges as how to better address the issues related to availability of additional farming machinery required for the enlarged double-cropping rice production. On the other side, as climate will continue to warm, the early rice may be negtively affected by high temperature (≥35 °C) on filling stage of rice, and therefore it is imperative to develop and use heat-resistant rice varieties to mitigate the high temperature-induced crop damages.

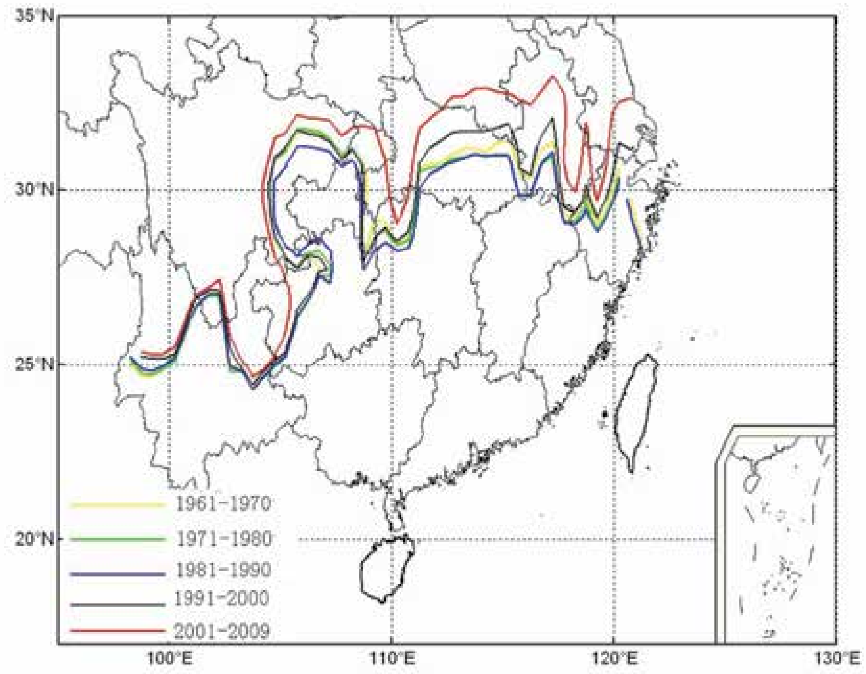


Fig. 11. The influence of climate change on growing northern boundaries of double-cropping rice in China from 1961 to 2009.

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8

Climate Change Adaptation using Agroforestry Practices: A Case Study from Costa Rica

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1. Introduction

Conventional agricultural practices in tropical latitudes, using modern plant breeding techniques, fertilizers, and irrigation, have resulted in an increased grain yield (Huxley, 1999). However, these agricultural practices have also played a major role in increasing the global total area of marginal land that is now substandard for the long-term production of food and livestock (FAO, 1990), and has contributed significantly to the accumulation of greenhouse gases in the atmosphere (IPCC, 2007). Such activities are most notable in developing countries which are strongly affected by climate change due to their lower capacity to adapt compared to developed nations (IPPC, 2007). Comparatively, developed nations have the infrastructure and financial capabilities to cope more effectively to a changing climate.

As a result of the inherent environmental degradation and poverty associated with deforestation and conventional agriculture, there is a resurgence in the implementation of sustainable land-use practices including agroforestry (Kandji et al., 2006). In this paper agroforestry is defined as the deliberate integration of woody species with agricultural crops and/or pastures on the same land-unit resulting in the integration of economical and ecological interactions between components (Young, 2002). The cultivation of trees in combination with agricultural crops was a common practice dating back to the beginning of plant and animal domestication. Since then, several models of various agroforesry practices, from Asia, Africa and Europe to North and South America, have been developed (King, 1987). In tropical latitudes, farmers imitated vertical forest structure and diversity by planting a variety of crops with different growth habits. It was not unusual to plant up to 24 species on a plot one-tenth of a hectare with each layer corresponding to the natural stratification of a tropical forest (King, 1987). Until the 1860s, the focus of agroforestry practices was on tree production. It was not until 1975, when the International Development Research Centre (IDRC) in Canada concluded that priority in research should be given to combined agroforestry production systems in tropical regions in order to optimize land-use, establish food security, and address the increasing problem of environmental degradation (King, 1987). Since then, agroforestry practices were promoted as a sustainable land-use management system in developed and developing countries. For example, agroforestry practices range from low-input systems such as alley cropping and short-term improved fallow with leguminous shrubs to shade-grown coffee (*Coffea arabica* L.) in tropical regions and high-input cereal-legume systems and riparian plantings in temperate biomes (Nair, 1993; Gordon & Newman, 1997).

In Central America, agroforestry practices were also diverse and commonly included a combination of trees with food crops, trees with livestock (pasture for fodder) or all elements combined (Budowski, 1987). In this region, pre-Columbian people mixed trees with food crops in a system similar to shifting cultivation. Other land-use techniques included home gardens and the integration of trees and crops along banks. Agroforestry practices in Central America were first described by O.F. Cook in a 1901 report to the U.S. Department of Agriculture, noting that coffee plants were growing under shade trees. Cook also noted the beneficial effects of leguminous shade trees on soil fertility. Since then there has been a plethora of information published on Central American, particularly Costa Rican agroforestry practices. For example, Holdridge reported on the practice of planting *Alnus acuminate* Kunth. in pastures in the Costa Rican highlands (Holdridge, et al. 1977). Budowski (1987) noted the use of *Cupressus lusitanica* L. windbreaks in the highlands and the use of *Cordial alliodora* L. in lowland pastures in Costa Rica. Other research from Costa Rica reported secondary forest management on abandoned coffee plantations (Budowski, 1987), and use of life-fences and increased biodiversity (Harvey et al., 2005). Alley cropping was established in Costa Rica as a new agroforestry practice in the early 1980s, where crops were grown between rows of trees (Kass et al. 1995). The aim of this modern agroforestry practice was to minimize the need for external nutrient inputs from fertilizers or manure, which are difficult or not economically feasible for small producers. Instead this agroforestry practice relied on the biannual input of organic material derived from leguminous plants, high in nutrient content, of completely shoot pruned of trees. The application of the organic material to the soil as mulch was synchronized with the seeding of crops, resulting in the maximum release of nutrients from the decomposing organic material to the growing crops. Over the past decade the potential of agroforestry systems to sequester carbon (Oelbermann et al., 2004; Oelbermann & Voroney, 2011), and their role in providing ecosystem services (Pagiola et al., 2008) has become the forefront of research as a result of global climate change.

Agroforestry systems are unique because they are a land management practice that simultaneously addresses biophysical, economical, and socio-ecological components. Such diversity and interactions leads to a greater functional and structural complexity compared to conventional agroeosystems (Nair, 1993). Leaky & Simmons (1996) suggested that over the long-term agroforestry systems become successively similar to natural systems, where biodiversity increases with each stage in the development of this succession. Such functional and structural complexity has led to the great diversity currently observed in modern agroforestry practices.

However, the adoption of agroforestry practices is based on socio-cultural and sociecological considerations including land tenure and land rights, in addition to providing enhanced biodiversity and ecological services (McGinty et al. 2008; Sood & Mitchell 2009). Currently, agroforestry practices are increasingly adopted due to their potential of providing ecosystem services. Ecosystem services not only provide an economic incentive but are also of value to society by maintaining environmental sustainability (FAO, 2007). The benefits derived from agroforestry practices occur over a range of spatial and temporal scales (Jose, 2009). For example, when comparing the large-scale removal of trees due to deforestation and its resultant high levels of erosion, agroforestry systems provide ecological services by decreasing soil erosion and preventing the sedimentation of waterways; ultimately protecting downstream fisheries (Pearce & Mourato 2004). Thus, ecological services provided by agroforestry systems are derived at the farm- and / or landscape-scale but are enjoyed by society at regional- and / or global-scales (Jose, 2009).

Verchot et al. (2007) suggested that agroforestry practices, apart from providing ecosystem services, are a means of diversifying agricultural production and increase food security for smallholder agricultural producers, especially under current climate change scenarios. For example, recent observations on inter-annual changes in temperature and precipitation along Costa Rica's Pacific coast have shown more intense and longer dry seasons, coinciding with changes predicted by the IPCC in this region (IPCC, 2007). Although maintaining agricultural productivity under changing climatic conditions will be challenging (Watson et al., 2000), Sanchez (2000) suggested that structurally and functionally complex agroecosystem management systems, including agroforestry practices, may show a greater resilience to changing environmental conditions. Although several studies have been published on the adoption of agroforestry practices (Pattanayak et al., 2003; Mercer, 2004), few studies have investigated the efficacy of agroforestry as an agroecosystem management practice with greater resilience to climate change compared to less diversified (conventional) agroecosystems. Verchot et al. (2007) noted that the contribution of agroforestry practices to buffer against climate shifts is currently not well understood. Such knowledge is of great importance because agroforestry is also considered as a key player in achieving the Millennium Development Goals as described in the United Nations annual report (Verchot et al., 2007). The goal of this research was to present a case study from Costa Rica that evaluated the knowledge and perception of agricultural producers on climate change. This study also evaluated the implementation of agroforestry practices as a strategy to climate change adaptation.

2. Study site

The research area and agricultural producers described in this paper corresponded to those currently under evaluation by the GEF-Silvopastoral Study (Pagiola et al., 2007; Yamamoto et al., 2007; Pagiola et al., 2008; Hänsela et al., 2009). The Silvopastoral Approaches for Ecosystem Management, or Global Environment Facility-Silvopastoral Study (GEF-Silvopastoral Study), is a pilot project that was initiated in 2002 in rural Nicaragua, Costa Rica and Colombia where degraded pastures were prevalent. Land owners participating in the project received payment for the ecological services they generated including the integration of trees on their land, improvement of pasture management, maintaining habitat for biodiversity conservation, enhancing soil and water conservation, and increasing carbon sequestration. In association with the Global Environment Facility, the World Bank, the Regional Integrated Silvopastoral Management Project (RISEMAP) and researchers from the Tropical Agricultural Research and Higher Education Center (CATIE) in Costa Rica, each participating agricultural producer was surveyed to determine baseline data and the type of already existing or new agroforestry practices, that ultimately provided ecological services, they were interested in implementing. Financial incentives were received over a four-year period, and were based on the type and increment of ecological services they implemented relative to the previously collected baseline data (Pagiola et al., 2008).

The GEF Silvopastoral study and our study was conducted surrounding the area of Esparza (09°59′N, 84°38′W), located in the Central Pacific Coastal region of Costa Rica. The study area surrounding Esparza encompassed 432 km^2, with land-use consisting predominantly of mixed-agricultural production under conventional practices with beef, dairy, rice, sugarcane, and fruit. The majority of agricultural producers in this area have a beef-dairy production (62%), followed by beef (20%), mixed crop-livestock (14%), and beef/dairy breeding stock production (8%).

The area surrounding Esparza was characterized as a sub-humid tropical forest zone. The average annual temperature was 27.9°C and the mean annual daytime temperature was 32°C and the mean annual nighttime temperature was 22°C (Figure 1). The average annual precipitation of this region was ~1599 mm, with a distinct dry season from December to April and a distinct wet season from May to November. The mean number of sunshine hours in this region was 10 h/day from November to April, and 6 h/day from May to October. This area had a relative humidity ranging from 65% during the dry season and 80% in the wet season. This region is also influenced by large-scale inter-annual fluctuations such as the El Niño or La Niña. The elevation above sea level ranges from 50 m near the Pacific coast to 1000 m in inland areas. The geology of this region was based upon volcanic origin and alluvial sedimentation. This led to the development of Nitisols, with a predominantly loamy texture. The soils of the region were dark red, brown or yellow in color with the presence of an agrillic B horizon, but lack ferric and vertic properties.

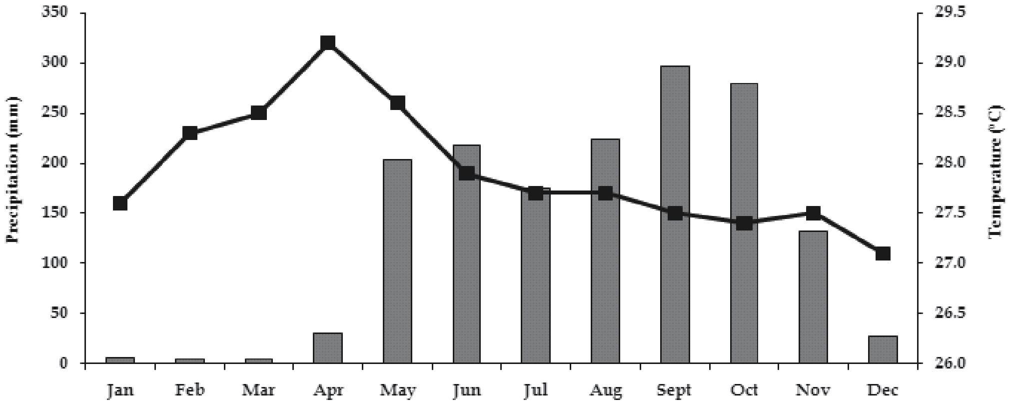

Fig. 1. Mean monthly maximum and minimum temperature (line graph) over 41 years and mean monthly precipitation (bar graph) over 64 years for Esparza, Costa Rica.

3. Sampling methods and statistical analysis

Agricultural producers that participated in this study were chosen because of their existing participation in the GEF-Silvopastoral Study. As such, the participating agricultural producers were already informed about climate change, ecological services, and payment for such services through interaction with CATIE researchers and extension personnel. In addition to conducting interviews with agricultural producers in association with CATIE rural extension officers and the Costa Rican Ministry of Agriculture, further information for this study was obtained from an existing database collected by the GEF-Silvopastoral Study. Information from this database, such as land biophysical characteristics and the type of agroforestry practices implemented provided more depth to the interviews conducted in our study.

In 2007, a total of 50 out of 105 agricultural producers were randomly chosen for our study; and were asked questions based on the following themes: 1) background and farming experience based on information not already collected by the GEF-Silvopastoral Study; 2) knowledge and perceptions about climate change; 3) knowledge on the effects of climate change on current agricultural production; 4) the type of agroforestry practice implemented and its outcome; and 5) why agroforestry practices were adopted. In order to evaluate the adaptive capacity of agricultural producers to climate change, and to contextualize how landowners perceived climate change, the survey included questions on changes in crop and livestock productivity, diseases and pests; changes in the amount and intensity of ambient rainfall and temperature, onset of rainy and dry seasons, frequency of droughts and how agroforestry practices helped to manage droughts. Additionally, landowners were also asked what strategies they were currently using to adapt to climate change and what their incentives (e.g. environmental, financial, extension support) were for implementing agroforestry practices. The semi-structured interviews lasted between 1-3 hours and each interview was recorded.

The surveys were developed and conducted in association with a representative from the Costa Rican Ministry of Agriculture as well as rural extension officers and researchers from CATIE. Details of the survey questions are presented in Smith (2008). Textual data included information provided by agricultural producers that elaborated on the questions of the survey. Recorded interview data was fully transcribed and organized manually into the different themes. In order to understand how the different themes are interconnected, each individual theme was analyzed using QSR NVivo® software (QSR International, Melbourne, Australia). This was done by counting who said what within each theme. Nodes and memos were created using NVIVO to mark relevant concepts, topics and themes. The model explorer tool in NVIVO was used to diagrammatically map out how the themes related to each other.

4. Results and discussion

4.1 Producer perception and understanding of climate change

Results from this study only incorporated agricultural producers with the greatest experience (more than 30 years) in farming because these participants were more likely to notice changes in climate. The majority of these producers (90%) understood the concept of climate change and its cause. Approximately 80% of those surveyed understood that climate change is currently impacting and will impact their land, their family and livelihoods in the future. Similar results were reported by Maddison (2007) who surveyed agricultural producers from 11 different African countries. He found that agriculturalists with the greatest amount of farming experience reported changes in climate. Our results found that many agricultural producers within the study region had knowledge on climate change likely as a consequence of their involvement with the GEF-Silvopastoral Study, and the social networks they established with other agricultural producers, the Costa Rican Ministry of Agriculture, and with researchers and extension personnel from CATIE. Agricultural producers in our survey noted that their primary source of information on climate change was derived from CATIE (56%) and from the Costa Rican Ministry of Agriculture (34%). Information from CATIE and the Costa Rican Ministry of Agriculture was gained through the participation of agricultural producers in organized workshops, seminars and / or on-farm visits.

Agricultural producers interviewed in this study observed several changes in climate, particularly relating to increased ambient temperatures and a prolonged dry season, in the Esparza region over the past 30 years and how this may potentially have affected agricultural productivity (Table 1). Approximately 90% of the agricultural producers noticed increased temperatures while 70% observed a more intense rainy season, but the overall amount of rainfall was lower. An additional 78% of the agricultural producers observed negative impacts on their land, crops, and livestock as a result of a prolonged and more intense dry season including a decrease in crop yield and water availability to livestock and their family. These observations coincided with those predicted by the IPCC (2007), who suggested that the Pacific region of Costa Rica is expected to be drier and hotter. A temperature increase of 0.1°C per decade was reported between the years 1901 and 2005 (IPPC, 2007). According to the IPPC, carbon dioxide (CO_2) started to have an effect on Costa Rica's temperature in the 1970s (IPCC, 2007). Walther et al. (2002) noted that Central America is one of the global regions where climate change impacts on the environment will be pronounced and the loss of species with climate change has already been identified. In the future, IPPC Climate models predict a minimum increase in temperature of 1.5°C and a maximum increase of 5.6°C, from current conditions for this region of Central America (IPCC, 2007). Predictions by the IPCC for changes in precipitation range from a decrease by 11 to 38% during the dry season and an increase of 7 to 21% during the wet season from current conditions. Agricultural producers in our study observed that changes in climate may have potentially led to a decrease in livestock weight, lower milk production, and a decrease in yield of their harvestable crops and pasture grasses. They also noted that the overall decrease in farm productivity affected food availability for their families and livestock. A prolonged dry season resulted in drought leading to a reduction of the farm's carrying capacity, thereby affecting the number of animals, harvestable crops, and the quantity and quality of milk produced. A mixed response, approximately 38% of the agricultural producers, also related climate change to increased pest outbreaks such as locusts (*Schistocera* spp.), ultimately affecting their crop productivity. Others, especially those at the higher elevations, noted an increase in snakes that are commonly found in lowland areas of the Pacific coast. These observations were similar to those reported by Raxworthy et al. (2008) who found that amphibians were moving upslope as a result of a warmer and drier climate at lower elevations.

Climate Characteristics	Potential Changes in Farm Production Quantity and / or Quality	Landowner Observation (%)
Increased Ambient Temperatures (IPCC, 2007)	Overall decrease in farm productivity	72
	Decrease in food production	76
	Livestock weight loss	80
	Decreased milk production	72
	Loss of harvestable products	38
Prolonged Dry Season (IPCC, 2007)	Decreased forage production	72
	Loss of livestock	76
	Loss of harvestable products	46
	Decreased milk production	74
	Decrease in water levels	64
	Overall decrease in water availability for livestock, crops, and people	54

Table 1. Agricultural producers observation of changes in quantity and / or quality of available food, feed and water potentially linked to the increase of temperatures and prolonged drought over the past 30 years in Esparza, Costa Rica (n=50).

4.2 Adaptation and implementation of agroforestry systems

As a result of the payment for ecological services (PES) program through the GEF-Silvopastoral Study, agricultural producers participating in our study had implemented a variety of agroforestry practices, including silvopasture with *Brachiaria brizantha* (Hochst. Ex A. Rich) Stapf. grass, fodderbanks, integration of trees on farmland or farmyards, and the establishment of live fences, that aided their adaptation to climate change. They were also aware that such activities helped in mitigating methane emissions from cattle and significantly increased the amount of carbon captured and stored for the long-term in trees and in soil. A total of 96% of the agricultural producers surveyed integrated trees on their land (Table 2). Specifically, agricultural producers adopted different strategies in order to cope with a longer and more intense dry season.

Agroforestry Land management Practice as a Climate Change Adaptation Strategy	Implementation by Landowners (%)
Silvipasture with *Brachiaria brizantha*	100
Maintenance/implementation of trees on farmland/farmyard	96
Fodder banks	56
Live fences	80
Shade for pasture grass and livestock	98
Enhanced nutrient cycling	98
Soil and water conservation	96
Fuelwood	100
Fruit production	69

Table 2. Percentage of agricultural producers implementing agroforestry land management practices as an adaptation strategy to a more intense dry season, and indicated other benefits (ecological services) as a result of implementing trees on their land in Esparza, Costa Rica (n=50).

For example, 100% of the agricultural producers in our study adapted *B. brizantha* as an improved pasture grass species when they initiated agroforestry silvopastural practices. *Brachiaria brizantha* is native to the African continent but it has been integrated in other tropical areas outside of its native range for use in permanent pasture, cutting for fresh feed, and as a ground cover for erosion control (Barnes et al. 2007). This grass species grows on a wide variety of soil types ranging from light to heavy soil textures and can tolerate a wide range in soil pH (4 to 8). *Brachiaria brizantha* is well adapted to a dry season ranging from 3 to 6 months in length during which time its leaves remain green while native species become dry, brown and unproductive. Additionally, *B. brizantha* can also endure wet soils and grows at an altitude up to 2000 m and thus can tolerate light frost (Barnes et al., 2007). Agricultural producers in our study found many advantages from growing *B. brizantha* on their land (Table 3).

Producers in our study observed an increase in milk production during the dry season by up to 70% as a result of establishing pastures with *B. brizantha*. Similar results were reported by Holmann et al. (2004) who found that the overall production of milk in Costa Rica increased by 55.5% as a result of establishing pastures or fodder banks with *B. brizantha*. This increase is likely due to the higher protein content in *B. brizantha* compared to other grass species traditionally used in Costa Rica (Cook et al., 2005). Results from our study showed that replacing conventional pasture grass with *B. brizantha* resulted in an improved management practice of grasslands, and also lowered grazing pressure and increased livestock carrying capacity, while at the same time provided a strategy to adapt to a changing climate. For example, Cameron (2002) observed that the implementation of *B. brizantha* grass into pastures resulted in soil and water conservation through a decrease in soil compaction and a reduction in external nutrient inputs.

Benefits Observed from *B. brizantha*	**Landowner Observation (%)**
Reduced erosion	96
Greater drought resistance	100
Increased forage production during dry season	98
Increased number of livestock per unit area	100
Livestock weight maintenance	92
Increased livestock meat and / or milk production	92
Improved calf health	96

Table 3. Benefits observed by agricultural producers by integrating silvopasture with *B. brizantha* grass in Esparza, Costa Rica (n=50).

Fig. 2. Fodderbank with *Gliricidia sepium* (Jacq.) Walp. The trees in the foreground show they were recently completely shoot pruned as fodder for livestock, and are already re-sprouting. Photo used with permission from M. Oelbermann.

Fodderbanks were another adaptive measure to climate change implemented by agricultural producers in our study (Figure 2). For example, a total of 56% of the agricultural producers surveyed used fodderbanks with commonly used tree species such as *Gliricidia sepium* (Jacq.) Walp. Pagiola et al. (2008) observed that adaptation of fodderbanks surrounding Esparza was much larger than that compared to other areas of Costa Rica, where they were virtually non-existent. This suggested that the integration of fodderbanks as an additional management practice was due to the close interaction between the agricultural producers, the Costa Rican Ministry of Agriculture, and CATIE researchers and extension officers taking part in the GEF-Silvopastoral Study. Agricultural producers found that *B. brizantha* fodderbanks helped to maintain livestock productivity during years with lower forage biomass and during drought or extended dry periods. A large proportion

(96%) of agricultural producers surveyed in our study implemented and maintained trees on their farmland or in the farmyard. Tree species most commonly established on farmland or in farm yards in our study included *Ficus hartwegii* (Miq.) Miq., *Guazuma ulmifolia* Lam., *Dipteryx panamensis* (Pittier) Rec. & Mell, *Enterolobium cyclocarpum* Jacq. Griseb., *Mangifera indica* L., *Byrsonima crassifolia* (L.) Kunth, *Psidium friedrichsthalianum* (O. Berg) Nied., *Gliricidia sepium* (Jacq.) Walp., and *Acrocomia aculeate* (Jacq.) Lodd. Ex Mart. Agricultural producers found that these trees served multiple functions such as the production of fruit for livestock and human consumption (69%), and the production of leaves for livestock fodder. They also expressed the hardiness of these trees during the dry season and as such did not shed their leaves. Other valuable services these trees provided included fuel wood (100%), shade for pasture grass and livestock, and enhanced nutrient cycling (98%), and soil and water conservation (96%).

Another agroforestry practice commonly implemented by participants in the GEF-Silvopastoral Study and widely used in Costa Rica included the use of live fences. In our study, all (100%) farmers surveyed implemented live fences and in a previous study by Harvey et al. (2005) over 80% of the agricultural producers surveyed in Costa Rica implemented live fences. In our study, the most common use of live fences was to provide an economical enclosure for livestock, and separating pastures from roads, forested areas, and waterways. Our study participants also observed that live fences provided shade for livestock and pasture grasses. In addition, many of the agricultural producers interviewed believed that live fences provided an ecological service by conserving biodiversity in addition to preventing soil erosion and protecting streams when they are used to separate pastureland from waterways. Live fences also provided foliage for cattle fodder. However, in our study, none of the agricultural producers surveyed discussed the use of live fences for this purpose. Similarly, Harvey et al. (2005) noted in their study that only 10% of Costa Rican agricultural producers used live fences for the production of fodder in addition to their use as an enclosure for pasture lands. This suggested that agricultural producers in Costa Rica were not aware of all possible benefits of live fences, but those that participated in the GEF-Silvopastoral Study had a greater knowledge on the diverse utility of live fences.

Other studies also revealed that the conversion of farmland previously containing few or no trees into areas dominated by agroforestry decreased the amount of degraded land by 15% over a 3-year period (Zamora-Lopez, 2006). Zamora-Lopez (2006) also found that the poorest agricultural producers were able to reduce pastureland degradation by introducing improved pasture with trees, by adopting fodder banks, and live fences. As such, a diversification in agricultural production systems included the implementation of a significant tree component that may buffer against income risks associated with current and future shifts in climate (Verchot et al., 2007). Kandji et al. (2006) also pointed out that agroforestry systems have the ability to improve the microclimate which in turn improves the adaptive capacity of land owners to climate change. Additionally, Kandji et al. (2006) suggested that the presence of trees in agricultural croplands can provide agricultural producers with an additional source of income that helps to strengthen their socioeconomic resilience. For example, tree products including fodder, resins, timber, and fruits provide a higher source of income than corps, and can also buffer against crop failure.

4.3 Producer contingency plans and adaptive capacity

According to the IPCC (2007) introducing a contingency plan to cope with unexpected changes in climate will increase food security and reduce financial losses. Our study showed that 28% of the agricultural producers researched the issue of climate change in detail and were able to explain what climate change is and how it will affect food security, their livelihood and families. These agricultural producers were able to link changes caused in the Earth's atmosphere to deforestation and industrial processes, and therefore had implemented a climate change contingency plan. These agricultural producers suggested, and were aware of, that those without a climate change contingency plan may face many additional challenges compared to those with a plan. An additional 50% of the agricultural producers in our study were seeking information about climate change contingency plans. This was because of their interaction with the GEF-Silvopastoral Study and the knowledge gained through this interaction. These agricultural producers expected that climate change will force them to make major adjustments to their land management practices in order to ensure food security and livelihoods for their family in the future. Approximately 56% of these agricultural producers relied on CATIE and 34% on the Costa Rican Ministry of Agriculture to obtain information on climate change and strategies for adaptation. The remaining agricultural producers from our study expressed that the different adaptation strategies they had already implemented as a result of their association with the GEF-Silvopastoral Study provided sufficient protection from negative impacts of climate change on their land.

Adger (2001) suggested that the capacity to adapt to climate change may be enhanced through the improvement of social networks that provide information about climate change. Such social networks, comprised of institutions and organizations fluent in issues surrounding climate change, should work in close association with agricultural producers to assist them in developing strategies to enhance their capacity to adapt to climate change (Gallopin, 2006). Our results showed that 84% of the agricultural producers sought assistance from CATIE and the Ministry of Agriculture to increase their capacity to adapt to climate change. Through the GEF-Silvopastoral Study, CATIE has played a key role in enhancing social networks in Esparza by connecting agricultural producers with the Costa Rican Ministry of Agriculture. A network specifically established for the agricultural producers in this region provided opportunities to connect with each other to learn about new climate change adaptation strategies through the implementation of agroforestry practices.

Nhemachena & Hassan (2007) observed that widespread information on climate change to agricultural producers enhanced their capacity to adapt to climate change, and led to the development and implementation of long-term contingency plans. Füssel (2007) also found that if agricultural producers understood the inherent changes expected as a result of climate change, then they improved their ability to adapt and decreased their overall cost of adaptation. Agricultural producers decided which land management practices to implement based on profit, grain yield and/or livestock productivity (Adger, 2001). Approximately 70% of agricultural producers in our study stated that market incentives either through credits or PES will increase their capacity to adapt to climate change. Based on the qualitative discussions with agricultural producers and the quantitative data collected in the surveys, several factors influenced their capacity and motivation to implement adaptation strategies (Figure 3). Our results showed that the producer's ability and motivation to implement climate change adaptation strategies was strongly influenced by financial incentives through a PES system which would also cover costs of tree planting and other expenses related to the adoption of agroforestry practices. Increased market incentives (e.g. eco-labelling) or other incentives to increase the marketability of their products, and non-financial assistance to help increase their capacity to adapt to climate change were requested by those surveyed in our study. Maddison (2007) pointed out that differences in the capacity to adapt to climate change may be due to the underlying differences in the perception of climate change. Some of the producers in his study expressed a lack of knowledge about adaptation strategies, rationing of key resources such as water, lack of appropriate seed, lack of market access and insecure property rights. Pagiola et al. (2008) also noted that the initial costs of implementing fodderbanks using *Brachiaria* grass species and the time lag before receiving any benefit from such activity in Costa Rica was a primary determinant of this management practice. Agricultural producers in our study, who thought climate change is not an environmental issue, were encouraged to implement environmental services for financial gain. The incentives offered by the GEF-Silvopastoral Study through a PES system and their increasing knowledge on the value of environmental services allowed them to understand and benefit financially through implementing these services.

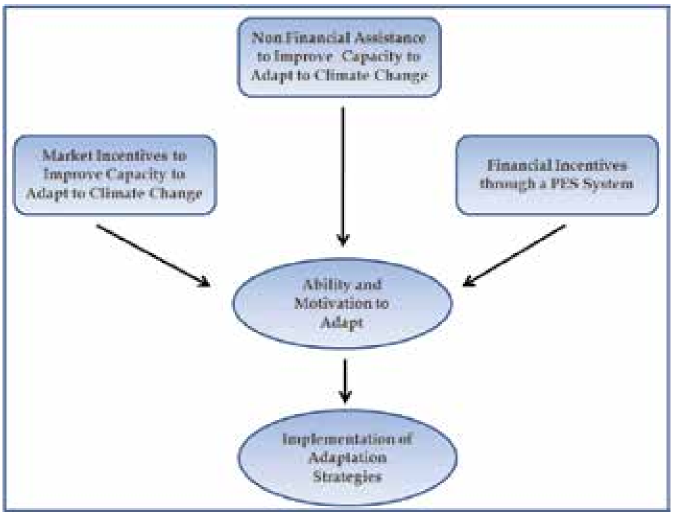

Fig. 3. Factors influencing the ability and motivation of agricultural producers to implement agroforestry systems as a climate change adaptation strategy, Esparza, Costa Rica (n=50).

5. Conclusions

Results from our study showed that the majority of agricultural producers had already implemented specific management practices to help cope with climate change. Our results also suggested that producers implemented specific agroforestry practices under the direction and guidance of CATIE extension personnel, researchers and the Costa Rican Ministry of Agriculture as part of the GEF-Silvopastoral Study. Through this interaction, agricultural producers became aware that the adoption of agroforestry practices also provided an ecological service, and therefore helped them to adapt to current and future climate change, for which they received a financial incentive. Only a small number of agricultural producers had a contingency plan in place which would help them cope with imminent climate change and reduce financial losses while maintaining food security and livelihoods for their families. However, a large proportion of agricultural producers were seeking further information on climate change contingency plans and relied on social networks built through their interaction with the GEF-Silvopastoral Study. A large number of agricultural producers in our study would readily adopt agroforestry practices as part of an incentive program including a PES system and market incentives, and receive further advice (non-financial assistance) from extension personnel on increasing their capacity to adapt to climate change.

6. Acknowledgements

Financial support was provided by Inter-American Institute for Co-operation in Agriculture, Canada, the Global Environment Facility Silvopastoral Study, and the University of Waterloo. We also thank Dr. M.A. Ibrahim and C. Cepulveda for assistance with research logistics and access to the GEF-Silvopastoral Study data base. We thank Francisco Casasola, and the Costa Rican Ministry of Agriculture for assistance in the field.

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9

Crop Production and Global Warming

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1. Introduction

Crop production will be affected by global warming, resulting in world-wide food shortages and starvation. Increased concentrations of carbon dioxide (CO_2), one of the main substances responsible for global warming, will promote plant growth through intensified photosynthesis. Some reports indicate that a rise in the levels of CO_2 would actually benefit plants, rather than harm them. The growth rates of C_3 plants increase in response to elevated concentrations of carbon dioxide. Thus, global warming might increase plant growth, because of higher temperatures and higher levels of atmospheric CO_2.

High atmospheric temperatures caused by elevated concentrations of CO_2 will induce heat injury and physiological disorders in some crops, which will decrease the incomes of farmers and agricultural countries. Photosynthesis is one of the most sensitive physiological processes to high temperature stress. Reproductive development is more sensitive than vegetative development to high temperatures, and heat-sensitivity differs among crops. In tomato, the optimal temperature for fruit set was reported as 21–24°C (Geisenberg and Stewart, 1986) or 22–25°C (Peet and Bartholomew, 1996), while pollen viability and release are adversely affected by high temperatures, and become major limiting factors for fruit set. Thus, global warming can have opposite effects on plant growth. From a long-term viewpoint, however, high atmospheric temperatures will drive the main sites of crop production further north, establishing new rules for the 'right crop for right land'.

Water shortages caused by global warming will be the greatest problem for crop production. Plants fundamentally rely on adequate fresh water, and agricultural water accounts for 70% of water use world-wide. As higher temperatures increase evaporation from water sources and decrease precipitation, arid regions will become further desertified. Particularly in semiarid regions, the cultivatable area will decrease because of drought, and this could result in famines and mass migration. As well, it is likely that there will be human conflicts over irrigation water and food.

Global warming is thought to be related to strong hurricanes, cyclones, and typhoons. These extreme weather events can seriously damage crop production, and destabilize farm management and the lives of consumers. However, these agricultural problems are most likely to occur in the medium and long-term future.

In this chapter, we summarize some of the agricultural problems and crop damage that result from global warming, and present some technical countermeasures (not political and administrative countermeasures) that could be used to ameliorate the effects of global warming on crop production. We also discuss parthenocarpy and grafting as potential countermeasures.

2. Effects of global warming on plant growth

2.1 Carbon dioxide

Carbon dioxide is a key molecule for photosynthesis. In plants, photosynthesis occurs mainly in the leaves. The chemical reaction driven by solar energy involves the reduction of CO_2 through water to create carbohydrates and release oxygen. The resulting carbohydrates are used for plant growth, and provide the energy source for living things. Under 'normal' conditions, the atmospheric CO_2 concentration is very low. The photosynthetic reactions under high temperatures and high light intensities are limited by the CO_2 concentration, and the photosynthetic rate does not exceed a certain value. Because CO_2 is the limiting factor, an increase in its concentration significantly affects photosynthesis. In general, increased CO_2 concentrations temporary promote photosynthesis; however, the photosynthetic rate decreases over an extended period of exposure to high CO_2 concentrations.

Photosynthesis is affected by various environmental conditions. In appropriate temperature conditions, the photosynthetic rate with the current CO_2 concentration of 370 ppm is strongly influenced by light intensity. Under low light conditions, the photosynthetic rate and the light saturation point are low, and so the CO_2 requirements are low. However, at higher light intensity, the photosynthetic rate and light saturation point are higher (Fig. 1). Thus, CO_2 is one of the major environmental factors affecting plant growth along with light, temperature, and water. However, unlike other environmental factors, the CO_2 concentration in the atmosphere does not fluctuate with climate change. Apart from anthropogenic sources, natural causes of changes in the atmospheric CO_2 concentration include plants, which at high density can change the CO_2 concentration by 25%, and respiration of soil microbes, which can change the CO_2 concentration by 30% near the soil surface.

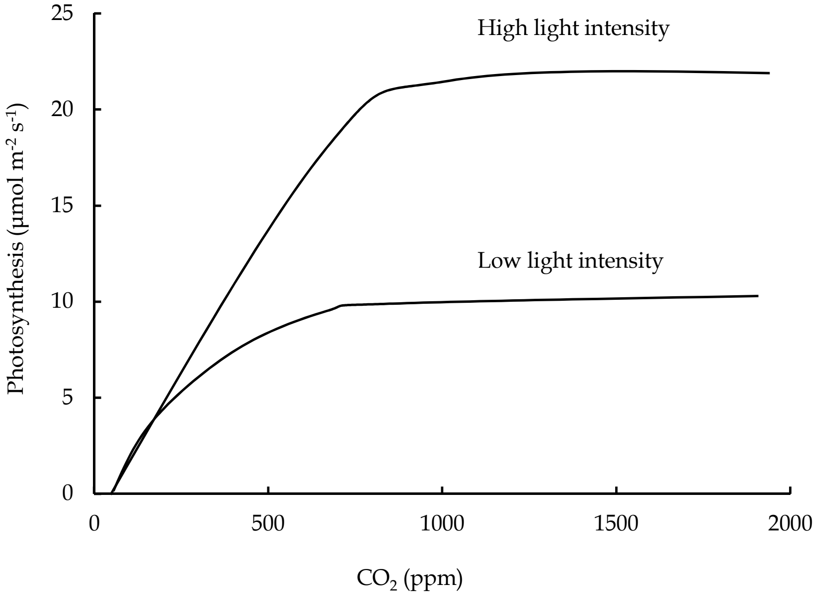

Fig. 1. Photosynthetic curves at high and low light intensities.

In plants, the promotion of photosynthesis under high CO_2 concentrations results in increased dry matter production. This is known as the "CO_2 fertilizer effect", and it is used to promote crop growth in greenhouses and plant factories. This effect is more pronounced in C_3 crops, such as wheat, soybean, and rice, but less so in C_4 crops, such as maize, millet, and sugarcane. This is because the current atmospheric CO_2 concentration limits photosynthesis in C_3 plants, but not in C_4 plants because of their ability to concentrate CO_2 in the cells (Fig. 2). If the concentration of CO_2 is doubled, the photosynthetic rate of many C_3 plants increases by 30–60%, but in most C_3 plants these promoted rates are temporary, and there are no promotion effects in the long term. Thus, it is thought that the changes in the photosynthetic apparatus or other photosynthetic factors that occur during short-term responses to increased CO_2 differ from those during long-term exposure to increased CO_2. This phenomenon often occurs when photosynthetic production exceeds plant growth (Nakano et al., 1997; Makino, 1994).

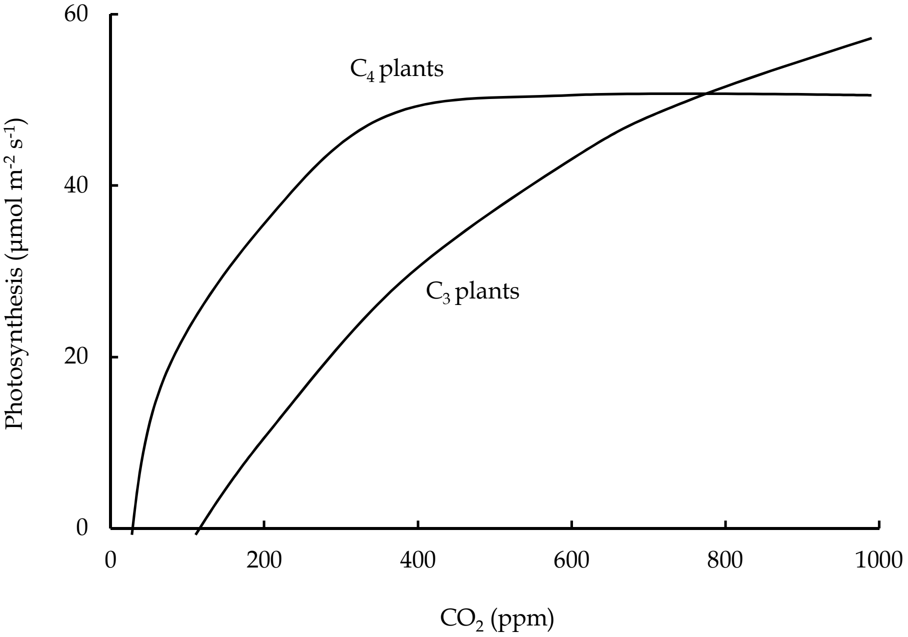

Fig. 2. Photosynthetic curves for C3 and C4 plants (Rogers &Runion, 1994).

The effects of CO_2 concentration on crop yield will become greater as the atmospheric CO_2 concentration increases. For many crops, the predicted yield increase in response to a 700 ppm CO_2 concentration is approximately 30%; specifically, a yield increase of 31% in wheat (Amthor, 2001), 29–35% in rice (Cock and Yoshida, 1973; Imai et al., 1985) 55% in soybean (Rogers et al., 1983), and 50% in maize (Rogers et al., 1983). However, the promoting effects will vary according to the specific nature of the plant and its sinks, e.g., seeds or bulbs. Even though photosynthesis in C_3-type crops is generally inhibited by long-term exposure to high CO_2 concentrations, those that have separate organs to accumulate photosynthetic products appear to be unaffected. For example, inhibition of photosynthesis in crops such as radish and potatoes has not been observed (Sage et al., 1989; Usuda and Simogawara, 1998). Also, if water and mineral nutrients become limiting factors, the promoting effects of increased CO_2

concentration on crop production are minor. This may because there is insufficient water and mineral nutrients to support an increase in photosynthesis, because of the balance of growth between the root and the shoot.

2.2 Temperature

Crop germination and growth rely on optimal temperatures during the period of greatest growth rate. Therefore, non-optimal temperatures slow the growth rate or stop growth altogether. The limiting temperatures for growth are minimum and maximum temperatures, and these vary among crops (Table 1), crop varieties (Table 2, Prasad et al., 2006), and among different growth stages in the same crop. In particular, temperature strongly affects crops during their reproductive period, from pollen formation to fertilization (Table 3). Low or high temperatures during this period can prevent crop fertilization and cause seed abortion.

Temperature type	Crops	Germination (°C)			Growth (°C)		
		Optimum	Min	Max	Optimum	Min	Max
High	Eggplant	20-25	15	33	22-28	17	33
	Pepper	20-30	15	35	25-30	15	35
	Water Melon	25-30	15	35	25-30	13	35
	Melon	25-30	15	40	25-30	18	35
	Soybean	25-30	10	35	25-30	10	35
	Maize	25-30	10	40	20-30	10	35
Midle	Wheat	25-30	2	40	20-25	4	30
	Tomato	15-27	11	30	21-26	5	35
	Cucumber	25-30	18	30	18-25	12	35
	Pumpkin	20-25	15	40	17-25	10	35
Low	Lettuce	15-20	4	25	15-20	8	25
	Carrot	15-25	11	30	16-20	5	28
	Potato^z	-	-	-	15-24	10	29
	Strawberry^z	-	-	-	17-23	10	23
	Cabbage	15-30	8	35	15-20	5	25
	Spinach	15-20	5	30	15-20	3	25

^{z}: Potato and strawberry are mainly vegetatively propagated.

Table 1. Temperatures for germination and growth of crops (recasting and adding of Saitoh, 2008).

	Vegetative biomass (g plant^{-1})			Grain yield (g plant^{-1})		
	AT	HT	% decrease from AT	AT	HT	% decrease from AT
L-204	11.9	12.3	0.0	11.9	1.3	89.1
M-202	12.0	10.6	11.7	13.6	1.9	86.0
Labelle	22.7	12.3	45.8	21.8	4.5	79.4
Italica Livorma	8.7	11.6	0.0	12.5	1.4	88.8
S-102	9.2	9.6	0.0	15.3	1.6	89.5
Koshihikari	9.1	9.9	0.0	12.3	2.7	78.0
M-103	8.7	9.3	0.0	12.2	4.4	63.9
N-22	17.4	23.8	0.0	17.7	9.2	48.0
IR-8	17.7	11.2	36.7	8.2	6.2	24.4
IR-72	15.9	12.6	20.8	8.4	5.5	34.5

Table 2. Effects of ambient temperature (AT) and high temperature (ambient +5 °C, HT) on vegetative biomass and grain yield of different rice cultivars (Prasad et al., 2006).

Crop	High-temperature injyury
Wheat	Male serarity (over 30 °C)
Tomato	Male serarity (over 30 °C)
Cucumber	Male serarity (over 30 °C)
Pumpkin	Abnormal differentiation of male and femal flower (over 30°C)
Potato	Poor potatp formation (over 21°C), No potato formation (over 29°C)

Table 3. High temperature injury of crops (Yamazaki, 1985).

2.2.1 Effect of high temperatures on crop production in different areas

The increase in temperatures resulting from higher concentrations of CO_2 in the atmosphere may inhibit or promote crop growth. Naturally, such climatic changes will directly affect agricultural production. It is anticipated that for moderate global average temperature increases (1–3°C) there will be an overall increase in global food production. Additional temperature increases, however, would result in an overall decrease in food (IPCC, 2007). In low-latitude regions such as seasonally dry tropical areas, even moderate temperature increases (1–2°C) are likely to negatively affect major cereal crops, increasing the risk of famine. By the mid-21st century, crop yields in East and Southeast Asia may increase by up to 20%, while those in central and South Asia may decrease by up to 30% if the direct positive physiological effects of CO_2 are taken into account. Western New Zealand is likely to receive more rain, but large areas of mainland Australia and eastern New Zealand are likely to have less soil moisture. Therefore, the increased drought and frequency of fires could decrease crop production. In North America, it is predicted that there will be climate-related yield increases of 5–20% over the first decades of the century, with overall positive effects of climate persisting through much or all of the 21st century. However, crops that are currently growing in areas that are close to their climate thresholds (e.g., wine grapes in California) are likely to show decreases in yield and/or quality in response to even modest increases in temperature (Hayhoe et al., 2004; White et al., 2006). In drier areas of Latin America, climate change is likely to lead to salinization and desertification of agricultural lands, and therefore, food production and security will fluctuate. In some African countries, climate change could exacerbate erosion, and decreases in yields from rain-fed agriculture of up to 50% during the period from 2000 to 2020 (Agoumi, 2003).

2.2.2 Effect of high temperatures on crop growth

Rice

In rice, seed abortion occurs when plants are subjected to temperatures above 35°C. When the average temperature exceeds 26–27°C at 20 days after ear emergence, grain filling and grain quality are decreased, and there are more immature grains.

Wheat

The number of wheat tillers decreases in response to high temperatures, especially high night-time temperatures. In such conditions, shoot elongation is promoted but there are more immature grains and decreased yields because of dark respiration. Moreover, unusually early panicle initiation caused by warm winters can increase the risk of frost damage.

Soybean

The growth of soybean decreases above 38°C, but soybean is relatively heat-tolerant. However, pollen viability was lower at day/night temperature conditions of 37/27°C than at 27/27°C, and the rate of pod setting at 32/27°C was lower than that at 27/27°C (Kitano et al., 2006).

Tomato

At high temperatures, seedlings grow faster and the differentiation and development of flowers is also promoted. However, the rate of flower set decreases and flowers are of poor quality. High temperatures during flowering induce flower abscission, malformed flowers, and pollen sterility in tomato plants. High temperatures also result in poor flowering, poor fruit quality, and color disorders.

Cucumber

High temperatures result in faster seedling growth. However, the development of pistillate and bisexual flowers is suppressed, the node order of the flowers increases, and the number of flowers decreases. High temperatures inhibit flower differentiation and development, and result in smaller ovaries in pistillate and bisexual flowers.

Lettuce

Since lettuce is a cool-temperature crop, it is likely to be adversely affected by higher temperatures. Higher temperatures induce floral differentiation and flower stalk development in lettuce plants, both of which decrease yield and quality of the crop.

Carrot

Carrot is another cool-temperature crop, and so higher temperatures and drier conditions inhibit seed germination and plant growth. Moreover, high temperatures and wet conditions result in shorter, thicker roots. The major risk for carrots, however, is the predicted increase in disease damage in warmer, wet conditions.

Potato

The night-time temperature is important for formation of potato tubers. The optimum temperatures are 20°C days and 10–14°C nights, but almost no tubers form if night-time temperatures exceed 20°C. In warm, wet conditions, the stolon-formation period is shorter, the tubers are smaller, and the tuber quality is poor (e.g. some have hollow hearts).

Strawberry

Floral differentiation of strawberry is strongly affected by temperature and photoperiod. At low temperatures (5–10°C), flower buds form regardless of the photoperiod. At 11–15°C, flower buds can form, but only with increased light intensity under long-day conditions. At 16–26°C, flower buds form under a short-day photoperiod (less than 12-h days), and no flower buds form above 27°C. Therefore, high temperatures will delay floral formation and result in small fruits.

2.2.3 Weeds, harmful insects, and diseases

To achieve high yields, crops must be protected from pests, diseases, and weeds. Of the total cropping area worldwide, crop yield is decreased by 10–20% by weeds (Mirrabelli et al., 2005). Many C_4 weeds are found in arable C_3 crops and many C_3 weeds in arable C_4 crops. Therefore, under high temperatures and increased atmospheric CO_2 concentrations, weed damage to arable C_4 crops in tropical and subtropical semiarid areas is predicted to increase. It is likely that global warming will result in pests and diseases that are currently found in low-latitude regions spreading to high-latitude regions. Bacteria and fungi are the main causal agents of plant diseases, and their optimal growth temperatures are approximately 25°C and above 30°C, respectively. Temperature also affects the growth of insects, with higher temperatures increasing their growth rate. Therefore, continued warming is expected to increase damage to crops from bacteria, fungi, and insects.

3. Water shortages, desertification, and tropical cyclones

As global warming progress, there will be increased evaporation from the earth's surface and from plants. Even a 1°C temperature increase would increase the amount of evaporation from the earth. As well, increased temperatures result in more concentrated, heavy rainfall, and crops show decreased rainfall use efficiency in such circumstances. Snowfall, which results in stored water resources, also decreases with higher temperatures, and snow melts more rapidly. Together, these factors could combine to increase drought in the major agricultural regions—the mid-latitude continents. This could significantly restrict the world's food supply.

Desertification of dry areas is very likely to result from global warming. In dry areas, water moves from subsurface to surface layers of the soil. Therefore, when capillary water reaches the ground or irrigation water evaporates, the soluble salts that dissolved into the water in the lower layers are concentrated in the surface soil layer. As a result, salt accumulates at the soil surface, where it negatively affects or prevents plant growth. In dry regions, more water will evaporate as temperatures increase, turning these areas into deserts. Desertification decreases the amount of vegetation, reducing CO_2 absorption by plants, and further progressing global warming. The area of the world's deserts is expanding by 60,000 km^2 each year, and the desertification of humid and semi-arid areas and the dry sub-humid areas used to cultivate wheat and other grains could cause a serious food crisis.

Strong tropical storms, hurricanes, typhoons, and cyclones severely damage farmland. The numerous tropical storms in recent years are thought to be a result of global warming. Theoretically, the increase in the number of strong tropical storms is because of increased evaporation—the energy source for tropical storms—due to the rise in the temperature of the ocean's surface (Emanuel, 1987). Walsh (2004) indicated that the tropical cyclone intensity will increase by 5–10% around 2050, along with increased peak rainfall rates of approximately 25%. More recent climate model predictions are that the number of cyclones will decrease by approximately 30% under global warming, but their duration will be longer (Oouchi et al., 2005). Therefore, low-lying areas could be at high risk because of longer tropical storms and increased sea levels.

4. Countermeasures

Some strategies to ameliorate the effects of global warming on food production include the development and use of heat-tolerant varieties, appropriate nutrient and water management, coordination of growing periods, and control of pests and diseases. In particular, pest/disease control and the use of heat-tolerant crops are thought to be the most promising approaches. Soybean is sensitive to drought, and so adequate irrigation must be provided when its evapotranspiration rate increases in response to higher temperatures. Although wheat is relatively drought-tolerant, water shortages in dry areas are a concern, so efficient irrigation techniques, e.g. drip irrigation, should be used. The male sterility that results from high-temperature injury decreases the yields of wheat and maize, but treatment with the plant hormone auxin can restore fertility (Fig. 4; Sakata et al., 2010).

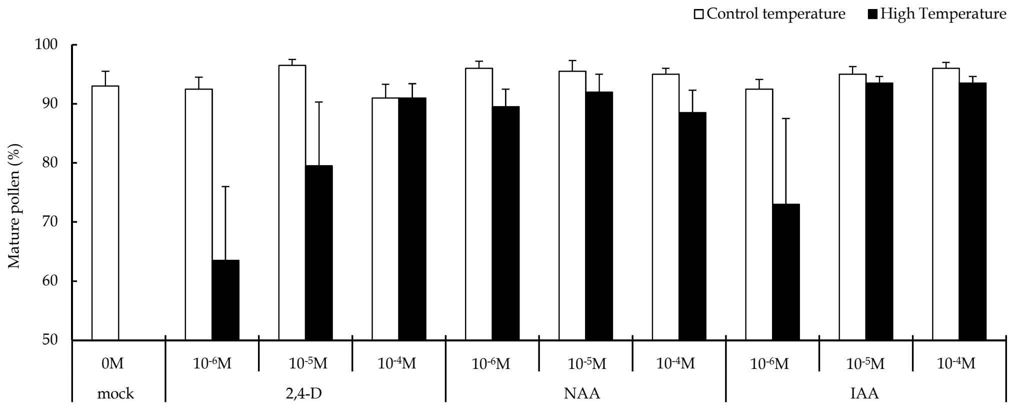

Fig. 4. Effects of exogenous auxin on high temperature injury of pollen developments in barley. A population of mature pollen grains were recovered from anthers after all auxin applications testeed. (Sakata et al., 2010).

For leafy crops, mulching and shading are useful techniques to prevent increases in the soil temperature. For fruit crops, useful techniques include the use of various materials to shade and heat-shield trees, and coordination of the growing period. A night-chilling treatment is a useful countermeasure to induce floral differentiation of strawberry. For crops in protected cultivation, the combination of heat pumps, evaporative cooling, air ventilation, and shading can achieve optimum growth conditions.

Rootstock	Desination	NaCl (mM)			
		0		50	
Moneymaker	M/M	201.2 ± 12.4	a	128.4 ± 10.1	b
Radja	M/R	242.9 ± 16.8	a	145.8 ± 24.3	b
Pera	M/P	238.2 ± 34.1	a	202.4 ± 24.4	a

Table 4. Shoot fresh weight (g plant−1) of self-grafted Moneymaker plants and Moneymaker grafted onto two rootstocks (Radja and Pera) after 35 days of salt treatment (Martinez-Rodriguez et al., 2008).

Results as means±S.E. (n = 6). Means within each column followed by different letters are significantly different according to the LSD test (P≤0.05).

4.1 Parthenocarpy

Fruit develops from the ovary, which itself develops in response to plant hormones that are produced by seeds formed after fertilization. Fertilization is the fusion of pollen (formed in the anther) and the ovule (formed in the ovary). However, because pollen is temperature-sensitive, high temperatures during pollen formation induce male sterility. If global warming proceeds at the current rate, fruit production could be affected in fruit and vegetables that require fertilization. Parthenocarpy is the natural or artificially induced production of fruit without fertilization of ovules, so this is a promising strategy for fruit production under global warming. Natural parthenocarpy involves using varieties that have parthenocarpic genes, while artificial parthenocarpy is induced by hormone treatment. Examples of parthenocarpy include the production of seedless grapes using GA treatment, and tomato, eggplant, and cucumber production using auxin treatment. Crops in which natural parthenocarpy is exploited include oranges, pineapple, banana, tomato, eggplant, and cucumber. In general, parthenocarpic fruit trees are propagated by vegetative propagation and parthenocarpic vegetables are propagated by F_1 seeds. Therefore, the use of parthenocarpic vegetables is limited because few seeds are formed in these vegetables. Recently, a method was reported to enhance seed production in parthenocarpic tomato fruits (Fig. 5; Johkan et al., 2010). This method can be applied to other crops, and therefore, it may allow more extensive use of parthenocarpic fruits in the future.

4.2 Grafting

Grafting is the vegetative propagation of fruit trees, but in Japan, it has also been used to avoid injury by continuous cropping of vegetables and soil pests and diseases. Vegetable fruits that can be grafted include cucurbits such as melons, watermelon, and cucumber, and

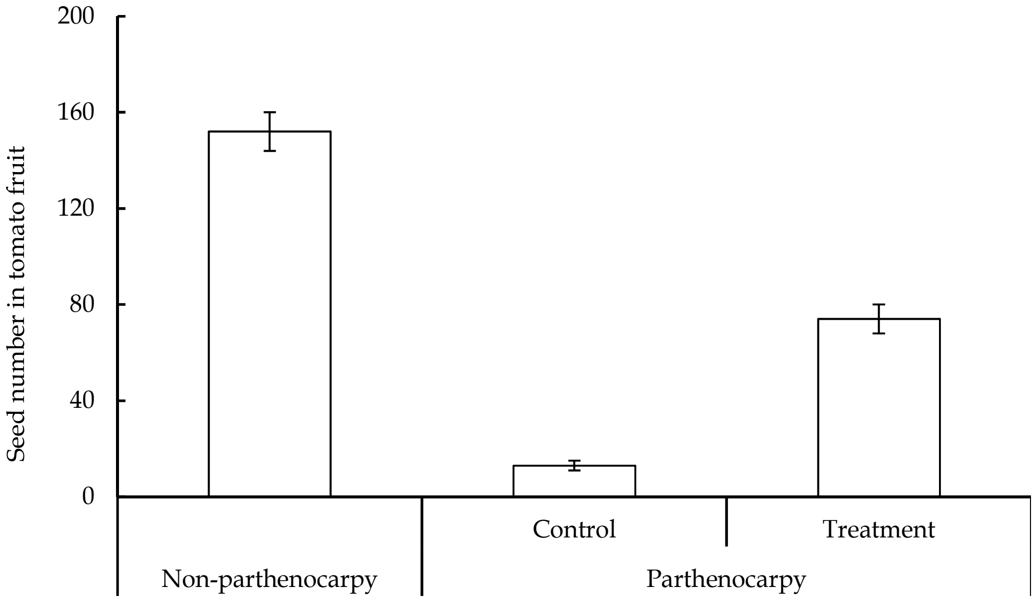

Fig. 5. Increase of seed formation in parthenocarpic tomato fruit (Johkan et al., 2010).

solanaceous species such as tomato and eggplant. Grafting can give the characteristics of the rootstock to the scion. Some rootstocks will be more tolerant to adverse environmental conditions. In particular, grafting scions to rootstock with high drought- or heat-tolerance can increase growth and yield under high temperatures (Fig. 6, Rivero et al., 2003). In addition, crops that are not salt tolerant can be cultivated in saline areas if grafted onto salt-tolerant rootstock. As mentioned above, grafting is an effective countermeasure for crop production without the need to breed lines that are tolerant to heat or drought.

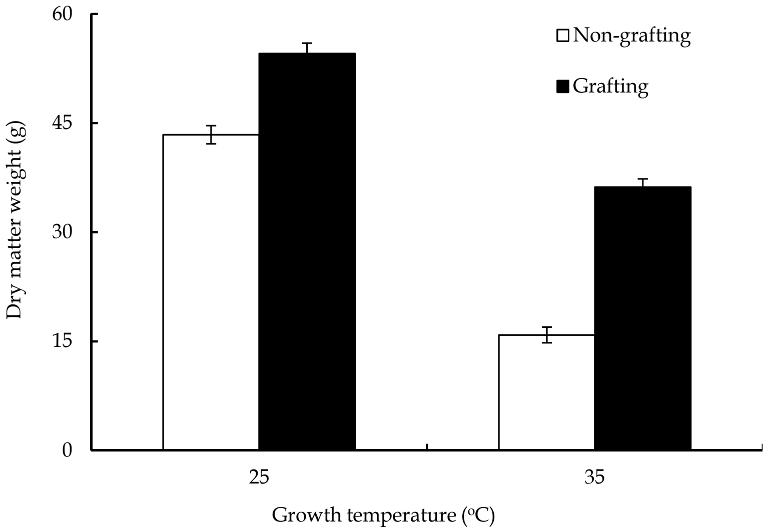

Fig. 6. Effect of grafting on growth of tomato shoots at high temperature (Rivero et al., 2003).

4.3 Vegetative propagation

The use heat-tolerant cultivars are an effective countermeasure against global warming. Breeding of heat-tolerant varieties is required if there are no suitable varieties for the local area. However, propagation by seeds requires genetic fixation, which is a lengthy process. In contrast, vegetative propagation does not require genetic fixation, so it can be used for rapid release of pathogen-resistant or desirable cultivars. One disadvantage of vegetative propagation is that it is less efficient than seed propagation. However, an *in vivo* mass propagation method was recently reported for tomato. This method markedly increased the multiplication rate (Johkan et al., 2008), and could be applied to other plants. As mentioned above, if immediate action is required to ameliorate the effects of global warming, vegetative propagation may be one effective method.

5. Conclusion

The effects of global warming on food production are complex, and are a combination of increased CO_2 concentrations in the atmosphere, higher temperatures, fluctuations in rainfall and solar radiation, and pests and diseases. The 'fertilizing effect' of elevated CO_2 concentrations on crop yields will decline slightly because of the negative effects of rising temperatures. Particularly in developing areas with undeveloped agricultural technologies, there is a high risk that a hotter, drier climate will negatively affect crop production. In mid- and high-latitude regions, even a moderate increase in the global average temperature (1–3°C) could increase food production, but additional temperature increases would cause an overall decline in food production. In low-latitude regions, especially seasonally dry semitropical areas, temperature increases of only 1 or 2°C are likely to negatively affect cereal production because of drought. Although the effect of global warming on food production will vary among regions and crop types, it is anticipated global food production will decrease, and the North-South gap in food production will become greater than it is at present. Therefore, it is important to reexamine existing varieties, to introduce new varieties with increased tolerance to high temperatures and pests/diseases, and to improve methods of pest and disease control.

Parthenocarpy, grafting, and vegetative propagation should also be considered as useful countermeasures against global warming. However, temperature strongly affects crop production, and the extent to which countermeasures can ameliorate the effects of global warming are limited. Global warming is a common problem for all people living on earth. There is no doubt that to address the issue of global warming together is the most effective strategy to guarantee stable crop production.

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10

Effects of High Night Temperature on Crop Physiology and Productivity: Plant Growth Regulators Provide a Management Option

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1. Introduction

Crop production is experiencing both increases in the frequency and intensity of high night temperatures (HNT) (IPCC, 2007). The HNT threatens the sustainability of crop production both currently and in the future. Recent meteorological data indicated faster increases in night temperatures (NT) than day temperatures (Alward et al., 1999). Experimental evidence also indicated the importance of assessing the effects of NT separately from the day temperature, as a smaller increase in NT can show a drastic decrease in crop production (Peng et al., 2004). Studies have indicated decreased crop yields as a result of HNT (Hall, 1992; Mohammed & Tarpley, 2009a). Apart from HNT, climate change will also increase a variety of environmental stresses affecting crop production, namely heat, drought, salinity, and relative humidity, hence farming in the future climate will have to be better adapted to a range of abiotic and biotic stresses. A long-term approach to negate the effects of abiotic stress is to develop stress-tolerant cultivars. The short-term approach includes the use of agrochemicals, especially those with plant growth regulator (PGR) capabilities, for the prevention and/or amelioration of various environmental stresses, including heat stress. Studies focusing on day temperature stress and, more recently, on NT stress have increased, but, studies looking at the effects of PGR under heat stress are rare (Ashraf & Foolad, 2007). This chapter primarily focuses on the effects of HNT on crop production and the beneficial effects of PGR (glycine betaine [GB] and salicylic acid [SA]) application against heat stress on crop production with special emphasis on rice (*Oryza sativa* L.) production.

2. Night temperature and its impact on crop production

Global climate change is a dynamic process affecting global air temperature, oceanic temperature, rainfall, wind and quality of incoming solar radiation. Global circulation models predict 1.4 to 5.8 °C rise in global temperature because of projected increase in the concentrations of all greenhouse gases by the end of the 21st century (Intergovernmental Panel on Climate Change [IPCC], 2007). Much of this increase in average daily temperature is projected to be due to an increase in NT. Night temperatures are expected to increase at a faster rate than day temperatures due to less radiant heat loss because of increased cloudiness (Alward et al., 1999). In some cases, increases in NT have been documented. For example, the scientists at the International Rice Research Institute (IRRI) reported an increase of 1.13 °C in NT over a period of 25 years (1979-2003) in the Philippines (Peng et al., 2004). The HNT increased at a rate of 0.18 °C per decade over a period of 45 years (1950-1995) in Libya (Jones et al., 1999).

Long- and short-term episodes of heat stress are predicted to occur more frequently as a result of global warming, affecting many aspects of crop growth and development, reducing crop yield and decreasing crop quality. Many studies have reported the impacts of long- and short-term temperature stresses on crop production. However, most of the studies assume no difference in the influence of day versus night temperature (Peng et al., 2004). High night temperature is known to decrease yield in several crops like cereals [rice, wheat (*Triticum aestivum* L.) and corn (*Zea Mays* L.)], legumes [cowpea (*Vigna unguiculata* L. Walp.)], oil seeds [soybean (*Glycine max* L. Merr.) and sunflower (*Helianthus annuus L.*), vegetables [tomato (*Solanum lycopersicum* L.)], fruits [apples (*Malus domestica* L.) and pineapple (*Ananas comosus* L.)] and fibers [cotton (*Gossypium hirsutum* L.)] (Chang, 1981; Gibson & Mullen, 1996; Izquierdo et al., 2002; Kondo & Takahashi, 1989; Loka & Oosterhuis, 2010; Mohammed & Tarpley, 2009a; Neales et al., 1980; Peters et al., 1971; Seddigh & Jolliff, 1984; Warrag & Hall, 1984; Willits & Peet, 1998).

High night temperature decreases crop production by decreasing photosynthetic function, sugar and starch content (Loka & Oosterhuis, 2010; Turnbull et al., 2002), increasing respiration rate (Mohammed & Tarpley, 2009b), suppressing floral bud development (Ahmed & Hall, 1993), causing male sterility and low pollen viability and hastening crop maturity (Mohammed & Tarpley, 2009a; Seddigh and Jolliff, 1984). Another effect of HNT that can contribute to reduced crop yield is decreased antioxidant capacity of the plants. Under normal physiological conditions, the toxic effects of reactive oxygen species (ROS) are minimized by enzymatic and non-enzymatic antioxidants. Under stress conditions, oxidant levels can overwhelm the antioxidant levels leading to cell damage. The increased production of ROS [oxide radical (O_2^-), H_2O_2, and the hydroxyl radical (-OH)], or the plant's decreased ability to neutralize ROS, as a result of heat stress negatively affects many physiological processes in plants, thus decreasing yield.

2.1 Methodology for determining rice plant response to high night temperature stress

Plant height and the numbers of tillers and leaves were recorded at harvest. Daily observations were made for the appearance of panicles. At harvest, leaves were separated from the stems and leaf area was measured using a CI-251 area meter (CID Inc., Camas, Washington, USA). During the rice plant vegetative stage, leaf photosynthetic rate, internal CO_2 concentration and respiration rate were measured using LI-6400 portable photosynthesis system (LI-COR Inc., Lincoln, Nebraska, USA). Leaf nitrogen content was determined using a FP-528 Nitrogen/Protein analyzer (LECO Corporation, St. Joseph, Michigan, USA) and was expressed as percentage (%; w/w). Total chlorophyll content, pollen germination and spikelet fertility were determined using the procedures from Mohammed & Tarpley (2011a), and relative injury to the membrane and total antioxidant capacity were determined using procedures from Mohammed & Tarpley (2009b).

2.2 Effects of high night temperature on plant morphology

Plant morphology deals with plant development, form, and structure. In a narrow sense, plant morphology refers to the external appearance of the plant. For example plant height and the numbers of tillers, leaves, panicles and grains are referred as rice morphological parameters. The effects of HNT on plant morphology vary from negative to positive, including no effect. Seddigh & Jolliff (1984) reported that HNT promoted early vegetative growth and hastened physiological maturity, but did not affect morphological characteristics such as plant height, number of auxiliary branches and number of nodes in soybean. The HNT has no effect on rice (cultivar Cocodrie which is a japonica cultivar) plant height and number of tillers but can increase number of leaves and leaf area (Fig. 1). However, Cheng et al. (2009) and Yoshida et al. (1981) reported reduction in plant height, number of tillers and total biomass for rice cultivar 'IR 72' (indica cultivar) as a result of HNT. Similar results were seen in redstem stork's bill (*Erodium cicutarium* L.) for which HNT decreased number of branches, leaf area and plant dry matter (Blackshaw & Entz, 1995). The decreased production of plant dry matter was directly correlated with decreased production of photosynthates.

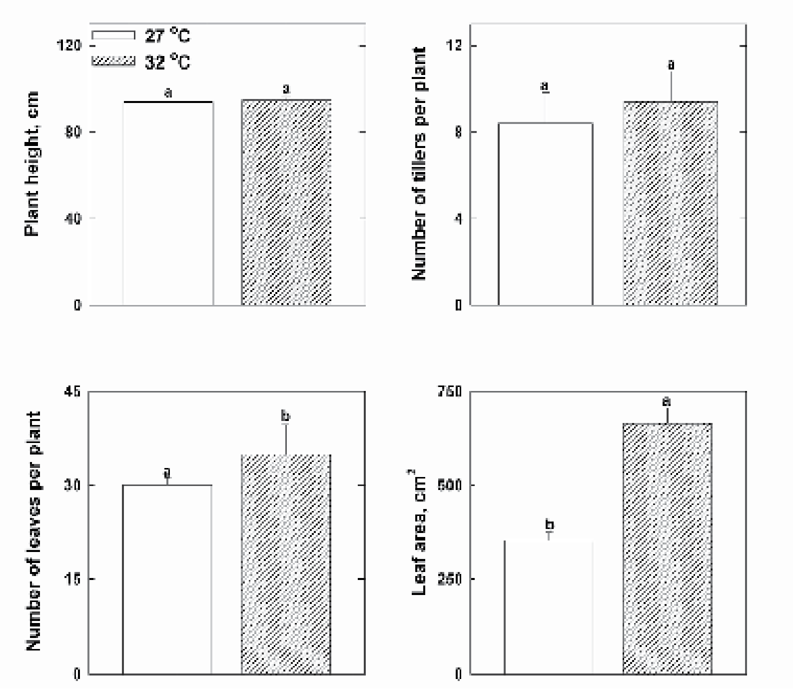

Fig. 1. Effects of high night temperature on rice morphology. Each bar represents average ± S.E. Different letters indicate means are significantly different at the P<0.05 level.

2.3 Effects of high night temperature on plant physiology

Plant physiology deals with the functioning of plants and is closely related with plant morphology. Fundamental processes such as photosynthesis, respiration, plant water and nutrition status, plant hormone functions and translocation of photosynthates are encompassed in plant physiology. Photosynthesis is a complex process and leaf photosynthetic rates depend upon leaf chlorophyll and nitrogen content, photosystems, stomatal characteristics and enzyme activities. The environmental stresses have a direct effect on leaf photosynthetic rates and an indirect effect through their effects on leaf chlorophyll and nitrogen content, stomatal characteristics and enzyme activities. The HNT had positive and negative effects, including no effect, on the following day's photosynthetic rates (Frantz et al., 2004; Mohammed & Tarpley 2009a). Rice leaf photosynthetic rates showed negative correlation with HNT (Fig. 2). The decrease in photosynthetic rates as a result of HNT was accompanied with decrease in leaf chlorophyll and leaf nitrogen content in rice (Fig. 2). Premature loss of chlorophyll as a result of heat stress has been noticed in many crop species (Guo et al., 2006; Reynolds et al., 1994). Damage to the photosynthetic electron transport particularly at the site of photosystem II (Havaux and Tardy, 1996) and inhibition of photosynthetic CO_2 fixation (Sayed et al., 1989; Yamane et al., 1997) as a result of heat stress can also reduce photosynthetic rates, thus leading to decrease in yield. Apart from decreases in photosynthetic rates, increased respiration rates can also decrease the crop yield.

Plant respiration is one of the important processes in terms of understanding plant growth and development when subjected to stress. Increase in respiration from climate warming is of serious concern as respiratory processes can consume a larger portion of total photosynthates (Paembonan et al., 1992). On average, the carbon lost from respiratory metabolism within an individual plant ranges between 30 and 70% of the carbon gained through photosynthesis (Peterson & Zelitch, 1982). Respiration is typically partitioned into the functional components of construction (growth), maintenance and ion uptake to facilitate our understanding of the impact of the environment on respiratory processes (Amthor, 1986; Farrar, 1985; Lambers, 1985). Maintenance respiration is mainly associated with turnover of proteins and lipids and maintenance of ion concentrations across membranes (Penning de Vries, 1975). It is the most responsive to environmental changes among the functional components of respiration (Ryan, 1991). At high temperatures, the cost of maintenance increases to support protein turnover and to maintain active ion fluxes across the membranes (Penning de Vries, 1975), thereby increasing maintenance respiration. An increase in NT from 27 ^{o}C to 32 ^{o}C increased respiration rates by 40% in rice leaves (Fig. 2). Previous studies on rice, cotton, lettuce (*Lactuca sativa* L.), tomato and soybean indicated an increase in maintenance respiration with warmer nights (Frantz et al., 2004; Loka & Oosterhuis, 2010, Mohammed & Tarpley, 2009b). Hence, HNT can stimulate respiration rates, thereby negatively affecting the yield (Zheng et al., 2002). The other consequence of increased respiration is increased production of ROS.

The production of ROS is an unavoidable consequence of aerobic respiration, with the majority of the ROS produced in photosynthetic tissue (mostly leaves) in the dark by mitochondrial electron transport chain activity (miETC) (McDonald & Vanlerberghe, 2005). The production of ROS by mitochondria has been shown to increase in many plants as a result of biotic and abiotic stresses (McDonald & Vanlerberghe, 2005; Moller, 2001). An increase in NT increases maintenance respiration and thus increases production of ROS. Physiological injury due to heat stress has been associated with increases in oxidative damage to the membrane in plant species (Larkindale & Knight, 2002). Plants increase maintenance respiration to support repair mechanisms of the membranes due to oxidative damage (Amthor & McCree, 1990). Thus, an increase in respiration occurs 1) with an increase in temperature (Huang et al., 1998) and 2) to support repair mechanisms of the membranes due to oxidative damage (Amthor & McCree, 1990). In addition, ROS interferes with photosynthesis and respiration by disrupting water, ion, and organic solute movement across plant membranes by affecting membrane stability (Christiansen, 1978).

Destabilized membranes are leaky membranes, thus interpreting the amount of electrolytic leakage from the membrane can be used as an indicator of cell membrane stability (Sullivan & Ross, 1979). Many studies have examined stability loss of the membranes subjected to environmental stresses by measuring electrolytic leakage from the membranes (Blum & Ebrercon, 1981; Dexter, 1956; Ibrahim and Quick, 2001; Ismail and Hall, 1999; Sullivan, 1972). An increase in NT from 27 °C to 32 °C increased injury to the membrane by 60% in rice leaves (Fig. 2). Similar results of increased injury to the membrane as a result of heat stress were seen in many crop species (Ibrahim & Quick, 2001; Ismail & Hall, 1999;, Martineau et al., 1979; Mohammed & Tarpley, 2009b). The properties of the photosynthetic system, including key enzymes and thylakoid membrane activities depend on the stability of membranes (Björkman et al., 1980). Moreover, it is well known that a functional cell-membrane system is central to crop productivity and acclimation of plants to high temperature (Raison et al., 1980). Mohammed & Tarpley (2009b) and Reynolds et al. (1994) positively associated membrane stability with yield performance under heat-stressed conditions in rice and wheat.

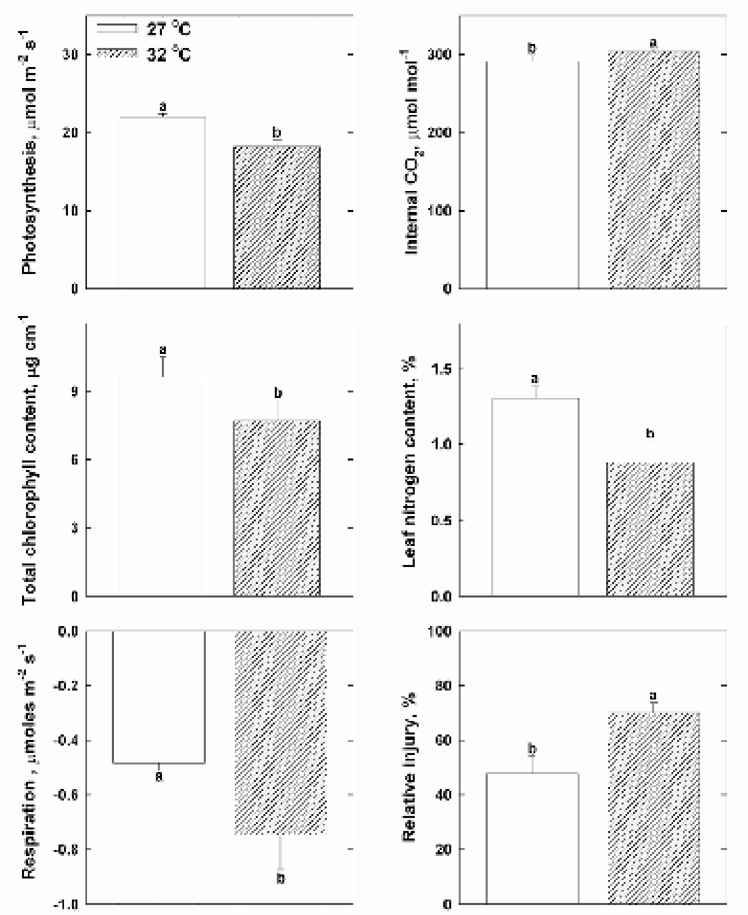

Fig. 2. Effects of high night temperature on rice physiology. Each bar represents average ± S.E. Different letters indicate means are significantly different at the P<0.05 level.

2.4 Effects of high night temperature on yield and yield-related parameters

The reproductive phase is relatively more sensitive than the vegetative phase to heat stress in many crop species (Hall, 1992). Moreover, differential temperature sensitivity for reproductive and vegetative growth has been reported in rice (Baker et al., 1992), soybean (Baker et al., 1989), wheat (Mitchell et al., 1993) and many other crops. Warrag & Hall (1984) reported that HNT induced male sterility and excessive floral abscissions in cowpea, whereas high day temperature had no adverse effect. The HNT can decrease crop yields by decreasing crop growth duration, suppressing floral bud development and decreasing pollen production and viability (Ahmed & Hall, 1993; Mohammed & Tarpley, 2009a; Prasad et al., 1999; Prasad et al., 2006). Increase in NT from 27 °C to 32 °C decreased crop growth duration by 2 days, as indicated by emergence of 1st panicle, in rice (Fig. 3). Decreased crop duration due to HNT decreases the time for carbohydrate accumulation, thus decreasing the yield (Cantarero et al., 1999). Badu-Apraku et al. (1983) attributed dramatic yield loss under high temperatures during the period of grain filling to sucrose availability (Afuakwa et al., 1984) and activity levels of enzymes involved in starch and sugar metabolism (Singletary et al., 1994). Moreover, the suppression of floral buds and flowering under HNT was also attributed to a shortage of photosynthetic assimilates supplied to the floral buds (Guinn, 1974), and/or an inability of floral buds to mobilize carbohydrates under heat stress (Dinar & Rudich, 1985). Decreased pollen germination due to heat stress has been noticed in many crop species (Hall, 1992; Matsui et al., 2001; Mohammed & Tarpley, 2009a). This decrease in pollen germination at high temperatures is due to poor anther dehiscence and pollen reception (Prasad et al., 2006), reduced pollen swelling and decreased anther pore size (Matsui & Kagata, 2003).

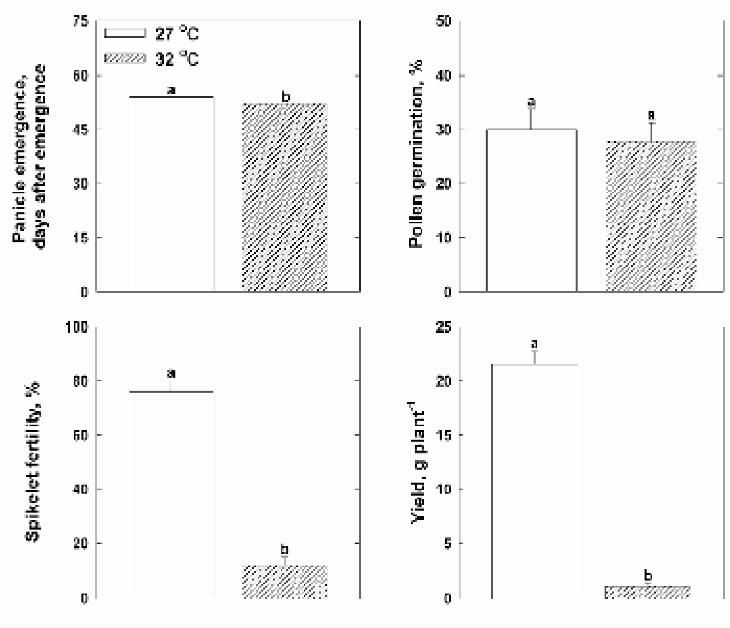

Fig. 3. Effects of high night temperature on rice yield-related parameters. Each bar represents average ± S.E. Different letters indicate means are significantly different at the P<0.05 level.

In most cereal crops, spikelet fertility, described as the ratio between filled grains and total grains, decreased with decrease in pollen germination. Increase in NT from 27 °C to 32 °C decreased spikelet fertility by 70% in rice (Fig. 3). Apart from pollen germination, hormonal balance in the sink (Micheal & Beringer, 1980) and/or availability and transportability of photosynthates to the sink from the source (Afuakwa et al., 1984) and/or inability of floral buds to mobilize carbohydrates (Dinar & Rudich, 1985) and/or altered activities of starch and sugar biosynthesis enzymes (Keeling et al., 1994; Singletary et al., 1994) can govern the spikelet fertility at high temperatures. The capacity to survive heat stress varies with plant species, genotype and developmental stage. The PGR provide an option to protect the plants from heat stress, thus providing sustainability for crop productivity.

3. Plant growth regulators

Genetic improvement and the modification of agronomic practices can be beneficial for crop adaptation to future climate conditions. However, these approaches are more applicable for long-term episodes of heat stress. The use of agrochemicals, especially those with PGR capabilities, for the prevention and/or amelioration of various environmental stresses, such as those resulting from global climatic change, is a viable approach to make crop production more resilient to short-term episodes of heat stress. Plant growth regulators are natural or synthetic chemical compounds that are used to promote or inhibit plant growth and development or alter specific physiology or metabolic factors. Like plant hormones, small concentrations of PGRs are enough to influence plant growth and development. In recent years, numerous PGRs have been developed to promote crop production under stress conditions. Glycine betaine, SA, vitamin E, proline and choline are some of the agrochemicals which can induce stress-tolerance (thermotolerance, drought tolerance, cold tolerance and/or salinity tolerance) in various crop plants. In this chapter, we focus on the beneficial effects of GB and SA application against heat stress on crop production.

Oxygen is potentially toxic to all organisms because metabolism and environmental stresses generate ROS from the oxygen. Under normal physiological conditions, the toxic effects of ROS are minimized by enzymatic and non-enzymatic antioxidants (Kreiner et al., 2002). Under stress conditions, oxidant levels overwhelm the antioxidant levels leading to cell damage (Kreiner et al., 2002). Plants exposed to environmental stress, such as heat, cold, drought and salinity produce ROS, which damage macromolecules and cell membranes (Zhang & Kirkham, 1996). Angiosperms possess several enzymatic and non-enzymatic scavenging systems to minimize deleterious effects of ROS. These include lipid-soluble antioxidants (e.g. α-tocopherol and β-carotene), water-soluble reactants (e.g. ascorbic acid and glutathione), and enzymatic antioxidants (e.g. superoxide dismutase, catalase and enzymes of the ascorbate and glutathione cycle) (Zhang & Kirkham, 1996). Glycine betaine and SA are synthesized in the plants and play important but different, roles in preventing oxidative damage to the membranes (Bowler et al., 1992; Demiral & Turkan, 2004) and inducing theromotolerance in plants subjected to stresses (Ashraf & Foolad, 2007; Caldas et al., 1999; Farooq et al., 2008a, 2008b; Larkindale & Huang, 2004; Mohammed & Tarpley, 2009b; Pan et al., 2006; Raskin, 1992). The commercial availability of GB and SA provides potential crop-management options to reduce crop heat stress events.

Glycine betaine, an important osmoprotectant is an amino-acid derivative that is naturally synthesized and accumulates under stress conditions in some plants (Bohnert & Jensen, 1996; Demiral & Turkan, 2004). It enhances stress tolerance by protecting enzymes (Paleg et al., 1981), photosystem II (Allakhverdiev et al., 1996), membrane integrity and antioxidant status of the plant (Mohammed & Tarpley, 2009b). Glycine betaine may also protect plants from environmental stresses indirectly via its role in signal transduction and ion homeostasis (John, 2002; Yilmaz, 2004). It regulates signal transduction and ion homeostasis by affecting MAP kinases, and expression of many genes related to signal transduction (John, 2002). Exogenous application of GB improved growth, survival and induced stress tolerance in many crop species (Diaz-Zorita et al., 2001; Harinasut et al., 1996; Rajasekaran et al., 1997) and also increased total antioxidant capacity and antioxidant enzyme activities (Farooq et al., 2008a; Mohammed & Tarpley, 2009b).

Salicylic acid is an endogenous plant growth regulator of phenolic nature and is considered to be a potent plant hormone because of its diverse regulatory roles in plant metabolism (Raskin, 1992). It plays an important role in the regulation of plant growth, development and responses to abiotic and biotic stresses (Raskin, 1992; Senaratna et al., 2000; Yalpani et al., 1994) by affecting photosynthetic rate, stomatal conductance, transpiration, ion uptake and transport, respiration rates, membrane stability, antioxidant capacity and antioxidant enzyme activities (Farooq et al., 2008a; Harper & Balke, 1981; Khan et al., 2003; Mohammed & Tarpley, 2009b). In addition, SA is considered to be an important signaling molecule involved in stress tolerance. It also promotes pathogenisis-related (PR) gene expression and induces systemic acquired resistance (SAR) in plants (Ryals et al., 1994). Besides providing disease resistance to the plants, SA can modulate plant responses to a wide range of oxidative stresses (Shirasu et al., 1997). It plays an essential role in preventing oxidative damage in plants by detoxifying superoxide radicals (Bowler et al., 1992) and by altering antioxidant capacity and antioxidant enzyme activities in plants (Chen et al., 1997; Dat et al., 1998, Fodor et al., 1997; Larkindale & Huang, 2004; Mohammed & Tarpley, 2009b; Rao et al., 1997; Wang & Li, 2006). Plants pre-treated with SA have shown increased thermotolerance (Larkindale & Knight, 2002).

3.1 Effects of plant growth regulators on plant morphology and physiology under high night temperature

Exogenous application of PGRs on plants under high night temperatures have shown positive, negative or no effect on plant morphology. Exogenous foliar application of GB or SA did not affect plant height in rice (Fig. 4). However, Farooq et al., (2008a, 2008b) state that seed priming of maize (*Zea mays* L.) with GB or SA increased shoot length, root length and biomass production. Increase in plant height as a result of SA application is due to increased cell enlargement, endoreduplication and/or cell division (Kang et al., 2007; Vanacker et al., 2007).

Glycine betaine and SA have profound effects on crop production through their effects on crop physiology. Foliar application of GB or SA increases leaf photosynthetic rates and decreases internal CO_2 concentration, respiration rates and membrane injury in rice (Fig. 5). Similar results were seen in other crop species and growth conditions where application of GB or SA increased photosynthetic rates and decreased respiration rates and injury to the membranes (Farooq et al., 2008a; Khan et al., 2010; Zhou et al., 1999).

In rice, application of GB or SA did not affect leaf chlorophyll or nitrogen content (Fig. 5). However, studies have shown that exogenous application of GB stabilizes pigments and prevents water oxidation and photooxidation (Cha-um et al., 2006, Sakamoto et al. 1998). Stabilization of pigments (chlorophyll and carotenoids) aids in light energy capture as required for photosynthesis. Several studies have reported that application of GB aids in protecting the photosynthetic machinery of the plant organelles by stabilizing the ultrastructure of the chloroplast, photosystem-II reaction centers and maintaining the oxygen-evolving machineries (Allakhverdiev et al., 2003; Busheva & Apostolova, 1997; Lee et al., 1997; Makela et al., 2000; Pospisil & Dau 2000; Sakamoto & Murata, 2000). On the other hand SA increases photosynthetic efficiency by increasing pigment concentrations and protecting photosystem function via activation of antioxidant defense systems as a signaling molecule (Dat et al., 1998; Ervin et al., 2005; Senaratna et al., 2001). The other physiological parameters such as respiration rates, transpiration rate and injury to leaf membrane decreased with application of GB or SA (Mohammed & Tarpley, 2011b). Studies have reported antitranspiration effects of GB and SA applications in crop species suggesting that GB and SA play an important role in controlling stomatal opening and closing under stress conditions (Cha-um et al., 2006; Khan et al., 2010; Larque-Saavedra, 1978). The most important effect of PGR's on crop production is through their ability to maintain the integrity of the membranes. The functional cell-membrane system is central to crop productivity. Stable membranes facilitate free movement of ions and water across the membrane and provide a favorable environment for enzymes and thylakoid membrane activities (Björkman et al., 1980). Several studies have reported that GB or SA application can maintain membrane integrity under stress conditions (Bohnert & Jensen, 1996; Farooq et al., 2008a, 2008b; Hussain et al., 2008; Mohammed & Tarpley, 2011b; Pan et al., 2006) by up regulating antioxidant enzyme activities and total antioxidant capacity (Demiral & Türkan, 2004; Farooq et al., 2008a, 2008b; He et al., 2005; Mohammed & Tarpley, 2009b).

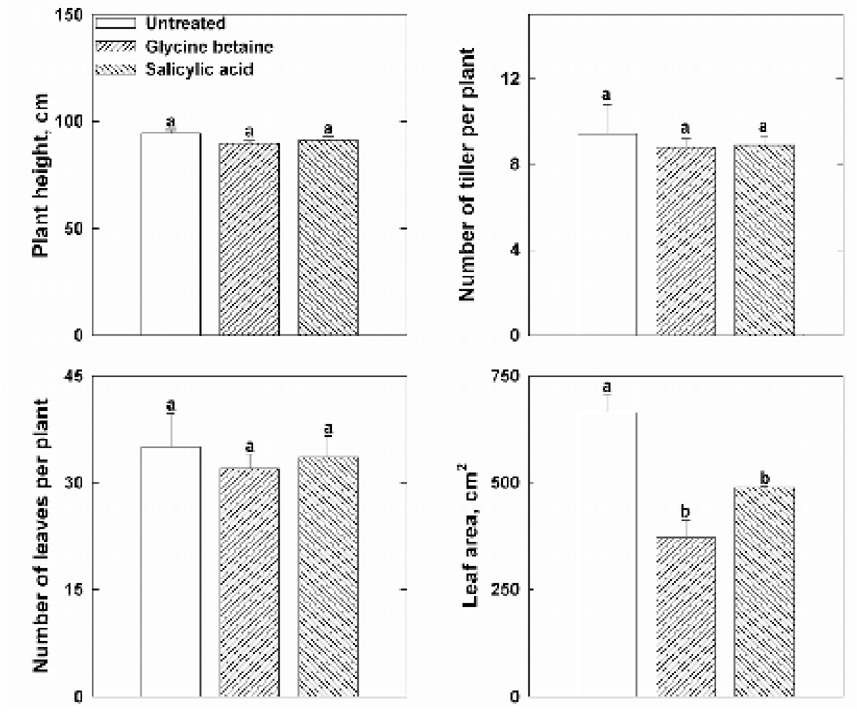

Fig. 4. Effects of glycine betaine and salicylic acid on rice morphology under high night temperature. Each bar represents average ± S.E. Different letters indicate means are significantly different at the P<0.05 level.

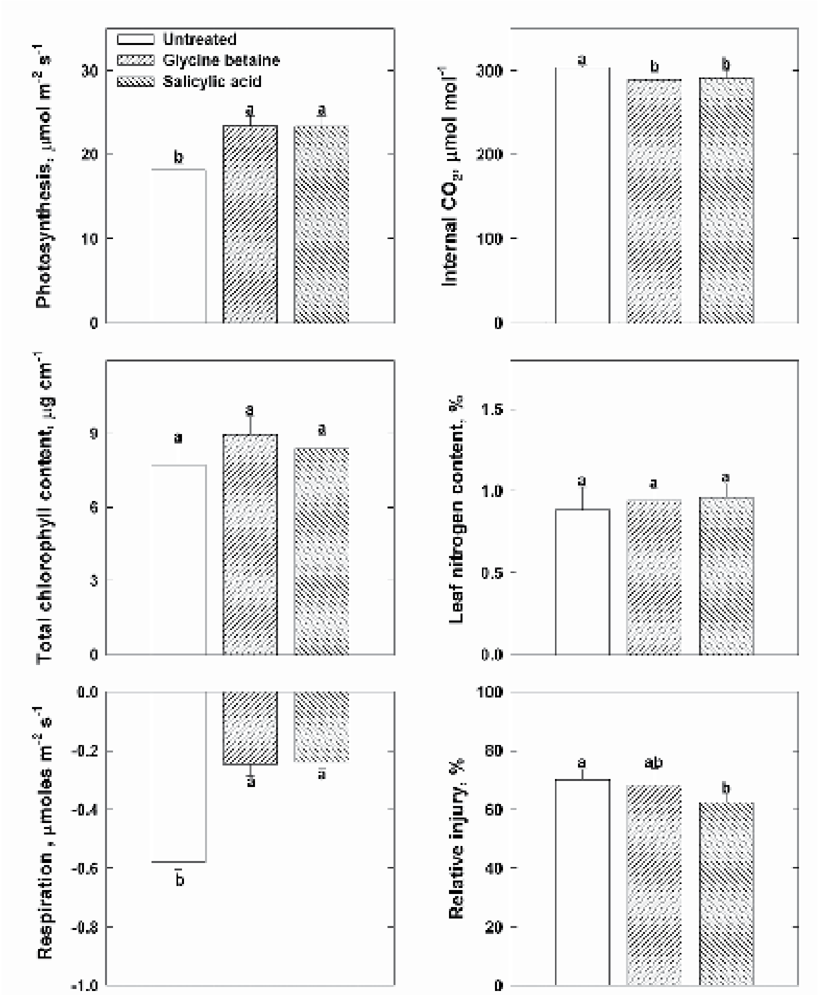

Fig. 5. Effects of glycine betaine and salicylic acid on rice physiology under high night temperature. Each bar represents average ± S.E. Different letters indicate means are significantly different at the $P<0.05$ level.

3.2 Effects of plant growth regulators on plant antioxidant enzyme activities and total antioxidant capacity under high night temperature

The antioxidant status of the plant is closely associated with its stress tolerance (Smirnoff, 1995). The severity of ROS-induced damage depends upon the antioxidant status of the plant and activities of antioxidant enzymes such as superoxide dismutase (SOD), ascorbate peroxidase (AP), catalase (CAT) and glutathione redutase (GR). Many studies have shown an increase in endogenous antioxidant levels as a result of exogenous application of GB or SA (Chen et. al., 1997; Diaz-Zorita et. al., 2001; Fang et al., 2009; Mohammed & Tarpley, 2009b). In rice, exogenous application of GB or SA increased total antioxidant capacity under high night temperature (Fig. 6). These increases in the levels of endogenous antioxidant are due to increases in antioxidant enzyme activities (Demiral & Türkan, 2004; Farooq et al., 2008a, 2008b; He et al., 2005; Khan et al., 2010).

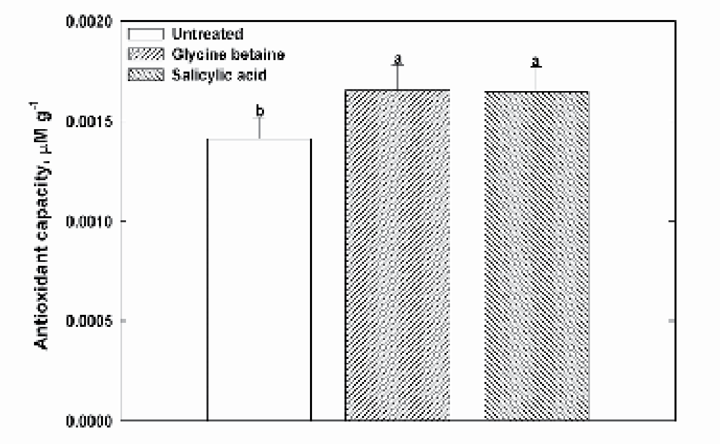

Fig. 6. Effects of glycine betaine and salicylic acid on total antioxidant capacity under high night temperature. Each bar represents average ± S.E. Different letters indicate means are significantly different at the P<0.05 level.

3.3 Effects of plant growth regulators on yield and yield-related parameters under high night temperature

Rice phenology under high night temperature was not altered by exogenous application of GB or SA as indicated by 1st panicle emergence date (Fig. 7). However, previous studies by Oota (1975) and Datta & Nanda (1985) showed that SA application induces early flowering in duckweeds (*Lemna gibba* L.) and chenna millet (*Panicum miliaceum* L.). Exogenous application of GB or SA increased spikelet fertility in rice (Fig. 7). The increase in spikelet fertility was due to increased photosynthesis, and decreased respiration and injury to the membrane stability as a result of GB or SA application. Exogenous application of GB or SA increases stability of the membranes as a result of increased antioxidant capacity of the plants. The enhanced membrane stability is responsible for increased photosynthesis and decreased respiration, which in turn increases crop production. In a nutshell, exogenous applications of GB or SA have been shown to increase stress tolerance, and often enhance plant growth and final crop yield under stress conditions, including HNT.

4. Conclusion

Yield, the final manifestation of all the physiological processes, decreased due to high night temperatures. The decrease in crop yields as a result of HNT was due to increased respiration and decreased photosynthesis and membrane stability. The decrease in photosynthesis was associated with decreases in photosynthesis-governing parameters such as stomatal conductance, internal CO_2 concentration, leaf chlorophyll content and leaf nitrogen, as a result of HNT. Moreover, decreased crop growth duration, pollen production and viability also contributed to decreased yields under HNT. Exogenous application of PGRs such as GB and SA increased production of photosynthates and decreased consumption of photosynthates and injury to the membrane, thereby increasing crop productivity under HNT. The exogenous application of GB and SA increases antioxidant levels, thereby protecting the membranes and enzymes against heat-induced ROS-mediated degradation, thus increasing crop productivity. However, there is a significant variation in

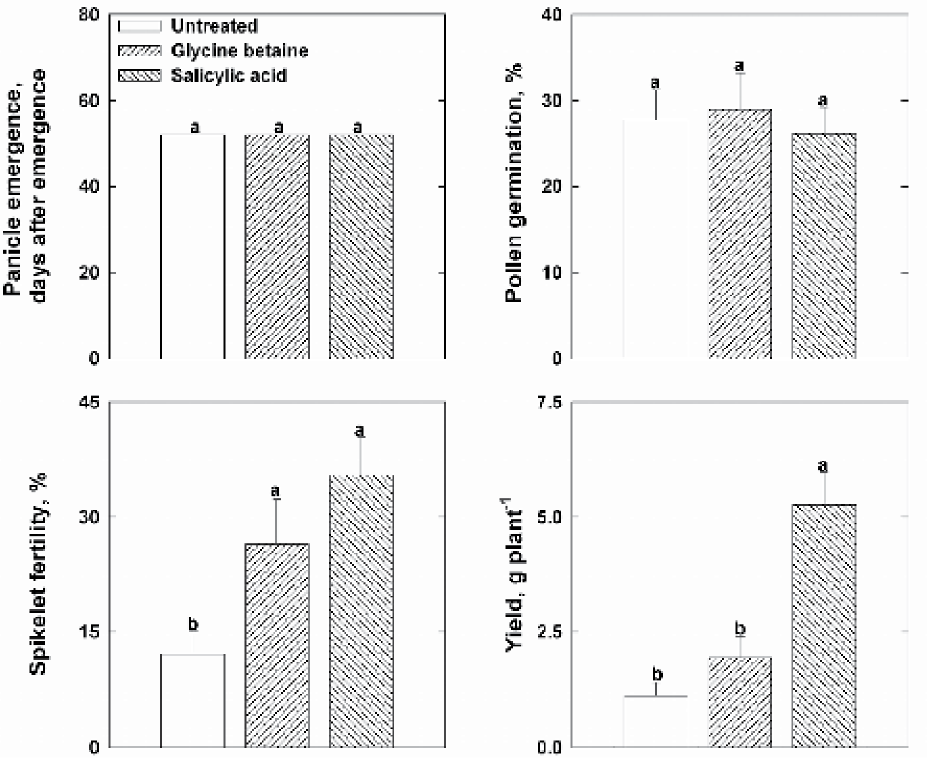

Fig. 7. Effects of glycine betaine and salicylic acid on rice yield-related parameters under high night temperature. Each bar represents average ± S.E. Different letters indicate means are significantly different at the $P<0.05$ level.

response to exogenous application of PGRs such as GB and SA among different plant species. This varied response among the plant species is due to 1) plant quantitative response to exogenous application of PGRs such as GB and SA at different stages of plant development, 2) plant exhibition of different responses to PGRs such as GB and SA at different stages of plant development and 3) variation in the effective concentration of a particular PGR among species. The PGRs such as GB and SA provide an option to protect the plants from different stresses like high day temperatures, high night temperature, drought and salinity, however, over-application of the PGRs such as GB and SA may be toxic to some plants resulting in growth inhibition or yield reduction.

5. Acknowledgment

We thank Texas Rice Belt Warehouse and Texas Rice Research Foundation for their support throughout this work.

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Part 5

Global Warming and Ecological Changes: Impacts on Forests, Mangroves and Sea Ecosystems

11

Effects of Temperature and Light Conditions on Growth of Current-Year Seedlings of Warm-Temperate Evergreen Tree Species and Cool-Temperate Deciduous Tree Species

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1. Introduction

It is suggested that global warming affects plant distribution along latitudinal and altitudinal gradients because vegetation changes with thermal conditions. Simulation studies predicted that global warming largely affects plant distribution (e.g., Morin et al., 2008). Actually, vegetation change during several decades has been observed (Penuelas et al., 2007; Lenoir et al., 2008). By contrast, some other studies did not observe vegetation changes (Holtmeier & Broll, 2007; Harsch et al., 2009). Interpretation of results of simulation models also needs caution because simulation results are different according to modeling methods even for same species (Thuiller, 2003). Therefore, there is still uncertainty of effects of global warming on plant distribution.

Plant distribution is determined by integrated demographic processes such as seed dispersal, seed germination, growth and survival of individual plants. Since early demographic phase such as seedling establishment is more susceptible to environmental conditions than the adult phase (Kullman, 2002), it is important to clarify effects of temperature on seedling growth to predict effects of global warming on plant distribution. There are many experimental studies that examined effects of temperature on growth of tree seedlings (Danby & Hik, 2007; Hoch & Körner, 2009; Munier et al., 2010). For example, Yin et al. (2008) reported that seedling growth of *Betula albo-sinensis* increased in the warm condition with 0.51°C higher than the ambient air condition. Many experimental studies that examined effects of temperature were conducted at bright conditions (e.g. Danby & Hik, 2007; Way & Sage, 2008). However, most seedlings distribute in dark closed-canopy conditions in forests. Therefore, it is necessary to examine effects of temperature on seedling growth not only in bright conditions but also in dark conditions.

Plants plastically change morphology according to light conditions. For example, relative biomass allocation to leaves is greater in dark conditions than in bright conditions, accompanied with reduction of leaf mass per area (LMA) (Ellsworth & Reich, 1992; Gould, 1993; Niinemets et al., 1999; Takahashi et al., 2005). These morphological changes increase light capture per plant, which is an adaptive strategy in dark conditions. Thus, plants adapt to changing environments through morphological plasticity. This study compared growth responses to temperature and light conditions among three species with different climatically distribution ranges. This comparison is important to clarify effects of global warming on distribution shift of vegetation.

Central Japan is a latitudinal vegetation ecotone between warm-temperate evergreen broad-leaved forests and cool-temperate deciduous broad-leaved forests. Ishigami et al. (2003) simulated net primary production (NPP) of forests by the modified model of BIOME3 (Haxeltine & Prentice, 1996). They predicted that NPP of warm-temperate evergreen broad-leaved forests is greater than that of cool-temperate deciduous broad-leaved forests above the current northern distribution limit of warm-temperate evergreen broad-leaved forests if air temperature is increased by global warming. According to the simulation result of NPP, Ishigami et al. (2003) suggested that the northern distribution limit of warm-temperate evergreen broad-leaved forests will move to the north. However, the northern distribution limit would not move to the north easily because of competition with existing northern vegetation (Kohyama & Shigesada, 1995). Therefore, it is important to compare growth responses of seedlings to temperature and light conditions between warm-temperate evergreen broad-leaved species and cool-temperate deciduous broad-leaved species to clarify vegetation changes due to global warming.

It is considered that warm-temperate evergreen broad-leaved species cannot distribute in the cool-temperate zone due to low winter temperature, not due to low summer temperature for the growth (Kira, 1949). Cold winter temperature decreases photochemical efficiency of leaves in warm-temperate evergreen broad-leaved species (Aranda et al., 2005; Taneda & Tateno, 2005). Reduction of photochemical efficiency due to cold temperature is more conspicuous in bright conditions than dark conditions (Matsuki et al., 2003). Therefore, it is necessary to examine growth responses to temperature and light conditions not only during growth period but also during dormant period (winter) to clarify how temperature affects growth of warm-temperate evergreen broad-leaved species.

This study examined effects of temperature and light conditions on seedling growth of a warm-temperate evergreen broad-leaved species and two cool-temperate deciduous broad-leaved species to answer the following two questions.

(1) Do the warm-temperate evergreen and cool-temperate deciduous broad-leaved species grow more in higher temperature and light conditions?

(2) Do high temperature conditions mitigate reduction of photochemical efficiency in winter for the warm-temperate evergreen broad-leaved species?

2. Materials and methods

2.1 Study site

This study was conducted at the two sites in Nagano Prefecture, central Japan: the campus of Shinshu University (N36˚15′04′′, E137˚58′41′′, 630 m above sea level) in Matsumoto, and the Yatsugatake experimental forest (N35˚56′40′′, E138˚28′11′′, 1350 m a.s.l.) of Tsukuba University in Nobeyama (Fig. 1). The mean annual precipitation of Matsumoto was 1035.7 mm during 2000–2009. The mean annual temperature was 12.2˚C. The mean monthly

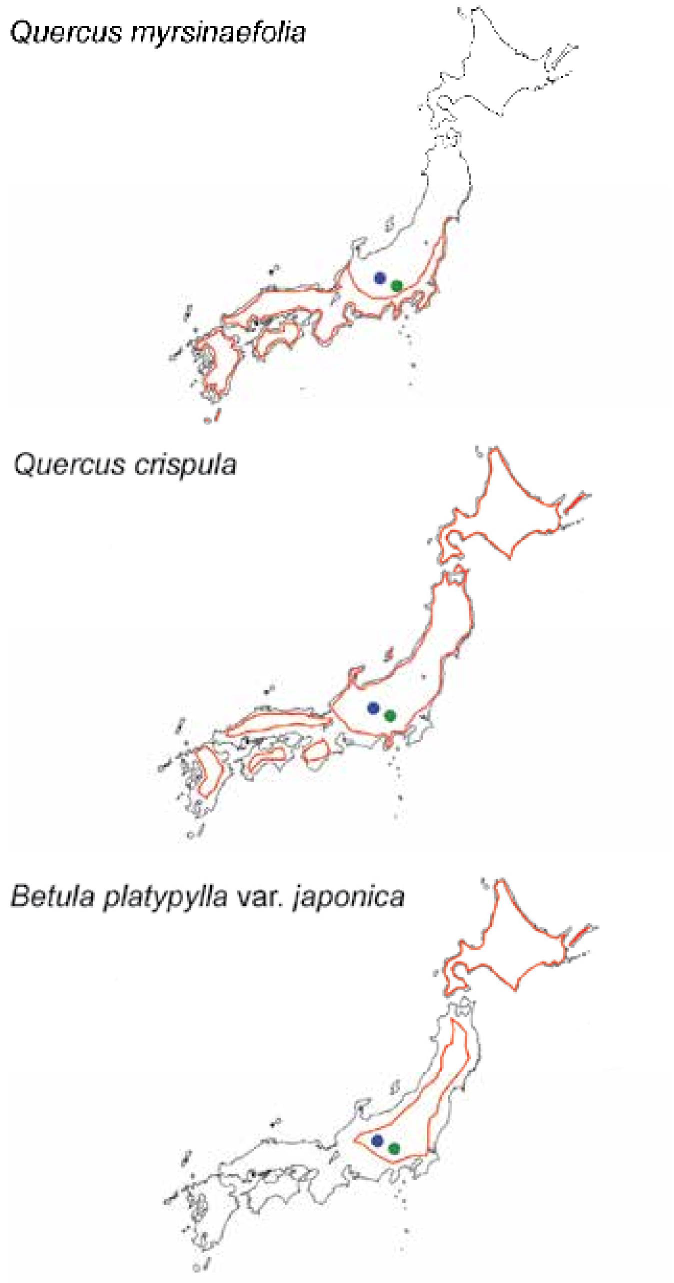

Fig. 1. Distributions (areas surrounded by red lines) of *Quercus myrsinaefolia*, *Q. crispula* and *Betula platyphylla* var. *japonica* in Japan. Distributions of the two *Quercus* species and *B. platyphylla* var. *japonica* were redrawn from Horikawa (1972) and Okuyama (1982), respectively. Blue and green dots indicate locations of two study sites, Matsumoto and Nobeyama, respectively.

temperatures in January and in August were –0.3 and 24.8°C, respectively. The mean annual precipitation of Nobeyama was 1435.3 mm during 2000–2009. The mean annual temperature was 7.2°C. The mean monthly temperatures in January and in August were –5.4 and 19.2°C, respectively.

2.2 Study species

This study examined a warm-temperate evergreen broad-leaved species (*Quercus myrsinaefolia* Blume) and two cool-temperate deciduous broad-leaved species (*Betula platyphylla* var. *japonica* Hara and *Quercus crispula* Blume) (Fig. 1). *Q. myrsinaefolia* is a shade-tolerant tall tree species that distributes in the northern part of warm-temperate zone (Horikawa, 1972). *B. platyphylla* var. *japonica* and *Q. crispula* are shade-intolerant and mid-shade-tolerant tall tree species, respectively (Samejima, 1979; Koike, 1988; Masaki et al., 1992). *B. platyphylla* var. *japonica* and *Q. crispula* often form pure stands after disturbances such as strong wind, forest fire and clear cutting (Samejima, 1979; Kamitani, 1993; Namikawa et al., 1997).

Q. myrsinaefolia distributes below 700 m a.s.l. in the warm-temperate zone, and the northern distribution limit is about N38° (Horikawa, 1972). Distribution of *Q. myrsinaefolia* is limited to below 500 m a.s.l. in the north of N36°. Although the southern part of Nagano Prefecture was the northern distribution limit of *Q. myrsinaefolia* (Horikawa, 1972), the distribution of *Q. myrsinaefolia* is recently observed in central part (Matsumoto area) of Nagano Prefecture probably because of escapes of seeds from planted *Q. myrsinaefolia* trees (Otsuka & Ozeki, 2008). *B. platyphylla* var. *japonica* distributes in central and northern Japan (Okuyama, 1981). *B. platyphylla* var. *japonica* distributes mainly at about 1000 m and 1300 m a.s.l. in Matsumoto and Nobeyama, respectively (Editorial Board of Flora of Nagano Prefecture, 1997). *Q. crispula* is one of the dominant species in cool-temperate deciduous broad-leaved forests, and widely distributes in the cool-temperate zone of Japan (Horikawa, 1972). *Q. crispula* distributes mainly at about 1000 m and 1300 m a.s.l. in Matsumoto and Nobeyama, respectively, like *B. platyphylla* var. *japonica*. Therefore, Matsumoto is the northern distribution limit for the warm-temperate evergreen species *Q. myrsinaefolia*, and Nobeyama is optimal thermal conditions for the two cool-temperate deciduous species *B. platyphylla* var. *japonica* and *Q. crispula*.

2.3 Seedling growth experiments

Growth experiments were conducted at Matsumoto and Nobeyama to examine effects of temperature and light conditions on the current-year seedling growth of *Q. myrsinaefolia*, *B. platyphylla* var. *japonica* and *Q. crispula*. A greenhouse experiment was also conducted at Matsumoto to make optimal temperature conditions for the warm-temperate evergreen *Q. myrsinaefolia* because Matsumoto is the northern distribution limit of this species. Windows of the greenhouse were opened in summer to avoid extreme rising of air temperature inside the greenhouse. Increase of air temperature in the greenhouse was 3°C on the average. Therefore, air temperature increased in the order of Nobeyama, Matsumoto and the greenhouse at Matsumoto. Nobeyama, Matsumoto and the greenhouse at Matsumoto are referred to T1, T2 and T3, respectively, in this study. Two light conditions (20% and 54% light) were set at each temperature condition by using shade cloth. 20% and 54% light conditions are referred to L1 and L2, respectively.

Species	Variables	T	L	T × L	*n*
Qm	Stem height	56.1^{***}	< 0.1	0.3	99
	Stem diameter	16.1^{***}	12.5^{***}	0.2	46
	Dry mass	24.2^{***}	15.1^{***}	1.5	46
	LMA	3.5^{*}	7.0^{*}	1.2	47
Qc	Stem height	46.2^{***}	3.1	1.3	94
	Stem diameter	18.0^{***}	36.2^{***}	1.6	94
	Dry mass	11.6^{***}	14.2^{***}	0.6	94
	LMA	32.4^{***}	67.4^{***}	0.4	93
Bp	Stem height	517.5^{***}	0.4	1.0	120
	Stem diameter	768.0^{***}	11.5^{***}	1.3	120
	Dry mass	595.9^{***}	49.5^{***}	8.3^{***}	117
	LMA	2.3	52.9^{***}	2.3	109

*: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$.

Table 1. ANOVA results of stem height, stem diameter, seedling dry mass and leaf mass per area (LMA) for *Quercus myrsinaefolia* (Qm), *Quercus crispula* (Qc) and *Betula platyphylla* var. *japonica* (Bp) to test three temperature conditions (T), two light conditions (L) and the interaction (T × L) on the four variables. *F*-values and the number of samples (*n*) are shown.

Seeds of *Q. myrsinaefolia*, *B. platyphylla* var. *japonica* and *Q. crispula* were collected in 2008. Seeds were sown in plastic pots (diameter 15 cm × height 13 cm) filled with horticulture soil and leaf mold. The number of pots was 20 for each light condition (L1 and L2) at each temperature condition (T1, T2 and T3) for each species. Seed sowing was conducted between late March and early April in 2009. However, seeds of *B. platyphylla* var. *japonica* were sown again at T1 in early June because seeds did not germinate. Pots were watered once a week or according to the need during the experiment period. All pots were randomly moved within each treatment once a week to minimize effects of pot position on seedling growth.

Seedlings of the three species were excavated and washed carefully in early October in 2009 after the cease of the current-year growth. In terms of *Q. myrsinaefolia*, only the half number of seedlings was excavated at each light and temperature condition, and the other seedlings were remained for the measurement of photochemical efficiency (see next paragraph). Stem diameter at the base and stem height were measured at the harvest for the three species. Seedlings were divided into stem, root and leaf, and then all leaves were scanned by using the free graphic software ImageJ (http://rsbweb.nih.gov/ij/) to measure total leaf area per seedling. Each organ was oven-dried at 80˚C for two days, and was weighed.

The ratio of light-induced variable to maximum fluorescence of chlorophyll (Fv/Fm) of *Q. myrsinaefolia* was measured as a surrogate for photochemical efficiency of PSII (Demmig-Adams et al., 1989). Photochemical efficiency was measured around the noon once a month from summer of 2009 to the next summer by using a chlorophyll fluorometer OS-30p (Opti-Science, NH, USA). The measurement was conducted after 30 min of dark acclimation.

Two-way ANOVA was done to examine effects of temperature and light conditions on stem height, stem diameter, LMA and seedling dry mass (including root) for the three species (*Q. myrsinaefolia*, *B. platyphylla* var. *japonica* and *Q. crispula*).

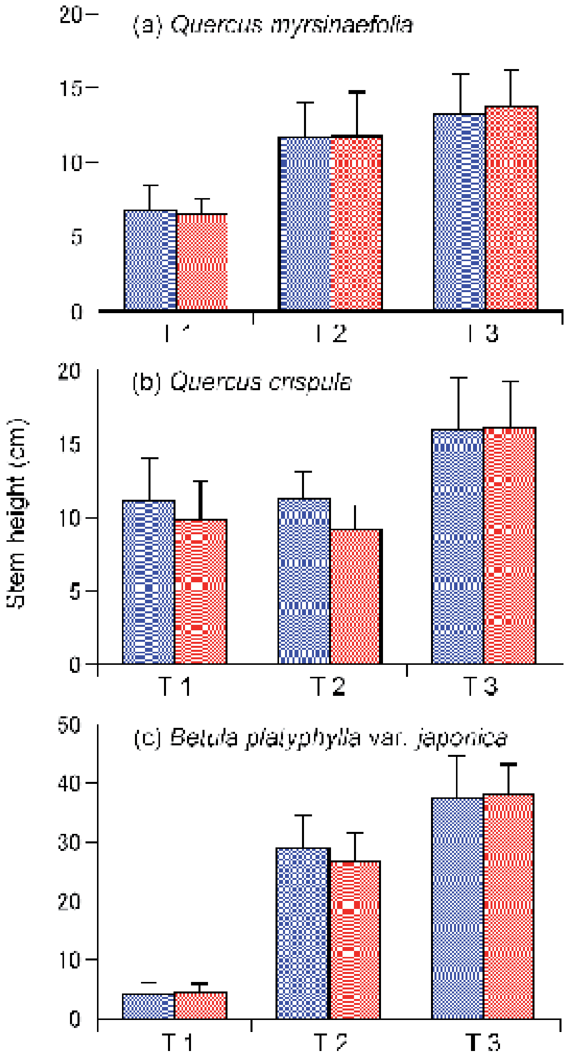

Fig. 2. Stem height for the three species at the three temperature and two light conditions. Blue and red bars indicate L1 and L2 light conditions, respectively. Mean values with positive standard deviations are shown.

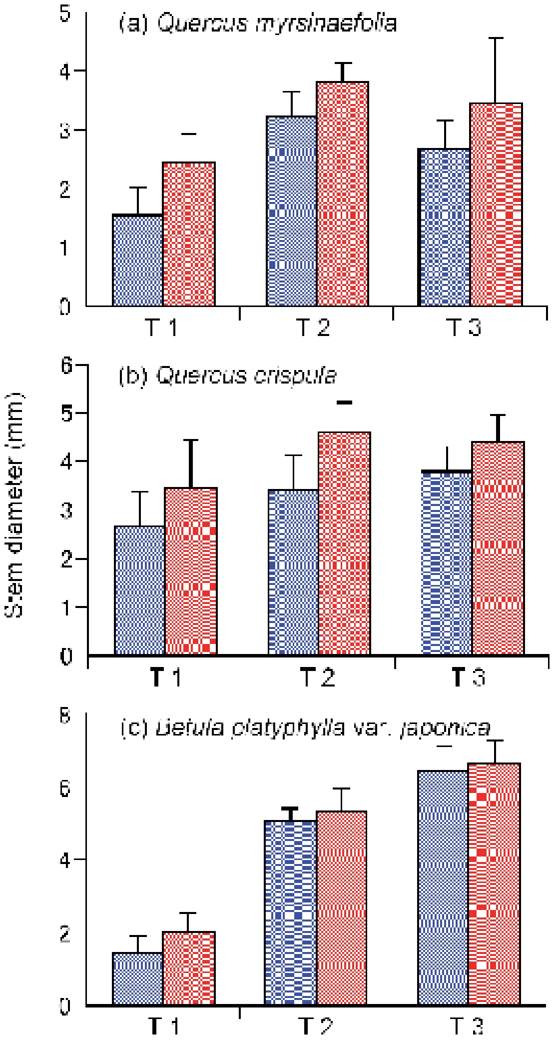

Fig. 3. Stem diameter for the three species at the three temperature and two light conditions. Blue and red bars indicate L1 and L2 light conditions, respectively. Mean values with positive standard deviations are shown.

3. Results

3.1 Growth of the three species

Effect of temperature on stem height was significant for the three species (Table 1), i.e., stem height was greater in higher temperature conditions, irrespective of light conditions (Fig. 2). However, stem height of *Q. crispula* was not different between T1 and T2 because of the shoot re-growth from the base after the shoot die-back in late May at T2. The difference in stem height of *Q. myrsinaefolia* between T2 and T3 was also not large (Fig. 2). Light conditions did not affect stem height for the three species (Table 1). By contrast, stem diameter of the three species was different not only among the three temperature conditions but also between the two light conditions (Table 1). Stem diameter of the three species was greater at L2 than L1 for each temperature condition (Fig. 3). Stem diameter was greater at T2 and T3 than T1 for *Q. crispula*. Stem diameter of *B. platyphylla* var. *japonica* increased in the order of T1, T2 and T3. However, stem diameter of *Q. myrsinaefolia* was slightly smaller at T3 than T2 for the two light conditions.

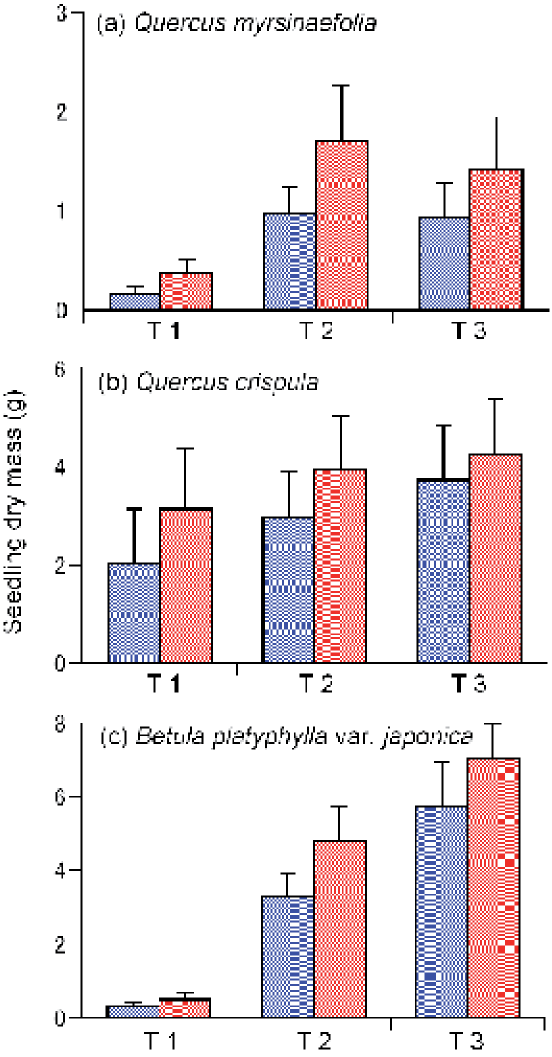

Fig. 4. Seedling dry mass for the three species at the three temperature and two light conditions. Blue and red bars indicate L1 and L2 light conditions, respectively. Mean values with positive standard deviations are shown.

Effects of temperature and light conditions on seedling dry mass were significant for the three species (Table 1), i.e., seedling dry mass was greater at higher temperature and brighter light conditions (Fig. 4). However, seedling dry masses of *Q. myrsinaefolia* at T3 were similar to and smaller than those at T2 for L1 and L2, respectively.

LMA was greater at L2 than L1 for the three species (Fig. 5, Table 1). LMA of *Q. myrsinaefolia* and *Q. crispula* was significantly different among the three temperature conditions (Table 1). Although LMA of the two species was greater at T2 than T1 and T3, the difference was not large (Fig. 5).

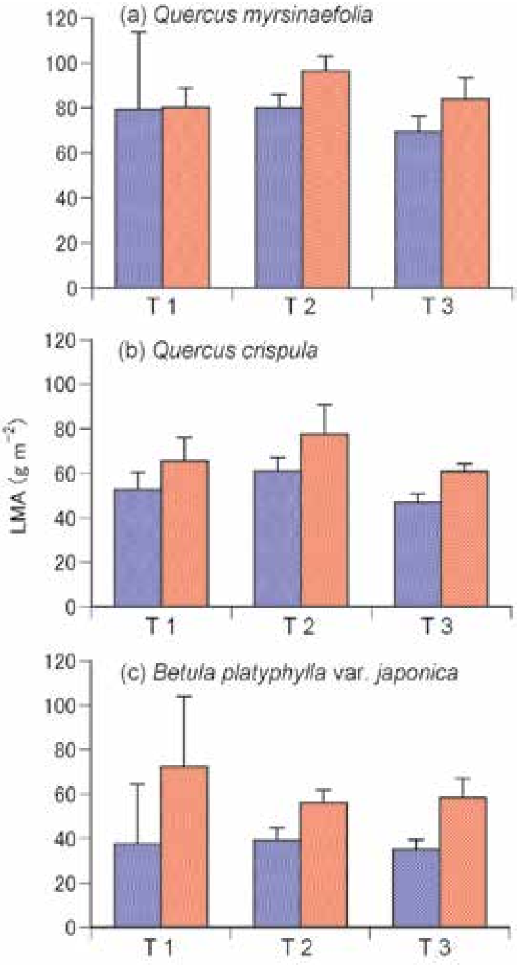

Fig. 5. Leaf mass per area (LMA) for the three species at the three temperature and two light conditions. Blue and red bars indicate L1 and L2 light conditions, respectively. Mean values with positive standard deviations are shown.

3.2 Photochemical efficiency of *Q. myrsinaefolia*

Values of photochemical efficiency (Fv/Fm) differed, according to temperature and light conditions and season (Fig. 6). In August of 2009, Fv/Fm values were similar between the two light conditions for the three temperature conditions. Although Fv/Fm value was about 0.8 at T3 in August, Fv/Fm values slightly decreased as temperature decreased from T3 to T1. Fv/Fm value was about 0.7 at T1 in August of 2009. Fv/Fm value decreased from autumn to winter in each temperature condition. This tendency was more conspicuous at L2 than L1 in each temperature condition. In addition, Fv/Fm value decreased to almost zero in February at T1, and all seedlings died by March (Fig. 7). By contrast, although Fv/Fm values decreased in winter at T2 and T3, these values increased again from spring to summer (Fig. 6) and the seedlings grew well by autumn (Fig. 8).

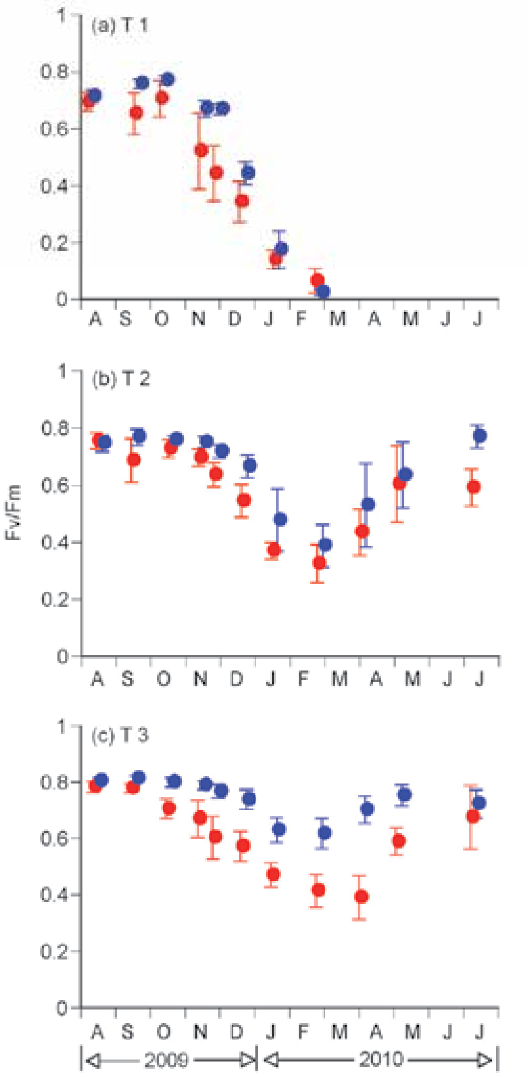

Fig. 6. Seasonal change of Fv/Fm of *Quercus myrsinaefolia* at three temperature and two light conditions. Blue and red circles indicate L1 and L2 light conditions, respectively. Mean values with standard deviations are shown.

4. Discussion

This study showed (1) that high temperature and light conditions increased the current-year seedling growth of the warm-temperate evergreen and the two cool-temperate deciduous species, except for the effect of light on stem height, and (2) that high temperature mitigated reduction of photochemical efficiency (Fv/Fm) of *Q. myrsinaefolia* in winter. Furthermore, winter temperature was so cold at T1 for *Q. myrsinaefolia* that all seedlings of this species died in winter. Therefore, this study showed that high temperature and light conditions increased the seedling growth of the three species and survival of *Q. myrsinaefolia* in winter.

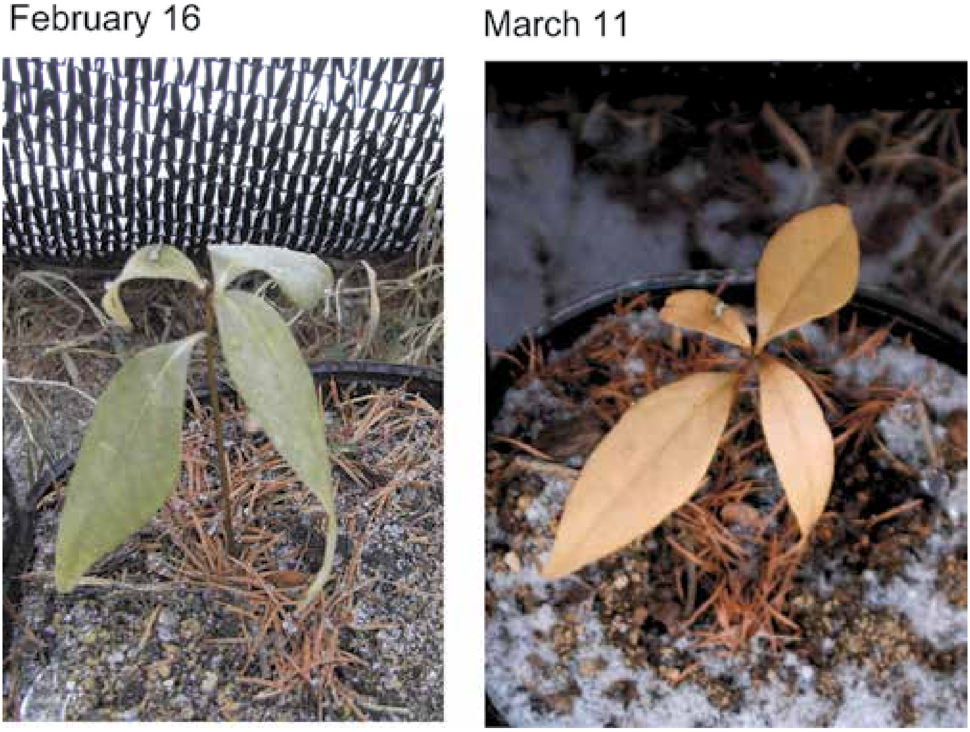

Fig. 7. A current-year seedling of *Quercus myrsinaefolia* at T1 with L1 light condition on February 16 and March 11, 2010. These photos were taken for a same seedling. Die-back was observed on March 11.

Light conditions did not affect stem height of the three species. Seiwa & Kikuzawa (1989) also reported that stem height of current-year seedlings was not different between bright and dark conditions for deciduous broad-leaved species with small seeds, while stem height was smaller in bright conditions than dark conditions for those of large seeds. Thus, stem height is not always taller in brighter conditions for current-year seedlings. This may reflect a survival strategy in forests. Litter accumulation on forest floor is a factor reducing seed germination and seedling survival (Goldberg & Werner, 1983). Therefore, the current-year seedlings germinated below litter layer have to grow over the litter layer. Furthermore, high growth of stem height is also advantageous for survival because of competition with other plants. Therefore, seedlings of the three species would preferentially grow stem height more than stem diameter in dark conditions as compared with bright conditions.

LMA was smaller at darker conditions for the three species at the three temperature conditions, which is advantageous for light capture efficiency per unit leaf mass. LMA of *Q. myrsinaefolia* and *Q. crispula* was also affected by temperature. Although LMA of the two species tended to be greater at T2 than T1 and T3, these differences were not large. By contrast, Woodward (1979) observed that low temperature increased LMA of *Phleum bertolonii* and *P. alpinum* because of increase of cell diameter. Unfortunately, this study did not examine cell diameter of leaves at the three temperature conditions. However, it is possible that light dominates the control of LMA of the current-year seedlings of the three species, compared with temperature.

Fig. 8. A 1-year old seedling of *Quercus myrsiaefolia* at T3 with L1 light condition on October 14, 2010.

Many previous studies about effects of temperatures on plant growth have been conducted so far in cold environments such as alpine region and tundra (Chapin & Shaver, 1985; Molau, 1997; Arft et al., 1999; Hollister & Webber, 2000). It is often reported that high temperature increases plant growth in such cold environments (Chapin & Shaver, 1996; Takahashi, 2005), meaning that cold temperature limits plant growth. Increase of temperature enhances photosynthetic rates in cold environments because of temperature dependency of photosynthetic rates (DeLucia & Smith, 1987). Furthermore, high temperature throughout a year expands the growth period of plants (Chmielewski & Rotzer, 2001). Nevertheless, seedling dry mass, stem height and diameter of *Q. myrsinaefolia* at T3 were similar to or smaller than those at T2 (the temperature conditions of the northern distribution limit). This suggests that temperature during the growth period is not a major factor limiting the growth of *Q. myrsinaefolia*. Northern distribution limits of warm-temperate evergreen broad-leaved forests tend to be determined by coldness in winter, not by warmth during the growth period (Kira, 1991). Thus, winter temperature may be important for the distribution of *Q. myrsinaefolia* along latitudinal gradients.

Increase of temperature clearly mitigated reduction of photochemical efficiency (Fv/Fm) of *Q. myrsinaefolia* during winter. This tendency was more conspicuous at brighter conditions. In forests, seedlings hardly grow in understory dark conditions, and grow vigorously in canopy gaps (Takahashi et al., 2001; Takahashi & Rustandi, 2006). Therefore, it is suggested that increase of photochemical efficiency of *Q. myrsinaefolia* by increase of temperature would enhance the growth in bright conditions. This effect may be large in the northern distribution limit of *Q. myrsinaefolia* because *Q. myrsinaefolia* co-dominates with many deciduous broad-leaved species there (Otsuka et al., 2004). Much light penetrates into forest floor in winter because of leaf fall of deciduous broad-leaved species. Understory seedlings and saplings of *Q. myrsinaefolia* can assimilate during winter after leaf fall of deciduous broad-leaved species, and the photosynthetic production during winter increases the growth and survival of *Q. myrsinaefolia* in the understory (Takenaka, 1986). Therefore, increase of winter temperature would enhance the growth and photochemical efficiency of *Q. myrsinaefolia* in the northern distribution limit.

The growth of the two cool-temperate deciduous broad-leaved species (*Q. crispula* and *B. platyphylla* var. *japonica*) was greater at T2 and T3 conditions than T1 (the optimal temperature conditions). Many studies showed that tree growth is greater nearer the southern and lower distribution limits along latitudinal and altitudinal gradients, respectively (Persson, 1998; Mäkinen et al., 2000; Li et al., 2003; Takahashi & Yoshida, 2009). Although the results of the previous studies were conducted in natural distribution ranges, the result of this study showed that tree growth increases in the temperature conditions warmer than the natural distribution range. Drought stress increases near southern and lower distribution limits (Buckley et al., 1997; Takahashi et al., 2003a; Adams & Kolb, 2005; Hart et al., 2010; Lebourgeois et al., 2010). On the contrary, increase of temperature prolongs the growth period (Sparks et al., 2000; Chmielewski & Rotzer, 2001; Fujimoto, 2008). Although increase of temperature induces drought stress to some extent, it would increase annual growth of plants by increasing annual carbon gain through increase of growth period.

The high growth of *Q. crispula* and *B. platyphylla* var. *japonica* at the two temperature conditions (T2 and T3) warmer than the current distribution range suggests that the natural distribution ranges of the two species are not determined by optimal temperature conditions alone (i.e., the concept of ecological niche). Although *Q. crispula* is a common species in old-growth deciduous broad-leaved forests (Masaki et al., 1992; Takahashi et al., 2003b), *Q. crispula* is recognized as a gap-dependent species (Yamamoto, 1989). It is reported that saplings of deciduous broad-leaved species distributed mainly in canopy gaps in an evergreen broad-leaved forest (Miura et al., 2001). In deciduous broad-leaved forests, understory saplings increases carbon gain by leafing before leaf expansion of canopy trees (Seiwa & Kikuzawa, 1996). However, understory of evergreen broad-leaved forests is dark conditions throughout a year, which have restricted saplings of deciduous broad-leaved species into canopy gaps. Therefore, actual distribution ranges are largely affected not only by temperature conditions but also by competition with other species (Takahashi, 2003).

5. Conclusion

This study predicted that high winter temperature mitigates the reduction of photochemical efficiency and reduces winter mortality of *Q. myrsinaefolia*. Furthermore, this study showed that increase of temperature enhances the growth of not only *Q. myrsinaefolia* but also *Q. crispula* and *B. platyphylla* var. *japonica*. It is possible that global warming intensifies competition between warm-temperate and cool-temperate broad-leaved species at their latitudinal ecotones. Therefore, it is unclear whether *Q. myrsinaefolia* will gain parts of the habitat now covered by *B. platyphylla* var. *japonica* and *Q. crispula* under global warming. This study examined only one warm-temperate broad-leaved species and two cool-temperate broad-leaved species, and the results of this study are not enough to show general responses of the two life forms to temperature and light conditions because of large variations in responses to temperature and light conditions within a life form (Parsons et al., 1994; Takahashi et al., 2003a; van der Werf et al., 2007). Therefore, it is necessary to analyze many species for each life form to clarify general growth responses to temperature and light conditions.

6. Acknowledgment

This study was partially supported by grants from the Ministry of Education, Culture, Sports, Science and Technology, Japan (Nos. 19580168, 22580160). We thank Dr. H. Kobayashi for constructive comments.

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12

Decreasing of Population Size of *Imperata cylindrica* Mangrove Ecotype and Sea-Level Rising

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1. Introduction

A very recent on-going trend worldwide is that sea level is found rising up due to global warming (Cazenave and Llovel, 2010). With one to two degrees temperature elevated, the polar iceberg will melt which eventually will lead to significant sea-level rise. There is increasing interest in knowing how mangrove population changes under sea-level rising. Mangrove forest (mangrove) is usually termed "kidney of the earth". The morphology and anatomy of these plants have unique structure, such as breathing roots, knee roots. Viviparous seedlings of the Rhizophoraceae plants further drift with the sea which results in implantation and reproduction. The origin of the name mangrove is derived from plants of a kind of mangrove tree *Rhizophora mucronata*. The plant's timber, tree trunks, branches, flowers are red. These trees grow in tropical and subtropical regions of rivers and coastal salt marshes, evergreen shrub or tree forest.

According to the literature, mangrove forests are mainly distributed in the western coastal estuary in Taiwan (Hsueh and Lee, 2000). Taiwan's largest and most well-known mangrove protected areas are in Danshui district, including Chuwei mangrove conservation area. These areas are along the Danshui River. The main object of the protected areas is *Kandelia* mangrove forests. *Kandelia candel* (L.) Druce is grouped into Rhizophoraceae *Kandelia* genera. Kandelia is the dominant species and turned out to be a precious national treasure along the Danshui River in Taipei, Taiwan. In addition to *Kandelia*, there are a wide range of plants associated with its surrounding area. These plants have also evolved special morphological and physiological characteristics to adapt to flooding and high salinity environment. These halophytes include *Phragmites austrakis* (reed), *Sporobolus virginicus* (salt sage), and *Imperata cylindrica* (cogon grass). In 1982 Lue carried out an ecological survey of Chuwei mangrove forest, and found the population of *Imperata cylindrica* (Lue, 1982).

Imperata cylindrica, a perennial herb, is a C4-type plant. It has 10 pairs of chromosomes. A single *Imperata* individual can generate many seeds. Seed dispersal can be assisted by wind. *Imperata* can also use their underground rhizome for asexual reproduction. It is adapted to a wide range of environmental factors and confers a high degree of stress tolerance. The underground rhizome is a commonly used medicinal herb. There are about 10 species of *Imperata* worldwide. In Taiwan there is only one genus one species, namely *Imperata cylindrica* (L.) Beauv. var. *major* (Nees) Hubb. (Hsu, 1975). Cheng & Chou (1997a) examined the leaves of *I. cylindrica* from Chuwei using scanning electron microscope (SEM) and found that Chuwei population differs from others in anatomy and morphology. The stele was empty instead of solid. The lower stem was surfaced with white wax instead of trichomes. In addition, polymorphism among populations was also analyzed by rapid amplify polymorphic DNA (RAPD) (Cheng & Chou, 1997b) and restriction fragment length polymorphism (RFLP) (Chou & Tsai, 1999) on ribosomal DNA (rDNA) (Chiang *et al.*, 1998; Tsai & Chou, 1999). In 2006 Chang found that Chuwei population is salt and flood tolerant (Chang & Chou, 2006). In 2008 Chang utilized proteomics approach and identified differentially expressed protein among Chuwei, Sarlun and Neihu Imperata populations (Chang, 2008). All these results revealed that Chuwei population was found to be a distinct ecotype.

Under salt pressure, plants accumulated various organic compounds *i.e.* proline, glycinebetaine, choline, glycerol, and sorbitol as compatible solutes in their bodies. Barley (Stewart & Michelle, 1983), tobacco (Binzel *et al.*, 1987), eggplant (Jain *et al.*, 1987), and spinach (Coughlan & Wyn Jones, 1980) accumulated large amounts of proline in response to salt treatment. The amount of proline increased with increased salinity. In addition, the expression of proline was regulated by abscisic acid (ABA) (Stewart, 1980; Stewart & Voeberg, 1985). Proline played diverse roles in stress physiology. Stewart & Lee (1974) pointed out that the accumulation of proline in plants correlated its tolerance to salt stress. They also indicated that high level proline would protect many N metabolism-related enzymes from harm. Moreover, large amount of proline would inhibit ACC from converting to ethylene so that plant would not hurt by ethylene (Chrominski *et al.*, 1988; Chrominski *et al.*, 1989). Proline could also be osmo-protectant which functions to maintain osmotic potential balance (Jain, 1987). It is suggested that proline in *I. cylindrica* from Chuwei may function as an osmo-regulator against salt stress.

Mangrove swamp environment is very unique. It is not only a salty land but is also subjected to periodic flooding which is very detrimental to plant growth. It has been discussed that sea-level rise may impact the survival of mangrove forests (Feller *et al.*, 2010). The rises of sea water may impact the survival of mangrove trees in the world. We suspect that the rise of sea water may be one of the causes of the population size decrease of Chuwei mangrove population of *Imperata*. A field work survey discovered that the population size of Chuwei ecotype is decreasing. The proline content of Chuwei population in the field before and after flooding was measured. In present study, we tried to investigate the relationship between the decrease of population size of *Imperata* Chuwei ecotype and proline content changes. We hypothesized that the dynamics of proline content may be related to the population size decrease. The study of how flooding affects proline accumulation may elucidate the possible impact of sea-level rise using Imperata mangrove population as an example.

2. Materials and methods

2.1 Sampling sites and plant materials

Imperata cylindrica (L.) Beauv. var. *major* (Nees) Hubb, Cogon grass, was used as plant materials. Chuwei mangrove salt marsh wetland (Hwang & Chen, 1995) where periodical flooding pressure threatens plant survival was chosen as a sampling site (Figure 1, Figure 2). Sarlun sandy beach was chosen as a control site (Figure 1, Figure 3) (Figure 1, 2, and 3 were adapted and modified as previously described (Chang, 1996)). These two sampling sites are close to each other in Danshui area, Taipei as shown in Figure 1. Plant leaves from Chuwei were harvested between July and October in 1995 and 2011 for proline content assay. Plant samples were collected on spring-tide days (high tide and flooding; Jul 14, Aug 13, Sep 11, Sep 28 and Oct 12 in 1995; Feb 20 in 2011). During harvesting, each leaf sample was excised by sterilized scissors and stored in zip-block in ice bucket with dry ice to keep it fresh and brought back to lab immediately for study the same day. Plant leaves harvested from each site were assay for water proline. Plants rhizomes collected from the field were washed by sterilized water and cultured in pots (60× 20 ×20 cm^3) in greenhouse for two weeks, then transplanted to Kimura's culture solution (Chang & Chou, 2006) to grow plantlet, the vegetative shoot. The culture solution was aerated with air pump without break. The culture solution was changed every week. These plantlets were used for differential display assay.

2.2 Hypotheses to be tested

We have two hypotheses for the interpretation of possible reasons for the population size decrease of Chuwei ecotype. The first hypothesis is a synecology hypothesis. This hypothesis address that the overpopulated *Kandelia* may threaten the survival of Chuwei Imperata. The second hypothesis is an autoecology hypothesis. This hypothesis address the local flooding may affect the survival of Chuwei Imperata. We hypothesized that Chuwei ecotype may respond to local flooding in a manner different from *Kandelia*. We suspected that local flooding may impact the survival of Chuwei ecotype even though it is flooding tolerant (Chang and Chou, 2006).

2.3 Proline content measurement

L-proline content was measured by the method as previously described (Bates *et al.*, 1973). Half a gram of plant fresh leaf tissues were chopped into pieces and quick-frozen in liquid nitrogen in 5 g sea sand and 5mL extraction buffer containing 3 % (w/v) 5-sulfosalicylic acid for grinding and homogenization. The homogenates were centrifugated at 538×g (Sigma, Model 2K15, Taiwan) for 10 minutes. The supernatant was obtained as proline crude extract. The reaction mixture contained 2 ml acid-ninhydrin solution, 2ml proline crude extract. Acid-ninhydrin solution contained a mixture of 0.14 M ninhydrin, 60 % (v/v) acetic acid, 2.4 M phosphatic acid and 2 ml acetic acid. The reaction took place at 100°C for 1 hour. Samples were then put into -20°C refrigerator to stop the reaction immediately. Four ml methane was mixed with samples and vortex viguously. The solution was divided into two layers, the upper methane layer and the lower water layer. Three ml upper ethane layer solution was placed in a cuvette. Proline content was analyzed spectrophotometrically at wavelength 520nm using spectrophotometer (Beckman, Model DU-50, Taiwan). Ten replicas were included for each data set. Data were analyzed by Student□s pairwise t-test in SPSS statistical package.

2.4 RNA extraction

RNA extraction was conducted by use of pine tree method as previously described (Chang *et al.*, 1993). Leaves of Sarlun and Chuwei population of *Imperata cylindrica* were ground in liquid nitrogen using mortar and pestle. About 2 grams of leaf powder were added into 15 mL extraction buffer containing 100 mM Tris-HCl pH 8.0, 25 mM EDTA, 2 M NaCl, 0.5 g/L

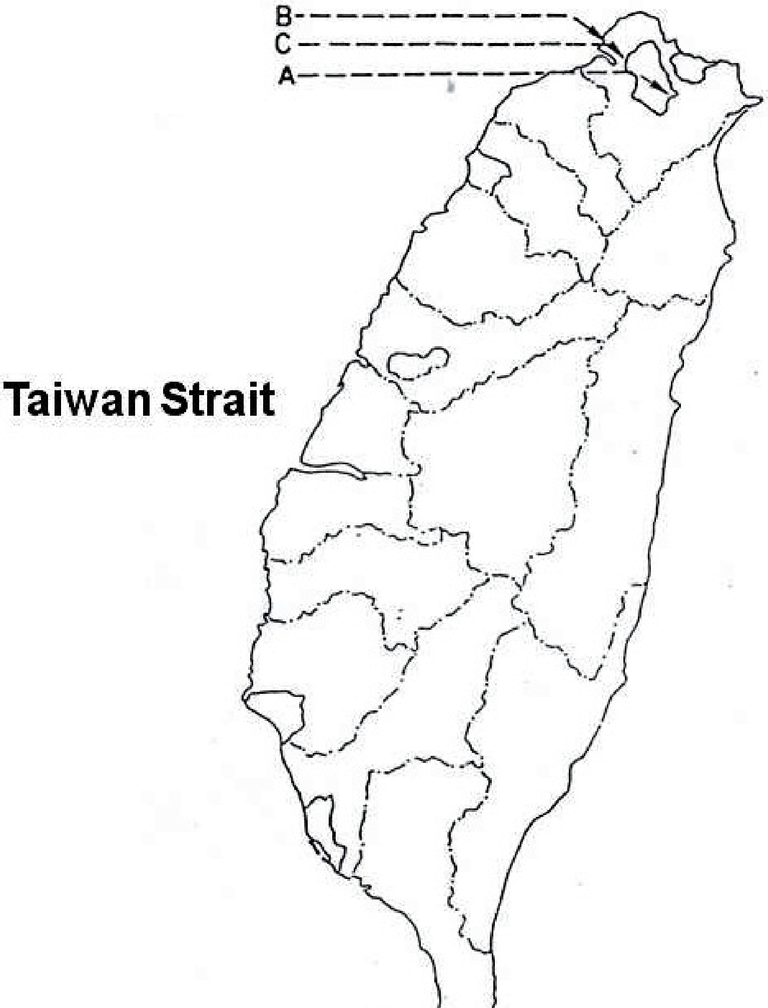

Fig. 1. Sampling sites of *Imperata cylindrica* in Danshui area, Taipei, Taiwan. *Imperata cylindrica* sampling sites were labeled as arrows indicated. A: Neihu; B: Sarlun; C: Chuwei.

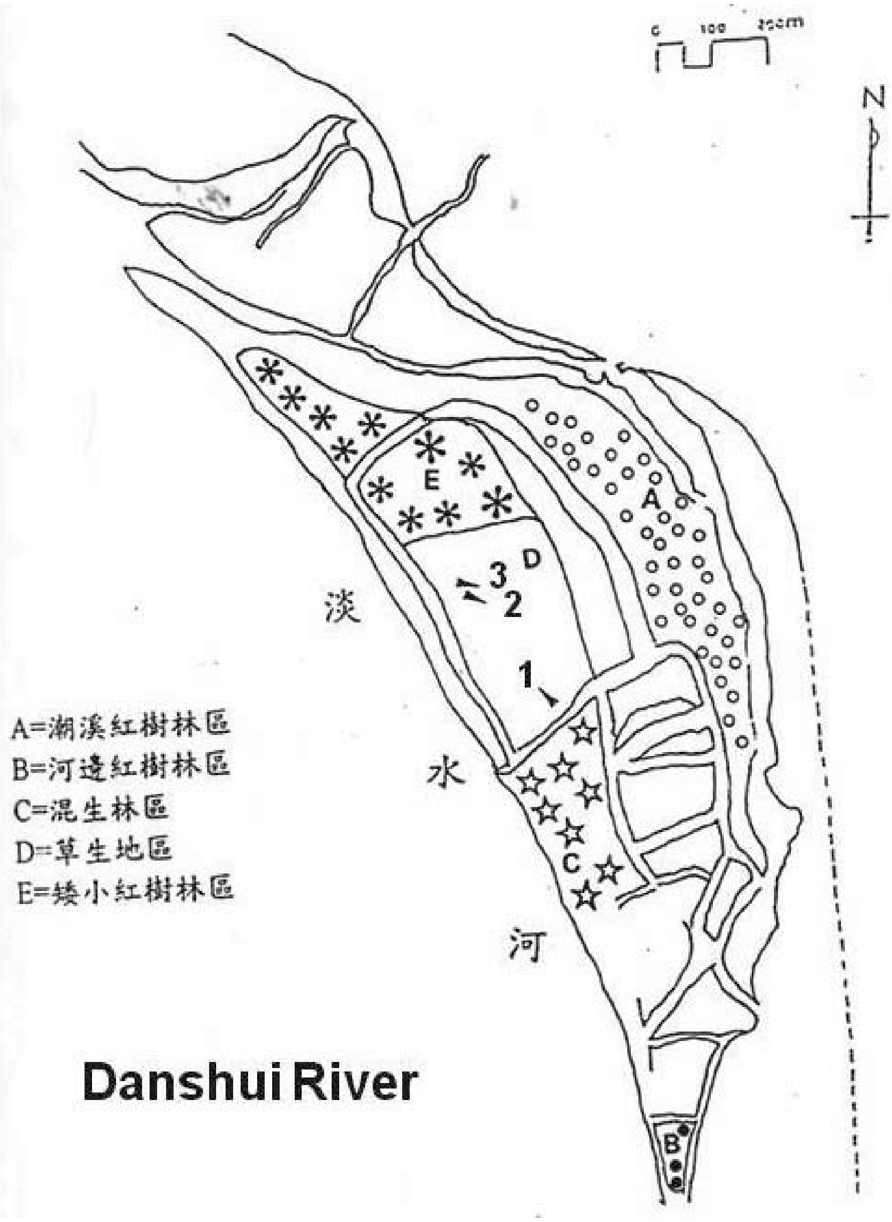

Fig. 2. Sampling sites of *Imperata cylindrica* in Chuwei, Taipei, Taiwan. *Imperata cylindrica* is populated in area D. In area D, sampling site 1, 2, and 3 were labeled as arrows indicated. Site 2 and 3 were lost just very recently for unknown reasons.

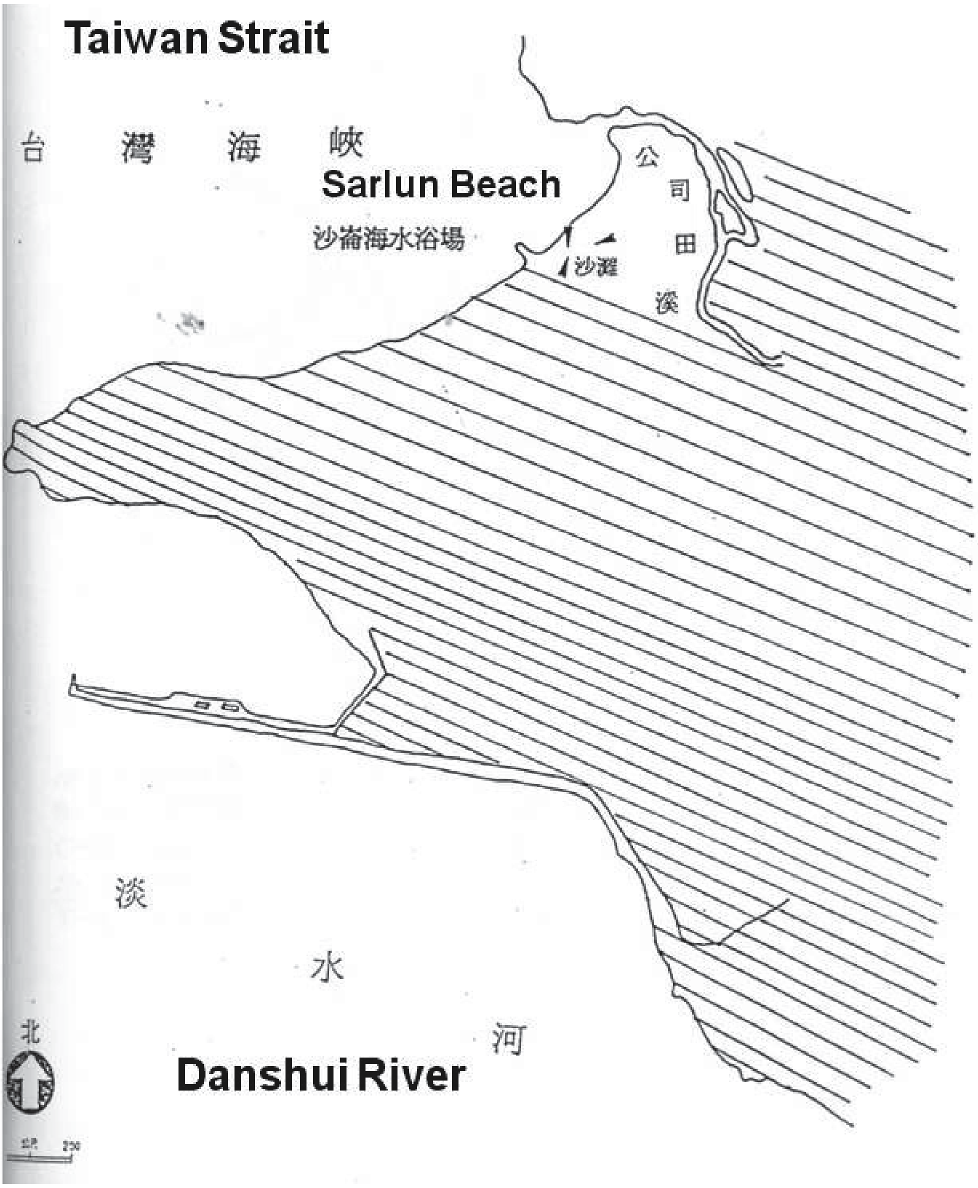

Fig. 3. Sampling sites of *Imperata cylindrica* in Sarlun, Taipei, Taiwan. Sampling sites were labeled as arrows indicated.

spermidine, 2% beta-mercaptoethanol, 2% CTAB, and 2% PVP. The homogenate was mixed well and subjected to water bath at 65°C for 10 minutes. The mixture was then centrifuged at 13000 rpm for 15 minutes at room temperature. The upper layer was recovered to a new centrifuge tube. Equal volume of chloroform:isoamyl alcohol (24:1) was added. After thorough mixing, centrifugation was carried out at 13000 rpm for 15 minutes at room temperature. This step was repeated twice in order to remove proteins and metabolites. The upper water layer was transferred to a new centrifuge tube. One third volumes of 10 M LiCl was added, mix well and subjected to incubation under 4°C overnight. The solution was centrifuged at 13000 rpm for 30 minutes at 4°C. The pellet was washed by 1mL 70% (v/v) ethanol. The solution was transferred to a sterilized microcentrifuge tube for centrifugation at 13000 rpm for 15 minutes at 4°C. The wash step was repeated twice to remove salt. The pellet was air dried. One hundred μL sterilized ddH_2O was added to resuspend RNA. RNA concentration was measured by NanoDrop spectrometer. The RNA integrity was checked by 2% agarose gel electrophoresis, and the solution was used as templates for reverse-transcription immediately followed by storage under -80°C.

2.5 Differential display assay

Differential display and the subsequent silver stain were carried out by following the manufacturer instruction (RNAimage Kit 5, GenHunter Corporation, Cat. No. G505; SILVER SEQUENCE™ Staining Reagents, Promega, Cat. No. Q4132). After reverse-transcription, cDNAs were used as templates to perform another PCR with AP primers provided by the manufacturer. PCR products were loaded into denature acryl-amide gel for electrophoresis at 1700V for 4 hours. The gel was stained by silver stain immediately after the electrophoresis was completed. The Air-dried gel was scanned by scanner (EPSON PERFECTION V750 PRO, EPSON). The electrophoretic bands were compared to identify gel bands specific to either Chuwei or Sarlun population.

2.6 Isolation of electrophoretic bands for DNA cloning and sequencing

The electrophoretic bands were excised from the acrylamide gel by sterilized dissection knife, and collected in 1.5 mL eppendorfs. The recovery step was conducted by use of QIAGEN II Gel Extraction Kit (QIAGEN, Cat. No. 28704). The DNA concentrations were detected by NanoDrop spectrometer. The recovered DNA was used for TA cloning. Cloning was conducted using TA Cloning Vector (RBC, # 200-09205) as cloning vector. T4 DNA ligase was used for ligation between TA vector and DNA. *E. coli* (DH5α) was used as hosts. The ligated plasmids were transformed into DH5α competent cells by heat-shock, and incubated under 37°C on LB medium (with ampicillin) for 14 hours. Five to eight colonies were selected from each plate to perform colony PCR and subsequent sequencing.

2.7 Database searching

Sequences acquired were searched against NCBI database using BLAST algorithm (http://blast.ncbi.nlm.nih.gov/Blast.cgi) (Altschul *et al.*, 1990). Plant Genome Database (PlantGDB, http://www.plantgdb.org/), the Gene Ontology（http://www.geneontology.org/）, the Arabidopsis Information Resource（TAIR, http://www.arabidopsis.org/）, and MIPS *Oryza sativa* database（MOsDB, http://mips.helmholtz-muenchen.de/plant/rice/）were also used. In nucleotide sequence searching, the cloned sequences were compared against databases by BLASTn program and

BLASTtx program for matches. In protein sequence searching, the acquired sequences were first translated by ExPASy Translate Tool (http://au.expasy.org/tools/dna.html), and then screen for possible protein sequences manually. The translated protein sequences were compared against databases by BLASTp program.

3. Results and discussion

3.1 Population size of Chuwei ecotype is much smaller than before

Imperata cylindrica (L.) Beauv. var. *major* (Nees) Hubb., a top-ten weed (Holm *et al.*, 1977), was found in Taiwan all around the island (Hsu, 1975). In America, *Imperata cylindrica* was found as a non-endemic species dominating Florida and neighboring states in both dry and wetlands (King & Grace, 2000). Interestingly, it was found growing in Chuwei mangrove salt marsh wet land as well. To track the dynamics of population size of Chuwei ecotype, we carried out field survey since 2008. Surprising, we observed decrease of population size of Chuwei ecotype. Two of the sampling sites (Chuwei and Sarlun) we selected for the field work (site 2 and site 3 as shown in Figure 2) before year 2000 were found missing since the beginning of 2009. Only sampling site 1 (around 30 m^2) still existed so far (Figure 2). In addition, the size of sampling site 1 is only less than half of the size as before. Therefore, we concluded that Chuwei ecotype is now decreasing its population and is endangered. However, the reason why the population size decreased is unknown.

3.2 Proline content in leaves of Chuwei ecotype decreased dramatically after flooding in the field

We have two hypotheses for the interpretation of possible reasons for the population size decrease of Chuwei ecotype. The first hypothesis is supported by the evidence that more and more *Kandelia* trees are invading the habitat of Chuwei Imperata. These *Kandelia* trees may threaten the survival of Imperata. It is expected that in ten years, this area will be dominated by *Kandelia* trees and Imperata Chuwei ecotype will eventually be extinct. In order to test the second hypothesis, we compare proline content in leaves of *I. cylindricain* in the field before and after local flooding on the spring tide (high tide) date. Samples were collected at monthly interval from August to December in 1995. For proline content analysis, leaves sampling was performed with 20 individuals within a day. To test if proline content changed in response to flooding, same leaf samples were collected before and after flooding (1 hr difference) on spring-tide days. Proline content analysis showed that proline content dropped dramatically after flooding. On July 14 in 1995, proline content decreased 53 % after flooding. On August 13, proline content decreased 46 % after flooding. On October 12, proline content decreased 67 % after flooding. Moreover, on February 20 in 2011, proline content decreased 40% after flooding (Table 1).

The decrease of proline content in response to local flooding in Chuwei supported our second hypothesis. In the salt marsh wetland, high level of proline content is helpful in maintaining the osmotic equilibrium in the cells. When local flooding occurred, proline dropped rapidly, which is harmful to plants since osmotic equilibrium was not maintained in the cells. This might eventually lead to cell death. In order to determine if proline content in leaves of plantlet increases in responses to flooding, flooding treatment was performed three months in the greenhouse to see long-term effect on proline. Leaf samples were collected and analyzed. Results showed that the accumulation of proline was not found in leaves of flooding-treated plantlet in the greenhouse (data not shown).

Sampling date	Before flooding	After flooding
07.14.1995	138.99± 7.53	64.62± 1.58[1]
08.13.1995	130.94 ± 8.29	70.49± 4.84[1]
10.12.1995	156.82± 14.84	52.16± 2.57[1]
02.20.2011	150.45 ± 2.37	89.97± 3.68[1]

[1] Values showed significant difference in Student's t-test at 5% level. S.E. was at 5% level. Proline count unit: micro g gfw^{-1}

Table 1. Average proline content in leaves of *I. cylindrica* from Chuwei population before and after flooding on spring-tide (high tide) days. Sampling was performed in 1995 and 2011.

3.3 Proline serves more than one function in *Imperata cylindrica* Chuwei ecotype? - A cross-talk between flooding and salt stress

In a previous study, *I. cylindrica* from Chuwei was tolerant to 1% salt treatment. Therefore, it was grouped as a salt-tolerant ecotype (Chang & Chou, 2006). The tolerance ability was even stronger than *Kandelia candel* (tolerant to 0.8 % salt), a dominant mangrove forest species in Chuwei salt marsh wetland (Hwang & Chen, 1995). Since Chuwei sampling site is a mangrove salt marsh land, how plants survived in such a high salt land is poorly known. According to our study, proline content of *I. cylindrica* from Chuwei was much higher than those from others in the field (Chang & Chou, 2006). They were also higher under salt treatment. In the greenhouse experiments, proline of *I. cylindrica* from Chuwei was highly accumulated in response to salt treatment.

However, does proline serve only single role in plants? It has been reported that the regulation of ion uptake and production of organic solutes (*i.e.* methyl proline) is related to combined salt and flood stress tolerance in some wetland plants (Carter *et al.*, 2006). In addition, mechanism of how some halophytes tolerate flooding is reviewed (Colmer and Flowers, 2008). In present study, proline content dropped dramatically (almost 50 %) after local flooding (only in one hour) in Chuwei ecotype, suggesting that proline may serve as a signal molecule in response to flooding. The dynamic of proline in leaves of Chuwei *Imperata* was suggested which might not only be involved in salt stress, but also in flooding stress response.

The decrease of proline content in response to flooding can be explained by two mechanisms. The first mechanism is that proline acts as a direct response to flooding. It has been reported the accumulation of proline was regulated by abscisic acid (ABA) (Stewart, 1980; Stewart & Voeberg, 1985). Alcohol dehydrogenase *ADH* gene expression was also known regulated by ABA (de Bruxelles *et al.*, 1996) through G-box, a promoter region (Walker *et al.*, 1987; Lu *et al.*, 1996). It is possible that *ADH* gene expression and proline accumulation cross-talks, and is regulated through ABA. Since proline accumulated in response to salt stress in Chuwei ecotype, decrease in proline content may be an easier way for cell to recognize to activate fermentation pathway, including activation of *ADH* gene. An alternative mechanism is an indirect response of proline to flooding. The accumulated proline transported downward toward root (shoot to root) to protect root from salt damage, and anti-transpirated with a flooding signal molecule from root to shoot (Else *et al.*, 1996) for stomata closes in response to flooding. This pathway might overlap with water-deficit pathway. Besides, a long distance transport of proline as a signal molecule was required. However, we did not confirm any of the possibility because it was very complicated to simulate a physiology experiment with two stresses acting at the same time. Timing makes the experiment even difficult to resolve. Maybe an easier way to keep tract on proline dynamic was to label proline using isotope as a tracer. Although the role of proline as signal molecule in response to salt stress has been proposed (Maggio *et al.*, 2002; Hare & Cress, 1997), the involvement of proline in flooding response has not been discovered before. Anyway, due to the fact that proline functioned in response to both flood and salt stress in present study, a crosstalk between two distinct pathways, salt and flooding response, was suggested.

3.4 Differential display reverse transcription assay revealed five genes which were differentially expressed in Chuwei ecotype as compared to Sarlun population

Differential display was first introduced In 1992, by Liang and Pardee as an easy application for comparison, identification and isolation of genes expressed as mRNA in various cells under designated conditions (Liang and Pardee, 1995). The basic steps of differential display include isolation of intact RNA from sample, reverse transcription of the RNA using an arbitrary primer to produce ssDNA, several rounds of polymerase chain reactions using the same primer to amplify the corresponding cDNAs, and display of the cDNAs as bands on a matrix gel, such as a DNA sequencing gel. In order to identify differentially expressed genes in Chuwei ecotype, differential display (DD) was introduced. The differences of gene expression between Chuwei ecotype and Sarlun population were compared. By comparing and collecting the bands uniquely appeared to either Chuwei or Sarlun populations. Population-specific ESTs was isolated and identified.

Three biological replicates were included. RNAs extracted from Chuwei ecotype and Sarlun population were subjection to QC. To check RNA integrity, RNAs extracted were used to perform electrophoresis in 2% agarose gel at 120V for 15 minutes. Differential display was conducted by three replicates with one of the replicate. Bands with high reproducibility were indicated and excised from the gel for subsequent cloning procedure. A total of twenty-six bands specific to Chuwei ecotype were detected, whereas seventeen bands were specific to Sarlun population.

Detail information about Chuwei-specific bands is listed in Table 2 and described as follow. BLAST search result of band C3 nucleotide sequence showed that part of the sequence of *Zea mays* chloroplast genome which coding for 16s rRNA was identified. This matched sequence was also found to be present in *Arabidopsis thaliana* chloroplast, *Zea perennis* mitochondrion and uncultured environmental bacterium. (Takeuchi *et al.*, 2005), whereas others had no significant matches. For BLAST search result of band C12 nucleotide sequence, a candidate uncharacterized mRNA sequence of *Triticum aestivum* was identified (Kawaura *et al.*, 2009). This cDNA had similar sequence matches in other plant species, including *Stellaria longipes*, *Sorghum bicolor*, *Oryza sativa*, and *Arabidopsis thaliana*. No hits were found in animals, which suggested it's a plant-specific gene. It appeared to be a putative disease resistance gene (Yang *et al.*, 2008, Sequencing Project International Rice, 2005, Tanaka *et al.*, 2008, Ohyanagi *et al.*, 2006), but remained to be a hypothetical one (Paterson *et al.*, 2009). For BLAST search result of band C12 nucleotide sequence, most ID matched hypothetical disease-resistance related genes in plants, which supported C12 to be an EST sequence of a plant-specific gene for a hypothetical protein. For BLAST search result of band C7 nucleotide and protein sequence, nevertheless no significant matches were found in NCBI, PlantGDB, TAIR and MOsDB databases.

Detail information about Sarlun-specific bands is listed in Table 3 and described as follow. BLAST search result of band S4 nucleotide sequence showed that an ATPase III subunit in *Dendrocalamus latiflorus* chloroplast, *Sorghum bicolor* chloroplast and *Zea mays* chloroplast

(Strittmauer and Kossel, 1984, Alexandrov *et al.*, 2009, Wu *et al.*, 2009) was identified. Moreover, BLAST search result of band S4 protein sequence showed that ATP synthase CF0 subunit III of many eudicotyledons such as *Geranium carolinianum* and *Erodium texanum* (Guisinger *et al.*, 2008) was identified. For BLAST search result of band S8 nucleotide sequence, the most likely candidate was a hypothetical protein of *Sorghum bicolor* (Paterson *et al.*, 2009). Similar sequences were also found in *Zea mays* and *Oryza sativa*, still hypothetical proteins (Yu *et al.*, 2005, Lai *et al.*, 2004). Moreover, for BLAST search result of band S8 protein sequence, eight possible queries out of six reading frames were blast against NCBI database. Five of these queries had no significant similarities, the others matched to hypothetical proteins of *Sorghum bicolor, Zea mays* and *Oryza sativa*.

For band S9 nucleotide BLAST search, a putative casein kinase of *Oryza sativa* was found. This sequence was also similar to another putative serine/threonine protein kinase of *Oryza sativa* (Sasaki *et al.*, 2002). For band S9 protein BLAST search, eight possible queries out of six reading frames were submitted to NCBI database. Two of them had matches indicating serine/threonine protein kinase of *Oryza sativa*; four were found to share similarities with hypothetical proteins among various vascular plants; the rest had no significant similarities found. For band S6 nucleotide BLAST search, no significant similarities were found among all databases mentioned above. For band S6 protein BLAST search, four possible queries were submitted. No significant similarities were found.

Band #	**Size (bp)**	**Accession #**	**Identity**	**Annotation of matched gene**
C3	776	AY928077	99%	*Zea mays* chloroplast, 16S rRNA
C12	553	AK333595	82%	*Triticum aestivum*, hypothetical

Table 2. Differential display bands specific to Chuwei ecotype.

Band #	**Size (bp)**	**Accession #**	**Identity**	**Annotation of matched gene**
S4	404	AY928077	98%	*Zea mays*, ATP synthase C chain
S8	468	AK333595	96%	*Sorghum bicolor*, hypothetical
S9	383	AAT44311	79%	*Oryza sativa*, casein kinase

Table 3. Differential display bands specific to Sarlun population.

3.5 Adaptational divergence of *Imperata cylindrica* Chuwei ecotype

Imperata Chuwei ecotype encountered both flooding and salt pressure. In order to survive, plants must possess adaptation mechanism against flooding and salt stress. The increase of

ADH activity and decrease of proline content may be a mechanism against flooding stress, and accumulation of proline may be a mechanism against salt stress (Chang & Chou, 2006). The working model for flooding stress tolerance of Chuwei ecotype was proposed. Before flooding, proline content accumulated in leaves of Chuwei ecotype in response to salt stress. After flooding, leaf ADH activity increased. By contrast, leaf proline content decreased after flooding. These changes can be reached in only one hour. In addition, we identified several differentially expressed genes in Chuwei ecotype and Sarlun population in present study. All these biochemical, physiological changes and genes may contribute to the tolerance of Chuwei ecotype to both flooding and salt stresses, and therefore drove this population diverged form other populations as a distinct ecotype through evolution. However, what was the signal transduction relationship among ADH gene activation and proline, and what was the crosstalk link between flooding and salt stress response remained unknown. More studies on crosstalk of flooding and salt stress physiology of Chuwei ecotype on the signal transduction level are needed.

3.6 Sea-level rise as a potential threat to the survival of *Imperata cylindrica* ?

In present study, we observed a decrease of population size of *Imperata* Chuwei ecotype. In the proline content assay, we also observed dramatic drop of proline content after local flooding in the field in Chuwei ecotype. The drop of proline may be detrimental to plants. These results suggested that sea-level rise can be a potential threat to the survival of *Imperata* Chuwei ecotype. However, it is still not sure that the decrease of population size of *Imperata* Chuwei ecotype is directly or indirectly related to sea-level rise. What can be expected is that in the near future the population may be totally wiped out due to sea-level rise. Since Chuwei ecotype may possess many unknown and valuable salt-tolerant genes, we urge to preserve Chuwei ecotype for conservation.

3.7 Conclusions

The results from present study showed that proline content dropped dramatically after the local flooding at Chuwei. The results supported our second hypothesis that local flooding-mediated proline drop may threaten the survival of *Imperata*. However, the first hypothesis was also supported by the fact of overpopulation of *Kandelia* trees in Chuwei. A concurrent contribution of the two is suggested. In addition, differential display identified Chuwei ecotype or Sarlun population-specific transcripts in the greenhouse. These differentially expressed genes can be important in salt or flooding stress tolerance. However, further validation and confirmation of gene expression using other molecular tools is needed.

4. Acknowledgments

We appreciated National Science Council, Taiwan for funding support (NSC# 98-2815-C-002-146-B, NSC# 98-2621-B-002-008-MY3, and NSC # 99-2815-C-002-041-B). We thank Technology Commons, College of Life Science, National Taiwan University for the equipment support. We appreciated technical support from Wuu-Yang Chen, Prof. Chan-Pin Lin, and Prof. Kuo-Chieh Ho at National Taiwan University.

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Change in Species Composition and Distribution of Algae in the Coastal Waters of Western Japan

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1. Introduction

Estuarine and coastal ecosystems are sensitive to human activities that lead to nutrient pollution, excess or insufficient sedimentation, and other types of pollution. The effects of climate change are particularly noticeable in these shallow ecosystems, and increases in non-native species and gelatinous zooplankton such as jellyfish can have harmful effects on fisheries. With climate change related to human activities well under way (IPCC, 2007), there is a need to assess the impacts of these changes on estuaries and coastal waters. Growing awareness of climate change has stimulated considerable recent interest in the possible shifting of biological events in marine ecosystems and the ecological consequences of these shifts. It has been suggested that enhanced stratification caused by an increase in surface water temperature decreases nutrient supply, leading to a decrease in primary productivity throughout a large area of the North Pacific Ocean (Ono et al., 2002; Watanabe et al., 2005). It has also been reported that the timing and magnitude of phytoplankton blooms have changed markedly, affecting the dynamics of zooplankton and fisheries resources (e.g., Edwards & Richardson, 2004; Chiba et al., 2008). Impacts on estuarine and coastal ecosystems remain unclear, however, because of the difficulty in distinguishing the effects of global warming from those of other anthropogenic factors. Although phytoplankton are major primary producers in most aquatic ecosystems, benthic primary production, such as macroalgae, can be often substantial and even dominant in shallow waters. *Sargassum* algal beds are highly productive and offer habitats for numerous marine animals. The decline and qualitative change of *Sargassum* beds in western Japan, which may be caused by global warming, and their impact on coastal ecosystems and fisheries that rely on them is of great concern. In last two decades, macroalgal beds composed of *Sargassum* and kelp (mainly *Ecklonia*) have been degrading or declining along the coast of the Kyushu and Shikoku areas in western Japan, which has southern temperate climate characteristics. It is estimated that the mass disappearance of local kelp and *Sargassum* beds in these regions totals several thousand hectares and more than 40% of the total macroalgal beds surveyed in the early 1990s. Degradation of macroalgal beds in these areas has coincided with increased water temperatures and grazing pressures by herbivorous animals (fish and sea urchins). Shifts of flora from temperate to subtropical components, accompanied by quantitative changes in macroalgal beds, have also been observed in many areas of western Japan.

Subtropical *Sargassum* species such as *S. duplicatum* and *S. carpophyllum* have begun to appear in many *Sargassum* beds in the Kyushu and Shikoku regions, sometimes becoming more dominant by replacing temperate species. These subtropical species exhibit an annual life cycle trait and develop their stocks only between winter and spring. This seasonality is attributable to the growth characteristics of the species in which shoot growth is triggered by cooler temperatures and is advantageous for avoiding active grazing by herbivorous animals during warmer seasons. Subtropical *Sargassum* species also have high regenerative ability at their holdfasts, which allows them to grow in severely turbulent conditions during which grazing activity is restricted. These eco-physiological characteristics of subtropical *Sargassum* species contrast greatly with those of their temperate counterparts and are well adapted to an environment with high grazing pressure from herbivorous animals. The quantitative and qualitative changes in macroalgal beds will extend to cooler regions in Japan if coastal water temperatures continue to increase. Monitoring and continuous surveying of coastal areas are needed in addition to countermeasures to protect biological and fisheries production against the coastal environmental changes induced by global warming.

Several species of dinoflagellates produce toxins responsible for paralytic shellfish poisoning (PSP). When these dinoflagellates bloom, their toxins accumulate in mussels and oysters that ingest them. Outbreaks of PSP in mussels and oysters caused by *Alexandrium*, *Gymnodinium catenatum* Graham, and *Pyrodinium bahamense* Plate var. *compressum* (Böhm) Steidinger, Tester & Taylor are currently a serious problem from both an economic and a food hygiene point of view. The occurrence of toxic *Alexandrium* blooms has increased in frequency, and these species are widely distributed in the coastal waters of Europe, North America, Japan, the Philippines, Australasia, India, and Argentina (Hallegraeff, 1995). Extensive taxonomic, physiological, and ecological studies have resulted in the recognition of some 10 species of the genus *Alexandrium* that are toxic or presumed toxic (Balech, 1995; Yoshida & Fukuyo, 2000). In Japan, *A. catenella* (Whedon & Kofoid) Balech, and *A. tamarense* (Lebour) Balech are the major *Alexandrium* species causing PSP. Appearances of the toxic tropical dinoflagellate species *A. tamiyavanichii* have been confirmed in the Seto Inland Sea since the 1990s, although it remains unclear whether global warming is directly responsible. Rising winter water temperatures in the Seto Inland Sea in Japan have occurred in response to progressing global warming caused by the massive exhaustion of carbon dioxide and the decomposition of the ozone layer related to civilization and industrialization (Yamamoto, 2003; Takahashi & Seiki, 2004; Wanishi, 2004; Tarutani, 2007).

Our purpose is to present and summarize some of the evidence of the impact of global warming on the coastal waters of western Japan. In this chapter, we discuss three topics that are closely related to global warming: 1) recent trends in environmental changes—mainly in surface water temperature (Section 2-1), 2) the degradation of macroalgal beds composed of algal genus *Sargassum* and kelp and their replacement by subtropical *Sargassum* species (Section 2-2), and 3) the new invasion of tropical species that cause harmful microalgal blooms and its settlement in the introduced area (Section 2-3).

2. Potential climate change effects on environmental characteristics in the coastal ecosystems of western Japan

2.1 Long-term changes in water temperature in the coastal waters of western Japan

According to the *Global Warming Projection*, published by the Japan Meteorological Agency (2008), the sea surface temperature (SST) around Japan has increased 0.8–1.7°C over the past 100 years (1900–2007). The SST around Japan is projected to increase, and the long-term SST trends for the 21st century predicted using the North Pacific Ocean General Circulation Model (Sato et al., 2006) are increases of 2.0–3.1°C and 0.6–2.1°C per century under scenarios A1B and B1, respectively. The findings for near-shore areas were not included in this report, however, and the impacts of global warming on environmental factors in these waters remain unclear. In this section, we take the Seto Inland Sea as an example of the coastal waters of western Japan and discuss recent trends in water temperature.

2.1.1 Site description

The Seto Inland Sea is the largest semi-enclosed coastal sea in Japan, surrounded by Honshu (the main island of Japan), Shikoku, and Kyushu Islands (Fig. 1). It is 500 km long, has an average depth of 30 m, and contains more than 700 small islands. The region of the Seto Inland Sea is meteorologically referred to as the Seto Inland Climate Zone. The annual average temperature and precipitation are 15°C and 1,000–1,600 mm, respectively. The watershed land covers 68,000 km^2, which corresponds to about 18% of the total land area of Japan. This region is one of the most industrialized areas in Japan. At present, approximately 35 million people—about 18% of the total population of Japan—live within the watershed, and the marine environment has been significantly affected by their activities.

Although the Seto Inland Sea is enclosed, phenomena in the Pacific Ocean can strongly influence its marine environment thorough two boundary regions, the Kii and Bungo Channels. Off the southeastern coasts of Kyushu, Shikoku, and Honshu, the Kuroshio Current flows northeastward. This current corresponds to the northeastern part of the subtropical ocean gyre that circulates clockwise in the North Pacific and transports a large amount of water and heat to the coast of Japan. The current path shows significant interannual variations off the southern coast of Japan (e.g., Kawabe, 2005; see Fig. 1) and strongly influences the thermal conditions and nutrient environment in the Seto Inland Sea, especially around the Kii and Bungo Channels.

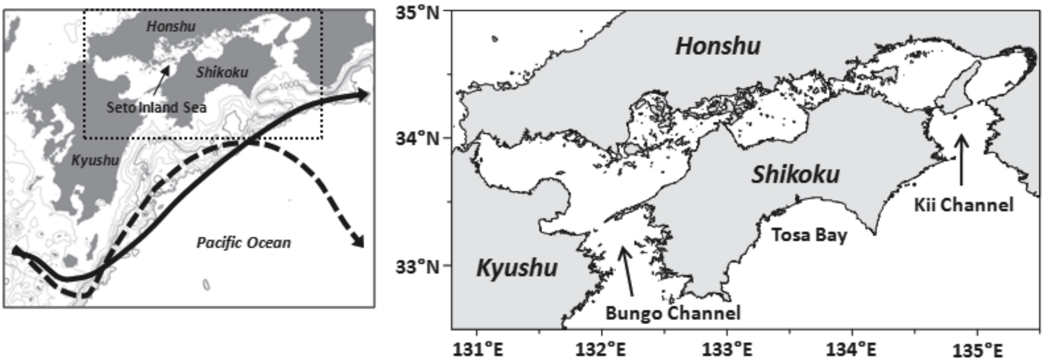


Fig. 1. Maps of the Seto Inland Sea and the typical Kuroshio Current path off the southern coast of Japan (left). The dashed and solid lines in the left panel represent the typical offshore (large meandering) and near-shore (non-large meandering) path, respectively.

The Seto Inland Sea has extremely high productivity per unit area of fishery products, which is the largest among comparable semi-enclosed coastal seas worldwide (e.g., Chesapeake Bay, Baltic Sea, North Sea, Mediterranean Sea; Takeoka, 2002). This high productivity is related to the extremely complex and semi-enclosed geography of the sea and the presence of essential nutrients supplied from the many rivers around the sea in sufficient amounts for the growth of phytoplankton. In recent decades, decreasing fishery production in the Seto Inland Sea has become recognized as a serious problem (Yamamoto 2003; Tarutani et al., 2009).

2.1.2 Recent trends in water temperature

The mean seasonal pattern for water temperature in the Seto Inland Sea has a maximum value in late summer (August to September) and a minimum value in late winter (February to March). The pattern differs somewhat spatially: the winter temperature is higher in the areas near the Kii and Bungo Channels, whereas the summer temperature is higher in the western part of the sea. Fig. 2 shows the long-term variations in mean water temperature throughout the Seto Inland Sea, and these variations were extracted from data gathered by the Fisheries Monitoring Program since 1973. After 1989–1990, the mean water temperature at a depth of 10 m generally remained higher than that measured during the 1980s (Tarutani, 2007). Considerable interannual variability is superimposed on long-term warming—for example, in Hiroshima Bay, located in the central part of the Seto Inland Sea, the annual mean temperature of water at 10 m of depth has warmed by about 1.0°C since 1973. The water temperature fluctuations differed seasonally, however. The warming trend was noticeable in autumn-winter, but was weak in spring-summer (Fig. 3). Such warming phenomena have occurred in several of the western coastal waters of Japan (e.g., Tosa Bay, located in the southern part of Shikoku Island; Setou et al., 2004).

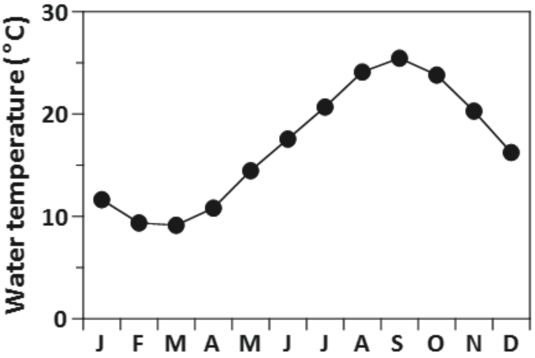


Fig. 2. Seasonal variations in water temperature in Osaka Bay, in the eastern part of the Seto Inland Sea (the mean from 1973 to 2002).

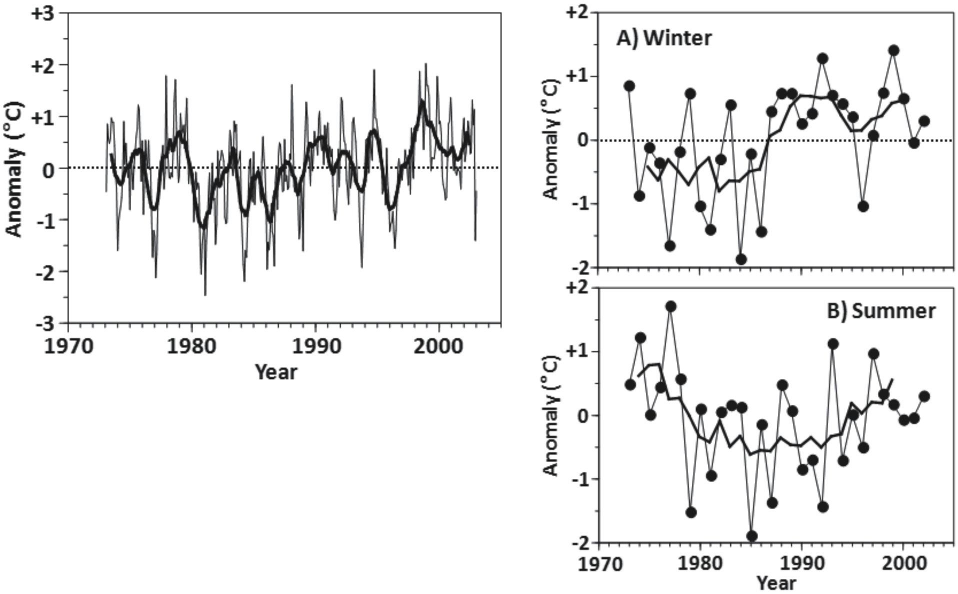


Fig. 3. Long-term variations in water temperature at 10 m depth in the Seto Inland Sea from 1973 to 2002. The thick line in the left panel indicates the running mean from 13 months of data. The right panels are (a) winter and (b) summer data, and the thick lines indicate the running means of 3 years of data.

The seasonality and future trends of water temperatures in the Seto Inland Sea are extremely important because they provide insight into the phenological changes in phytoplankton and macroalgae and may also play a role in regulating nutrient delivery to the sea from the Pacific Ocean. A hydrological modeling study revealed that the rising water temperature in the Seto Inland Sea was caused not only by changes in heat flux at the sea surface but also by changes in open oceanic temperature (Takahashi & Seiki, 2004). This discovery suggests that further detailed investigations of the mechanisms determining both regional atmospheric and oceanic temperature are required to accurately assess the impacts of climate change on hydrology in the Seto Inland Sea.

2.2 Changes in macroalgal vegetation on Japanese coasts

2.2.1 Degradation of macroalgal beds in southern temperate Japan

As mentioned in the introduction, coastal water temperatures have been increasing in Japan since the 1970s. The temperature increase is exerting a large influence on coastal ecosystems both directly and indirectly. Luxuriant macroalgal beds with diverse flora along the Japanese coast reflect variable climatic characteristics (cold and warm temperate to subtropical). These beds, called *Moba* in Japanese, were estimated to cover approximately 201,000 ha during the last research survey conducted between 1989 and 1991 (Environmental Agency & Marine Parks Center of Japan, 1994). In temperate Japan, large brown algae of the genus *Sargassum* and kelps (*Eisenia* and *Ecklonia)* dominate rocky shores and exhibit high productivity (Fig. 4). Along with the seagrass *Zostera* on sandy shores, these algae play important ecological roles as habitats for many marine animals. A recent report has shown that these brown algal beds have become extremely degraded or have disappeared during the last 20 years, especially in the southern part of temperate Japan (Fig. 5). In the southern area of the Miyazaki Prefecture in Kyusyu, for example, nearly 90% of local *Sargassum* beds have been lost (Aratake et al., 2007). In another case in the Kochi Prefecture, most kelp beds along the coast were lost after 1990 (Hiraoka et al., 2005).

The mass disappearance of local kelp and *Sargassum* beds in these regions is estimated to encompass several thousand hectares and 44.7% of the macroalgal beds reinvestigated after the survey by the Environmental Agency in 1989–1991 (Fujita et al., 2010). In most cases, the disappearance of macroalgal beds has seriously affected local coastal fisheries such as abalone fisheries (Serisawa et al., 2004). The scenery of the seabed after the decrease or loss of these large brown algae is called *Isoyake* (Fig. 6a). *Isoyake* has been known to occur occasionally since the 19th century with the approach of the Kuroshio Current offshore in the Pacific region (Fujita et al., 2010). The recent appearance of *Isoyake* is more frequent, however, and the phenomenon has extended to the entire Japanese coast. In the most remarkable case of *Isoyake*, the only dominant algae are crustose coralline algae on rocks or boulders that frondose macroalgae once occupied. Another common aspect among *Isoyake* regions is increased grazing pressure on algae by herbivorous animals (mainly fish and sea urchins; Fujita et al., 2010). Although it is unconfirmed whether these grazers are the cause of *Isoyake*, they prevent the recovery of frondose macroalgae and surely contribute to the continuity of *Isoyake* conditions.

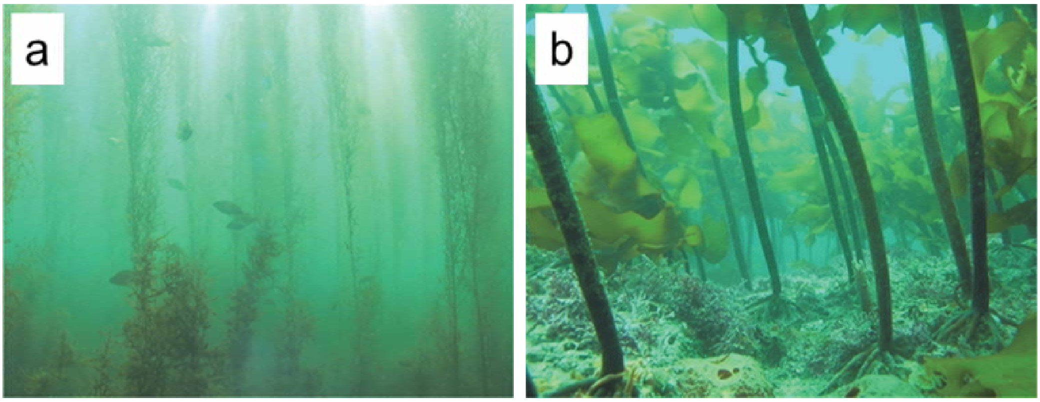


Fig. 4. Brown algal beds in southern temperate Japan. A *Sargassum* bed (a) in Hiroshima Bay, the Seto Inland Sea, and a kelp (*Ecklonia*) bed (b) at Sata-Misaki Peninsula in the Bungo Channel.

2.2.2 Changes in *Sargassum* flora in *Isoyake* areas

Concurrent with *Isoyake* during and after the 1990s, changes in the species composition of *Sargassum* beds that remain in *Isoyake* areas have also been reported in southern temperate Japan (e.g., Fujita et al., 2010). Along the coast of the Kochi Prefecture in the Pacific region, temperate species such as *S. micracanthum* and *S. okamurae* that dominated during the 1970s have been decreasing, and the subtropical species *S. duplicatum* (Fig. 6b) has become a major component of the flora since the 1990s (Hiraoka et al., 2005). In the Miyazaki Prefecture, *Sargassum* flora composed mainly of temperate species in 1970s has contained many subtropical species since 2000 (Aratake et al., 2007). The appearance of subtropical *Sargassum* has also been reported in the *Isoyake* area of Nagasaki, in the western Kyushu region (Fujita et al., 2010). Subtropical *Sargassum* exhibits annual characteristics in its life cycle that contrast greatly with the perennial characteristics of most temperate species (Fig. 7). Although the perennial species sustain shoots year round, subtropical species in Japan display shoot growth only in winter and spring. After reproduction in early summer, their shoots become senescent, and no visible thalli are observed in autumn (Shimabukuro et al., 2007).

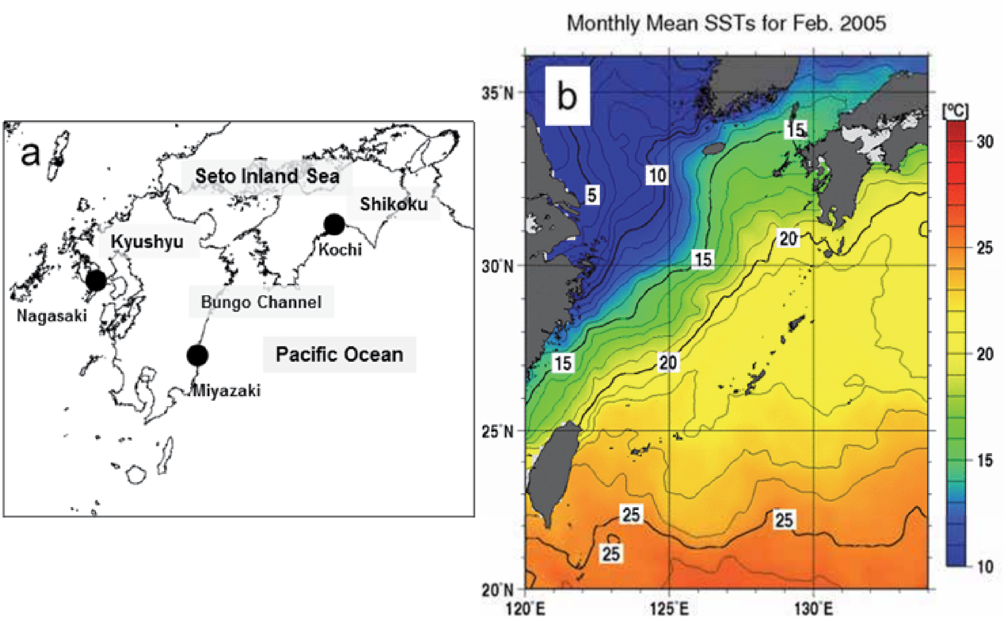


Fig. 5. Places cited in the text (a) and surface water temperature in winter (Feb. 2005) in the southern sea area of Japan (b) from the website of the Japan Meteorological Agency (2011).

To understand the physiological mechanism of subtropical *Sargassum* seasonality, we examined growth characteristics against variable temperatures for several common subtropical *Sargassum* species under experimental culture conditions. The results showed that the optimum temperature range for shoot growth in these species is 16–21°C, a range that coincides with winter coastal water temperatures in southern temperate Japan (see Fig. 5). Shoot development was inhibited above 24°C (Fig. 8), which is the average summer-autumn temperature in the field (Yoshida et al., 2009). This finding suggests that a drop in winter water temperature triggers shoot growth in subtropical *Sargassum*. On the contrary, the optimum temperature range for shoot growth is wider for temperate species. Even at summer temperatures (25°C), the shoots of many temperate species exhibit smooth growth (Haraguchi et al., 2005; Yoshida et al., 2008). These data seemed contradictory—a warmer temperature suppresses the growth of subtropical species more than it suppresses the growth of temperate species. Such a growth characteristic seems to be advantageous, however, because it allows subtropical species to escape grazing pressure by herbivorous animals. For example, the feeding activity of rabbit fish (*Siganus fuscescens*), a common herbivorous fish in warm temperate Japan, is temperature dependant. It grazes brown algae intensively under warmer temperatures (>25°C), whereas grazing activity is low below 20°C and almost stops at 15°C (Yamauchi et al., 2006). Owing to their growth characteristics, subtropical species can develop shoots during winter when the herbivorous fish is inactive. On the contrary, temperate species are defenseless and vulnerable to grazing by these fish owing to the year-round growth pattern of their stands.

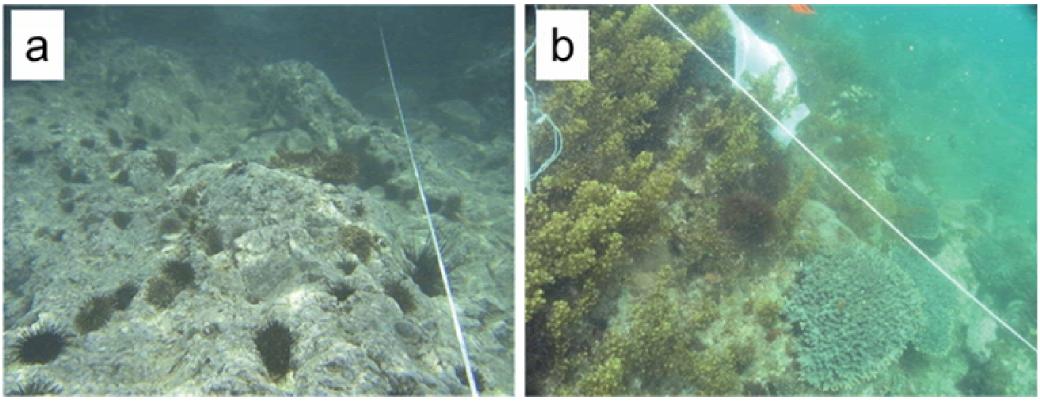


Fig. 6. *Isoyake* (a) and subtropical *Sargassum duplicatum* with co-occurring corals (b). Both were photographed at Ainan, Ehime Prefecture, in the Bungo Channel.

Another advantageous characteristic of subtropical species revealed by our study is their high regenerative ability, which enables them to develop stands under high grazing pressure. A high frequency of new budding production from holdfasts is observed in several subtropical species (e.g., *S. carpophyllum*) when the holdfasts are experimentally excised from their thalli (Fig. 9a). On the contrary, less or no budding occurs in the excised holdfasts of temperate species—e.g., *S. yamamotoi*, one of major species in warm temperate regions. Many subtropical *Sargassum* can develop stands in specific environments with relatively severe physical turbulence—for example, strong surge or frequent sand movement (Fig. 9b). Holdfasts of subtropical *S. carpophyllum* can endure being buried in sand for several months, and after reappearing, they can generate new thalli. Less grazing occurs in such severe environments, and even when grazing does occur, the high regenerative ability of subtropical species allows them to grow despite physical damage.

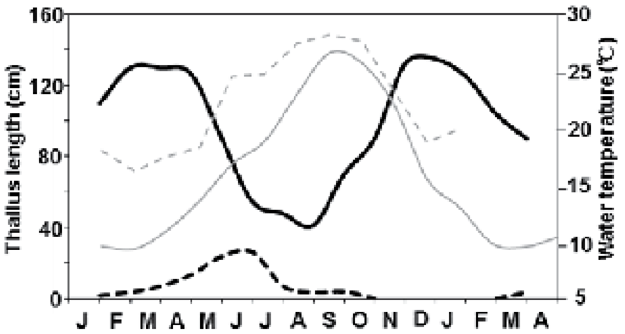


Fig. 7. Schemes of seasonality of temperate and subtropical *Sargassum*. The bold, solid line indicates seasonal growth of temperate *S. fulvellum* (from Yoshida et al., 2008), and the bold dotted line indicates subtropical *S. duplicatum* (from Shimabukuro et al., 2007). The thin solid and dotted lines indicate water temperature in their habitats, respectively.

2.2.3 Mechanisms of the changes and human countermeasures

Although many factors (e.g., nutrient depletion, change in food web structure related to overfishing of predators) are possible contributors to *Isoyake*, the increase in coastal water temperature is one of the most plausible (Fujita et al., 2010). In the past few decades, the mean yearly surface temperature along the warm temperate Japanese coast has increased 0.5°C to 0.7°C (e.g., Serisawa et al., 2004; Shimabukuro et al., 2007). Although extreme rises in summer temperature could cause physiological damage to macroalgae, long-term monitoring also indicates that the temperature increase has been larger in winter than in summer (Hiraoka et al., 2005; Shimabukuro et al., 2007). Rising water temperature in autumn and winter allows herbivorous animals to be active for longer periods. An increase in grazing by these animals may be the most potent cause for the ousting of temperate large brown algae in warm temperate regions. It has been reported that when grazing pressure increases, shallow coastal seabeds shift from being macroalgal dominated to being coral- or coralline algal dominated in tropical and subtropical regions (Lapointe et al., 1997). Are subtropical *Sargassum* extending their distribution in temperate regions of Japan? Some past records indicate that the subtropical species are minor but original members of the coastal flora once dominated by temperate species in southern temperate Japan (Aratake et al., 2007). As the result of environmental change over several decades, subtropical *Sargassum* ecologically adapted to high grazing pressure and has been becoming conspicuous, replacing major temperate species that are more sensitive to grazing (Yoshida et al., 2009).

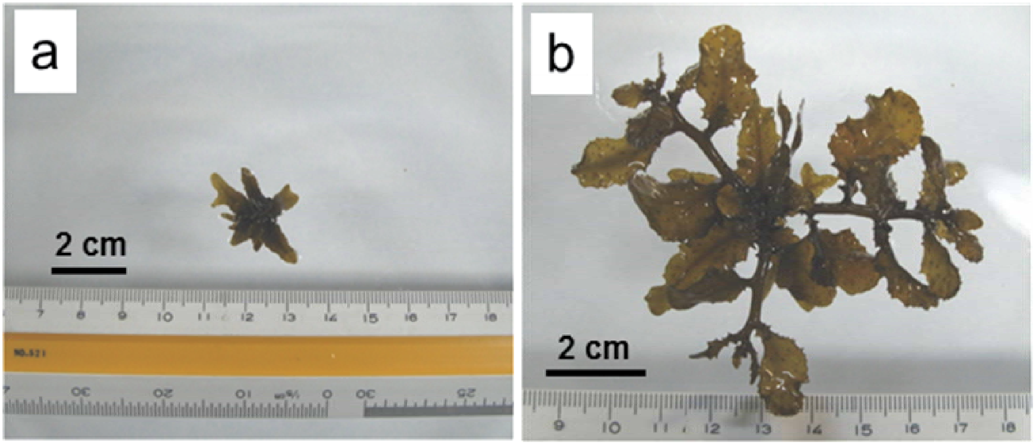


Fig. 8. Growth of subtropical *Sargassum duplicatum* cultured in a laboratory under (a) 24°C, and (b) <18°C.

The mass disappearance of macroalgae in warm temperate coastal Japan has had serious effects on coastal biological productivity, and countermeasures to sustain coastal fisheries are needed. It is well known that physical defense of *Moba* against grazing by using nets or cages and removing herbivores is often effective for recovering macroalgal beds in *Isoyake* areas (Fujita et al., 2010). Another possible countermeasure that protects fisheries production is the exploitation of productivity of the new vegetation of subtropical *Sargassum*. Because subtropical *Sargassum* species have characteristics that differ from those of temperate ones—e.g., seasonality, habitat, stand structure—the ecological roles they could play in the coastal ecosystem should be evaluated (Fujita et al., 2010).

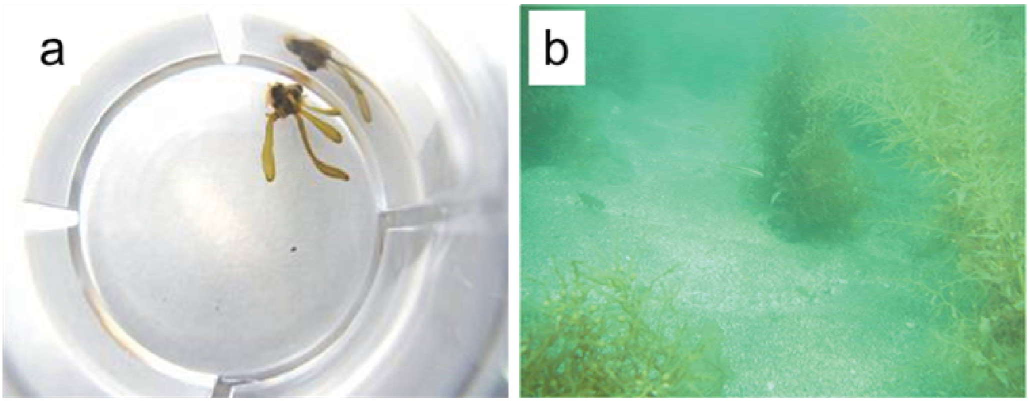


Fig. 9. (a) Regeneration of new buddings from an excised holdfast of *Sargassum carpophyllum*, and (b) a *Sargassum* habitat buried in sand (Kushima, Miyazaki Prefecture).

If coastal water temperature continues to increase as predicted, quantitative and qualitative change in macroalgal beds will extend to cooler regions in Japan. To recognize these changes as soon as possible, fixed survey stations around the Japanese coast have been established for a long-term national monitoring project (e.g., Biodiversity Center of Japan, 2011). One of the most interesting survey points is in the channels between the Pacific regions and the Seto Inland Sea in southern Japan. In the Bungo Channel, a gradient in winter seawater temperature ranges between 6°C and 8°C within ca. 200 km. Within this distance, both luxuriant brown algal beds and *Isoyake* with subtropical *Sargassum* and corals are observed (Yoshida et al, 2009), as shown in Figs. 4 and 6. Ecological and oceanological surveys in this transition zone, or ecotone, between temperate and subtropical areas will provide valuable information about the mechanisms of global warming effects on coastal ecosystems.

2.3 Appearance of a tropical harmful algal bloom species in temperate Japanese coastal waters

The first appearance of *A. tamiyavanichii* was confirmed in a towing plankton net sample at Aburatsubo in Sagami Bay, Japan, in 1988 (Ogata et al., 1990). After that, *A. tamiyavanichii* bloomed for the first time at Shioya Bay in Okinawa Prefecture, Japan, in 1997 and again in 1998, and an outbreak of PSP was confirmed in green muscles fed *A. tamiyavanichii* (Koja et al., 2001). This record is the first of toxification of shellfish caused by this species in Japan. The appearance of *A. tamiyavanichii* was also confirmed in the Seto Inland Sea in 1997 when 6.6 MU g^{-1} of PSP from the edible part of Japanese oysters in Uchinoumi, Tokushima Prefecture (Sato et al., 2001) and 8.8 MU g^{-1} of PSP from muscles and 5.0 MU g^{-1} of PSP from arch shells at Tsuta-cho in Kagawa Prefecture were detected in 1999 (Yoshimatsu et al., 2000)—the first record of PSP outbreaks attributed to this species in the Seto Inland Sea. In 2001, *A. tamiyavanichii* blooms were confirmed in almost all areas of the Seto Inland Sea, and 2.4 MU g^{-1} of PSP was detected in manila clams (Tanada et al., 2003).

The blooming of this species has often been observed not only the Seto Inland Sea but also around the Tsushima, Gotou, and Amami Islands (Fig. 10). This species has also been collected in the Gulf of Mexico, the Straits of Malacca in Malaysia (Usup et al., 2002), the Gulf of Thailand (Fukuyo et al., 1988), and Manila Bay in the Philippines (S. Sakamoto, personal communication). Research has provided some information on the morphology and the ultrastructure of vegetative cells (Phanichyakarn et al., 1993; Wisessang et al., 1993; Balech 1994; Nagai et al., 2003), life cycle (Nagai et al., 2003; Nagai et al., 2008), growth characteristics and toxin production (Kodama et al., 1988; Fukuyo et al., 1989; Ogata et al., 1990; Nagai et al., 2008; Oh et al., 2009), phylogenetic position (Usup et al., 2002), and distribution (Fukuyo et al., 1988) of this species and toxin accumulation in mussels that feed on it (Wisessang et al., 1991; Hashimoto et al., 2002).

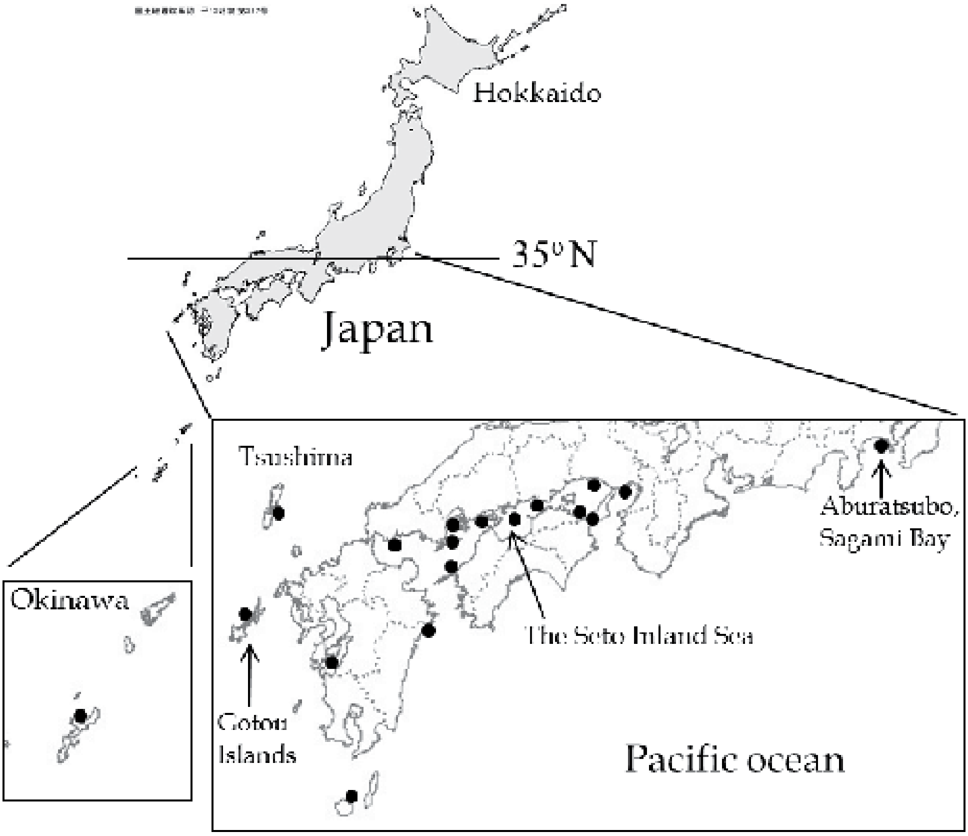
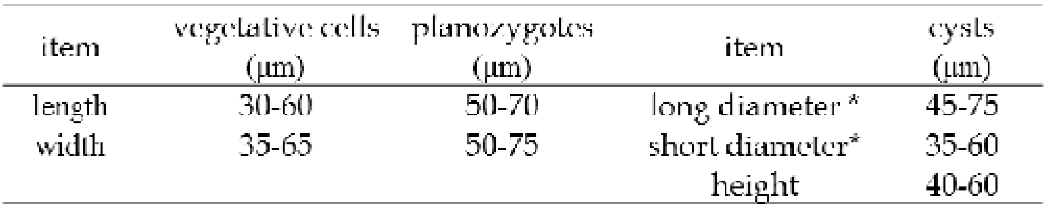


Fig. 10. Occurrences of the toxic dinoflagellate *Alexandrium tamiyavanichii* in Japanese coastal waters. Note that until now, the distribution has been limited in areas south of the northern latitude of 35°C.



item	vegetative cells (µm)	planozygotes (µm)	item	cysts (µm)
length	30-60	50-70	long diameter *	45-75
width	35-65	50-75	short diameter*	35-60
			height	40-60

Table 1. Measurements of cell sizes of *Alexandrium tamiyavanichii* in culture (n=50). *, They were measured from the upper side.

2.3.1 Morphological characteristics of *A. tamiyavanichii*

Vegetative cells of *A. tamiyavanichii* are yellow-brown and contain numerous chloroplasts (Nagai et al., 2003). This species forms long chains that often contain more than 200 cells during the early and middle exponential growth phases under laboratory conditions (Fig. 11a). Cell chains separate into smaller chains or even single cells in the stationary phase. Vegetative cells are 30–60-µm long and 35–65-µm wide, and the sizes drastically change in response to culturing (Table 1). The cell is round to subpentagonal in the ventral view and usually more wide than long. The first apical plate has a ventral pore at the posterior portion of the right anterior margin with the fourth apical plates (Fig. 11b). The most typical characteristic of this species is that the sulcal anterior plate has a triangular or rectangular anterior expansion, and the anterior and posterior portions are delimited by a transverse rib, but the two parts are inseparable (Balech, 1994; see Fig. 11b).

2.3.2 Toxin composition in *A. tamiyavanichii*

Vegetative cells of *A. tamiyavanichii* collected from the Tokushima Prefecture (eastern Seto Inland Sea) in 1999 showed PSP toxicity, of which 83 mol% was accounted for by gonyautoxin (GTX) 2, GTX3, and GTX4 with fluorescent high-performance liquid chromatography analysis. Its specific toxicity was 112.5 fmol cell^{-1}, and 1 MU was equivalent to 7,200 cells (Hashimoto et al., 2002). The toxic component of the Aburatsubo strains from Sagami Bay, Japan, was dominated by the highly potent carbamate toxin GTX4 (37–45 mol%; Ogata et al., 1990). The toxic composition observed in samples from the Tokushima Prefecture was closely related to that of strains isolated from the Gulf of Thailand (Ogata et al., 1990; Wisessang, et al., 1991). The toxic components of *A. tamiyavanichii* clonal strains, isolated from the Seto Inland Sea, showed that *N*-sulfocarbamoyl (C-) 2 and GTX4 were the main toxins, and C3+4, GTX2+3, GTX5, neo-saxitoxin (neo-STX), and STX were minor components (Oh et al., 2009). The percentages of the main toxins (C2 and GTX4) are closely related to those of *A. tamarense* and *A. catenella*. Potent toxic components including GTX2+3 and STX existed at higher concentrations than was the case with *A. tamarense* and *A. catenella*, however. Additionally, the average toxicity of *A. tamiyavanichii* was higher than that of *A. tamarense* and *A. catenella*. Toxic components detected from several shellfish, including the mussel *Mytilus galloprovincialis*, the Pacific oyster *Crassostrea gigas*, and the ark shell *Scapharca broughtonii* after the large-scale bloom of *A. tamiyavanichii* in the eastern Seto Inland Sea in early December 1999 were similar to those detected in *A. tamiyavanichii* plankton cells (Hashimoto et al., 2002), and the PSP toxicity in the shellfish that were higher than regulation levels (4 MU g^{-1}) were seen when the abundance of *A. tamiyavanichii* in the bloom was greater than 30 cells mL^{-1} (Yoshimatsu et al., 2000; Sato et al., 2001; Tanada et al., 2003).

2.3.3 Sexual reproduction in *A. tamiyavanichii* under laboratory conditions

In one study, encystment through sexual reproduction was observed in 54 pairs (39.7%) of 136 pairs of *A. tamiyavanichii*, which included 16 that were self-crossing, using 16 clonal strains under laboratory conditions (Nagai et al., 2003). Neither planozygote formation nor encystment was confirmed in any of the self-crossings. These results clearly show that *A. tamiyavanichii* is heterothallic—i.e., compatible strains of an opposite mating type are required for sexual reproduction. Crossing experiments have been carried out in a modified f/2 medium (made up with 1/6 nitrate and phosphate, 1/3 metals and 1/10 vitamins; see

Nagai et al., 2004) using a sexually compatible mating pair under the same conditions used in growth experiments. Vegetative cells in the mixed culture at 25°C grew exponentially, and the growth reached a peak (2,400 ± 200 cells mL^{-1}) on day 8, with density thereafter decreasing gradually owing to an increase in the number of planozygotes and resting cysts (Fig. 12). Suspected gametes began to appear in the culture 2–3 days after the crossing experiment started (see Fig. 12). These cells were morphologically indistinguishable from gametes (hologamy), but the swarming of single vegetative cells, which make an association of sexual mating behaviour as seen in *A. tamarense*, were often observed in the early and middle exponential growth phases.

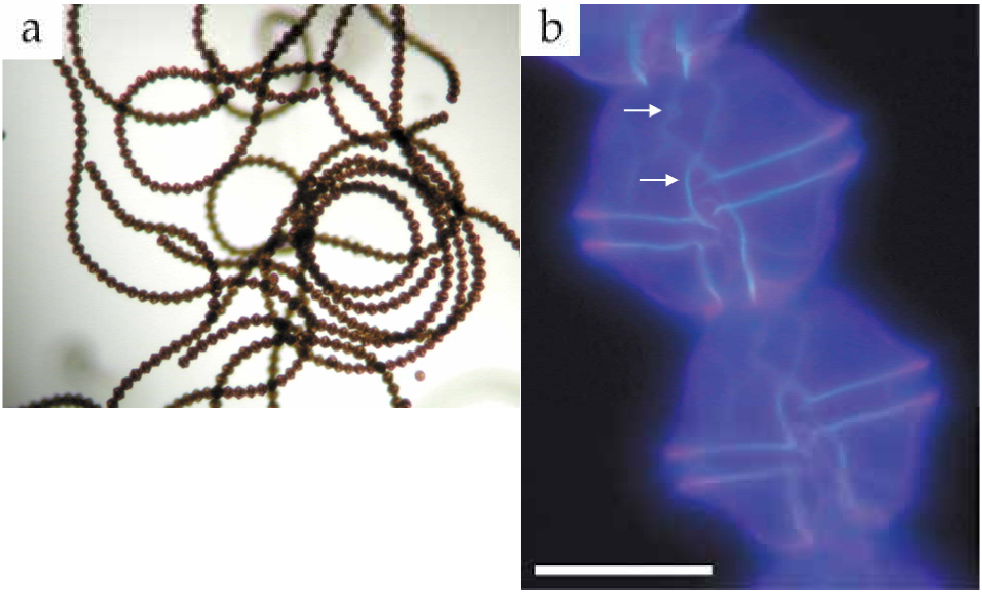


Fig. 11. Vegetative cells of *Alexandrium tamiyavanichii*. (a) A long chain consisting of more than 200 cells. (b) Vegetative cells stained with calcofluor-white. Arrows indicate a ventral pore and a transverse rib. Scale bar is 25 µm. Observation in (a) was made using a Nikon TE-300 light microscope (Tokyo, Japan) and in (b) using an epifluorescence microscope under ultraviolet and blue light excitation.

Pairs of fusing gametes were isolated in the wells of a microplate with 1 mL of the culture medium to observe the sequence of zygotes. The gametes swam rapidly and made contact with each other bilaterally (gametes remained side by side; Fig. 13a), and the couplets swam helicoidally with rotation due to the almost perpendicular orientation of their longitudinal flagella, as reported in *A. pseudogonyaulax* (Biecheler) Horiguchi ex Yuki et Fukuyo by Montresor (1995). The length of this phase was variable, and a couplet was observed swimming for more than 1 hour before conjugation, whereas others started fusing sooner and formed a planozygote (Fig. 13b, c). Conjugation took place through the progressive engulfment of one gamete by the other, which consequently increased in size (see Fig. 13c). Sexual reproduction was by conjugation of isogametes, although the cell length of one mating gamete was often up to 1.2–1.3 times longer than that of the other. Plasmogamy was completed 60–80 min after conjugation started and produced a planozygote with one transverse and two longitudinal flagella (Fig. 13d). There was no trace of thecal plates near the newly formed zygotes, and only the thecal plates of the gamete that engulfed the other gamete appeared to be maintained as the zygotic thecal plates.

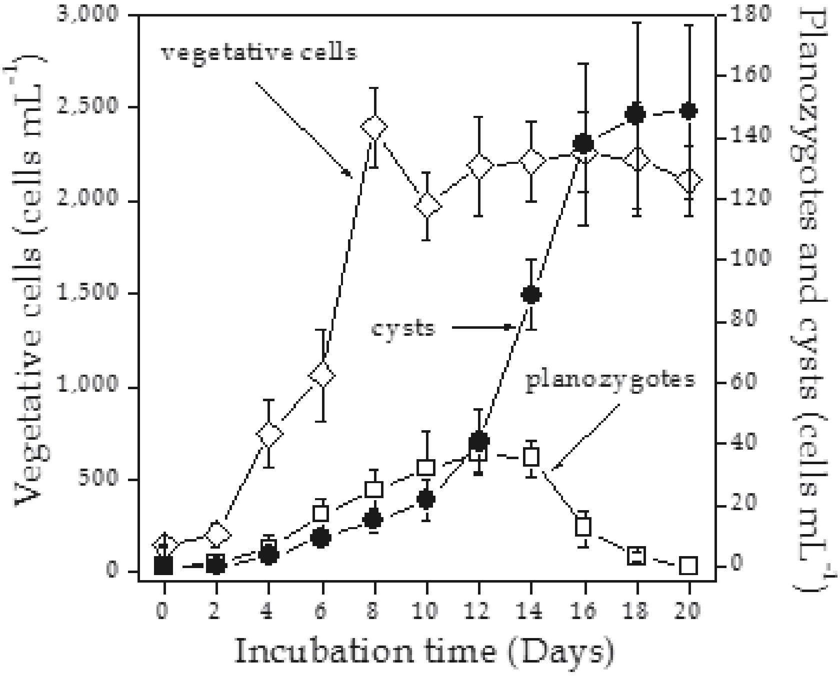


Fig. 12. Encystment of an *Alexandrium tamiyavanichii* batch culture at 25°C. Time-course measurements were carried out to observe the sexuality and the encystment process in 1.9 mL of modified f/2 medium in Iwaki 24-well microplates (Chiba, Japan) under an irradiance of 100–150 μmol m^{-2} s^{-1} provided by cool-white fluorescent lamps with a 12:12 h light:dark cycle (Nagai et al., 2003, 2008). The culture medium contained 1/6 nitrate and phosphate, 1/3 metals, and 1/10 vitamins. Two compatible strains of AT0112T06 and AT0112F06 were mixed and incubated for 20 days. A portion of the *Alexandrium* culture (100 μL) was sampled every 2 days, and the numbers of vegetative cells, planozygotic cells, and resting cysts were counted using a microscope.

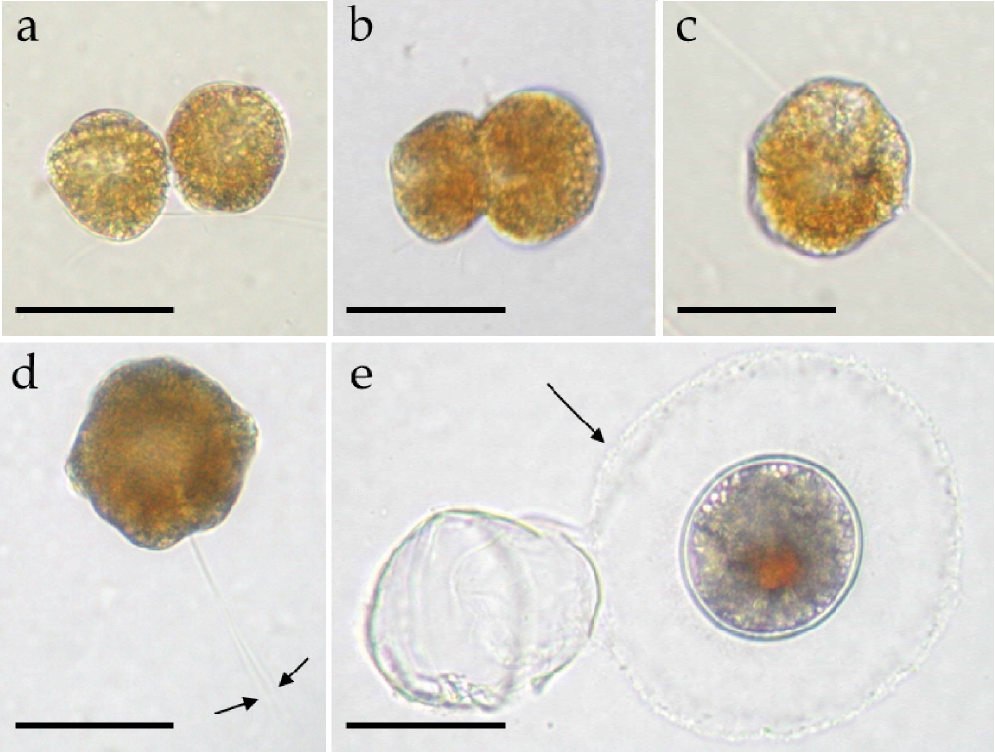


Fig. 13. Life cycle stages of *Alexandrium tamiyavanichii* obtained in the sexual reproduction experiment described in Fig. 12 (Nagai et al., 2003). Scale bars are 50 μm (all at the same magnification). (a) Mating pair of isogametes entwined by their flagella (initial contact phase). (b) Conjugating gametes. (c) Completion of conjugation in which one gamete engulfs the other. (d) Planozygote with two longitudinal flagella indicated by arrows. (e) Threshing during encystment and resting cysts covered with transparent mucilaginous matter indicated by arrows. Observation was made using a Nikon TE-300 light microscope (Tokyo, Japan).

Planozygotes were typically a more blackish color compared with vegetative cells and tended to swim more slowly; therefore, they were readily distinguishable. Planozygotes were 50–70-μm long and 50–75-μm wide and larger than vegetative cells (see Table 1). In the transformation process of planozygotes to hypnozygotic cysts, a small number of planozygotes failed to thresh, but most succeeded and after 2–3 days the cysts were covered with transparent mucilaginous matter as seen in *A. tamarense* and *A. catenella* reported by Turpin et al. (1978), Yoshimatsu (1981), and Nagai et al. (2004) (Fig. 13e). Cysts were vertically compressed (Fig. 14a, b) or spherical (Fig. 14c, d) and 45–75-μm long, 35–60-μm wide, and 40–60-μm high. Scanning electron microscopy clearly showed that the surface of *A. tamiyavanichii* cysts was smooth and lacked paratabulation (see Fig. 14). The density of planozygotes increased gradually until day 12 (74 ± 13 cells mL^{-1}) and then decreased on day 14 owing to transformation into cysts. The period from planozygote formation to transformation into cysts depended on the individual planozygote and varied from 2 to approximately 10 days. Cyst formation was observed on day 4 and encystment continued exponentially until day 16, with density slightly increasing until the end of the incubation (150 ± 30 cysts mL^{-1}; see Fig. 12).

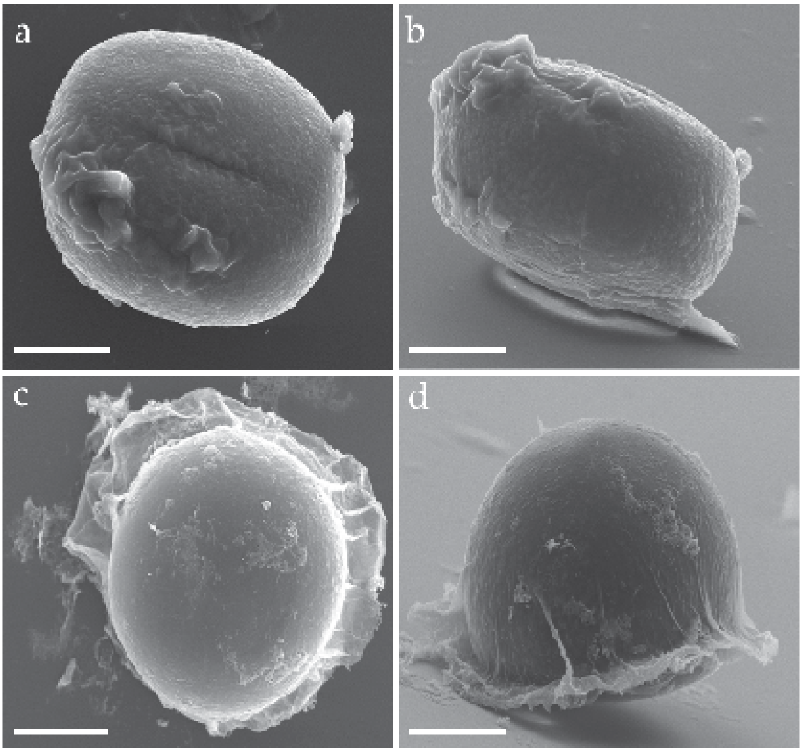


Fig. 14. Scanning electron microscopic observations of resting cysts in *Alexandrium tamiyavanichii* (Nagai et al., 2003). Scale bars are 20 μm (all at the same magnification). (a) Vertically compressed cyst without any paratabulation on the surface (view from above). (b) Side view of the cyst shown in (a). (c) Spherical cyst covered with transparent mucilaginous material (viewed from above). (d) Side view of the cyst shown in (c).

2.3.4 Effect of temperature on vegetative growth and sexual reproduction in *A. tamiyavanichii* and *A. tamarense* under laboratory conditions

Vegetative growth in *A. tamiyavanichii* has been observed at temperatures ranging from 20°C to 32.5°C, and the culture strains survived briefly at 17.5°C and 35°C but died quickly at 15°C (Fig. 15a). Optimum growth was seen around 27.5–30°C, and the growth rates were 0.71–0.76 divisions day^{-1} (Fig. 15b). The maximum yield of vegetative cells ranged from 300 ± 41 cells mL^{-1} at 20°C to 3,513 ± 452 cells mL^{-1} at 30°C, and the yields were highest at 27.5–30°C (see Fig. 15a). The effect of temperature on growth rate tended to be very similar to that for the maximum yield of vegetative cells. Encystment was observed at temperatures between 20°Cand 32.5°C and cyst yields ranged from 7.0 ± 2.6 cysts mL^{-1} at 20°C to 148 ± 28 cysts mL^{-1} at 25°C (Fig. 15c). The cyst yield was highest at 25°C and significantly higher than that at temperatures between 20°C and 32.5°C (*t*-test, $P < 0.005–0.001$). Cyst formation (cyst yield/maximum yield of vegetative cells × 100 [%]) ranged from 0.1 ± 0.1% at 32.5°C to 6.2 ± 1.1% at 25°C (data not shown).

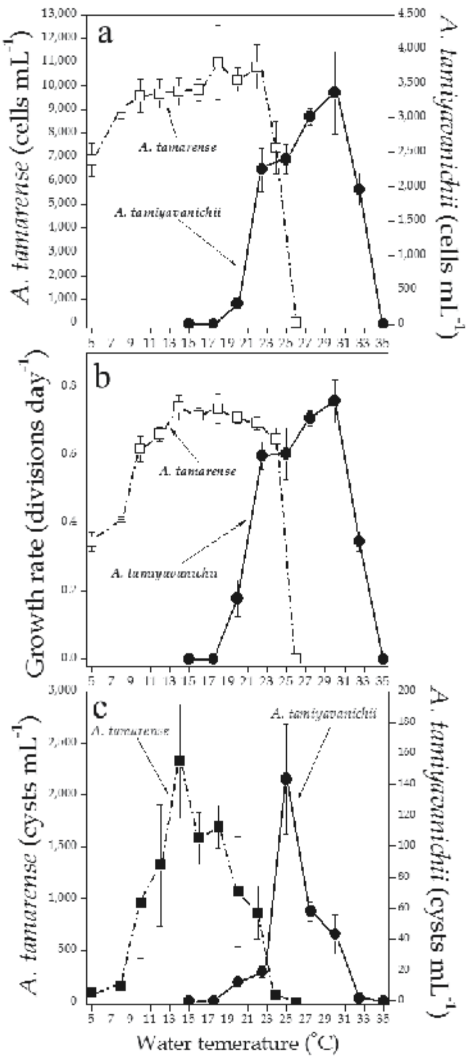


Fig. 15. Effect of temperature on vegetative growth and resting cyst formation in *Alexandrium tamiyavanichii* and *A. tamarense* under laboratory conditions. (a) Maximum yields of vegetative cells at each temperature. (b) Growth rates of vegetative cells at each temperature. (c) Maximum yields of resting cysts at each temperature. Effect of temperature on vegetative growth was investigated at nine temperatures between 15°C and 35°C in *A. tamiyavanichii*, and 11 temperatures between 5°C and 26°C in *A. tamarense* under the conditions described in Fig. 12 (except temperature). Two compatible strains of AT0104H15 and AT0104H26 were used to study *A. tamarense*. After pre-incubation, both strains were mixed at each temperature setting and incubated for 20 days (*A. tamiyavanichii*) and 30 days (*A. tamarense*). Five wells of each were used for counting motile cells and cysts, and the maximum yields of vegetative cells and cysts. The number of vegetative cells counted using the microscope, and the growth rates (divisions day^{-1}) in the exponential growth phase were calculated using the method of Guillard (1973).

In Japanese coastal waters, the toxic dinoflagellate *A. tamarense* was reported mostly along the northern Pacific coast, such as in the Hokkaido and Tohoku regions, until the 1980s (Uchida et al., 1980; Fukuyo, 1982; 1985; Sekiguchi et al., 1986). Since the 1990s, however, *A. tamarense* has become a conspicuous species in southwestern Japan (Yamamoto & Yamasaki, 1996; Kotani et al., 1998), especially in Hiroshima Bay (Asakawa et al., 1995; Yamaguchi et al., 1995; Itakura et al., 2002; Yamaguchi et al., 2002). In laboratory cultures of *A. tamarense* isolated from Hiroshima Bay, vegetative growth was observed at temperatures ranging from 5°C to 24°C, and the maximum yields of motile cells ranged from 6,880 ± 716 cells ml^{-1} at 5°C to 10,980 ± 1,553 cells ml^{-1} at 18°C. No growth was seen at 26°C (see Fig. 15a, b). The growth rate ranged from 0.34 ± 0.03 divisions day^{-1} at 5°C to 0.74 ± 0.04 divisions day^{-1} at 14°C and 18°C (see Fig. 15b), and the rates at 5°C and 8°C were remarkably lower than those at the other temperatures. The range of growth rates between 10°C and 24°C was 0.62–0.74 divisions day^{-1}. Encystment was observed at temperatures ranging from 5°C to 24°C using compatible strains with different mating types, and cyst yields ranged from 68 ± 34 cysts ml^{-1} at 24°C to 2,326 ± 551 cysts ml^{-1} at 14°C (see Fig. 15c). The cyst yields at 5°C, 8°C, and 24°C were remarkably lower than those at the other temperatures. The cyst yield at 14°C was significantly higher than that at temperatures between 10°C and 22°C (*t*-test, $P < 0.05$–0.001). Cyst formation (cyst yield/maximum yield of vegetative cells × 100 [%]) ranged from 0.9 ± 0.5% at 24°C to 23.8 ± 5.1% at 14°C. The effect of temperature on cyst formation tended to be similar to that for cyst yield. Cyst formation at 14°C was also significantly higher than that at temperatures between 10°C and 22°C (*t*-test, $P < 0.05$–0.001; data not shown, but see Nagai et al., 2004). Therefore, the optimal temperature for encystment of *A. tamarense* strains from Hiroshima Bay is approximately 14°C.

2.3.5 Effect of temperature on germination of resting cysts in *A. tamiyavanichii* under laboratory conditions

Experiments have been conducted to examine the germination physiology of resting cysts obtained from laboratory cultures of *A. tamiyavanichii* under laboratory conditions after storage at nine temperatures ranging from 5°C to 30°C for several months in darkness. The experiments were conducted at 25°C or at each temperature at which the resting cysts had been stored. In the experiment at 25°C, the first excystment (germination) was confirmed on day 7 because the cysts had been stored in darkness at 17.5°C to 30°C (3.3–10.8% germination success—i.e. germinated cysts/total cysts × 100 [%]), and germination was confirmed at all temperatures except 5°C on day 15 (4.2–91.2%). Germination success was higher than 60% at temperatures between 10°C and 17.5°C (Fig. 16a). After day 30, germination success at 10°C continued to be approximately 50%, but >80% at 15°C to 27.5°C. Germination success at 30°C increased after day 51, and high germination success (>80%) was observed after that. No germination was confirmed at 5°C throughout the experiment, however. At 7.5°C, germination was seen only on day 15 (4.2%) and day 30 (9.0%). In the germination experiment at each temperature at which cysts were stored in darkness, successful germination was observed at ≥17.5°C, but not at <15°C (Fig. 16b). High germination success (79.4–96.6%) was observed at 20°C, 27.5°C, and 30°C after day 64. At 17.5°C, germination was confirmed after day 79, but no vegetative growth was seen after germination. Accordingly, the optimum temperature for storage in darkness and germination in resting cysts in *A. tamiyavanichii* is around 25°C, and this species has no dormancy period, or if it does, it would be within 1 week. A germination experiment was carried out at 25°C to examine the germination potential of resting cysts after 3 months of storage in darkness at each temperature, and germination was observed on day 2, although germination success was low (0.8–8.8%). After that, active germination was confirmed in the resting cysts stored at 15–25°C, with germination success >70% on day 6 (Fig. 16c).

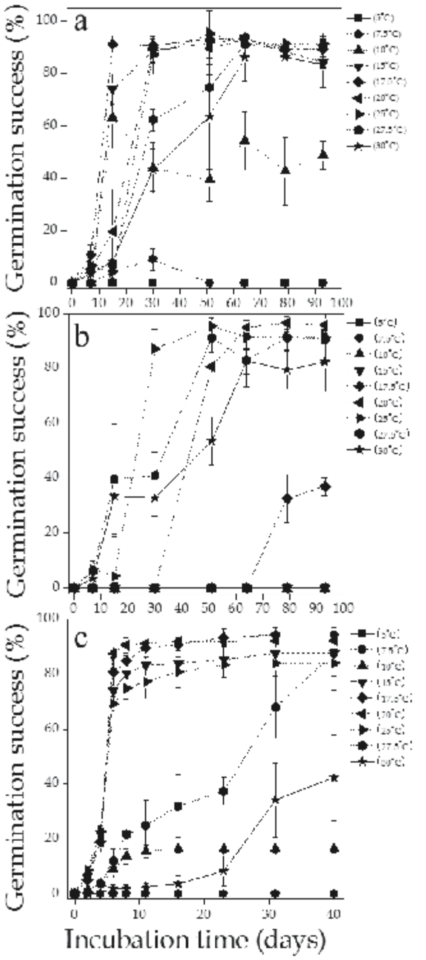


Fig. 16. Effect of temperature on germination in resting cysts of *Alexandrium tamiyavanichii* under laboratory conditions. Cysts were produced under appropriate incubation conditions at 25°C by mixing two compatible strains of AT0112T06 and AT0112F06 as described in Fig. 12. Resting cysts were harvested 3 weeks after the start of the encystment experiment. Cysts were stored in darkness at nine temperatures between 5°C and 30°C to investigate the period of mandatory dormancy of cysts. Some of the cysts (14–65 cysts) were picked up on days 7, 15, 30, 51, 64, 79, and 93 days and incubated at 25°C (a) and at the same temperature at which they had been stored (b). One month after incubation under the light conditions described in Fig. 12, the number of germinated cysts, dead cysts, and total cysts were measured under an inverted microscope. The percentage of germination success was calculated (germinated cysts/total cysts × 100 [%]).Resting cysts stored at the nine temperatures for 90 days were incubated under appropriate light conditions at 25°C (c). Germination success was calculated every 2–9 days for 40 days.

2.3.6 Difference in life cycle strategies of *A. tamiyavanichii* and *A. tamarense*

A. tamiyavanichii grows at temperatures ranging from 20°C to 32.5°C and the optimum temperatures for growth are 27.5–30°C (see Fig. 15). *A. tamiyavanichii* cannot survive below 15°C, however, demonstrating the growth physiology of a typical tropical microalgal species (Ogata et al., 1990; Nagai et al., 2008). Actively swimming vegetative chains of this species have been confirmed around 15°C in the Seto Inland Sea at the end of blooms in the middle of December (Yoshimatsu et al., 2000; Tanada et al. 2003; Nagai et al. 2008), suggesting a higher tolerance for low water temperatures in natural populations than in laboratory cultures. Anderson & Wall (1978), Anderson & Morel (1979), and Itakura & Yamaguchi (2001) have emphasized the importance of *Alexandrium* cysts as the seed population for overwintering, bloom initiation, and cyst dispersal within estuaries and near-coastal waters—i.e., the geographical spread of the population. Hallegraeff (1998) has also pointed out the role of dinoflagellate cysts in settling and spreading over a wider distribution through transportation either in ship's ballast water or associated with the movement of shellfish stocks from one area to another. *A. tamiyavanichii* produces resting cysts at temperatures of 20–32.5°C in laboratory cultures, and the optimal temperature for encystment is 25°C (see Fig. 15). Interestingly, this temperature is slightly lower than the optimal temperature for vegetative growth (see Fig. 15). Conversely, resting cyst production in *A. tamarense* is observed at temperatures of 5–24°C in laboratory cultures (see Fig. 15). The optimal temperature for encystment is around 14°C, and cyst formation is ca. 25%. Accordingly, these data clearly indicate that *A. tamiyavanichii* produces resting cysts at remarkably higher temperatures and does not produce resting cysts at high density compared with *A. tamarense*. In the coastal areas around Hokkaido in Japan, *A. tamarense* usually appears in early spring when the water temperature is 1–3°C (start of blooming) but appears when waters temperatures reach 8–10°C in western Japan. *A. tamarense* has a vegetative stage that usually lasts for <4 months in the water column (Itakura et al. 2002; Nagai et al. 2007), although the duration of the vegetative stage varies with the water temperature as well as with the pattern of annual water temperature fluctuation. This species disappears in the water columns when the water temperature exceeds ca. 15–16°C, clearly indicating an adaptation to cold waters (Itakura et al., 2002; Nagai et al., 2007; Shimada et al., 1996, 2010).

It is assumed that in the annual life cycle of *A. tamarense*, to appear for a limited time as vegetative populations in the water column in a year and to endure the most unsuitable season (high water temperatures), the organism has developed a survival strategy that produces high amounts of resting cysts at the end of blooms (Itakura et al., 2002; Nagai et al., 2007). Conversely, *A. tamiyavanichii* is a typical tropical species that blooms in stable environmental conditions—i.e., little fluctuation in annual water temperature. Therefore, no preparation is necessary to survive adverse environmental conditions (e.g., unsuitably cold winter season) through the production of high amounts of resting cysts as seen in *A. tamarense*. Regarding germination, *A. tamiyavanichii* also cannot germinate at temperatures below 20°C, and although occasional germination was observed at this temperature, the organism did not grow. *A. tamiyavanichii* loses the ability to germinate when kept at the temperatures below 10°C in darkness even for a week or so, even though the resting cysts look alive. Conversely, resting cysts of *A. tamiyavanichii* have high potential for germination, even when kept in darkness for more than 3 months at relatively high temperatures of 20–30°C (see Fig. 16). Thus, we can conclude from the results of these laboratory experiments that *A. tamiyavanichii* is the species with the life cycle strategy that adapts to tropical environmental conditions, thereby resulting in limited distribution, until now, in areas south of a northern latitude of 35 degrees.

2.3.7 Environmental conditions that allow the appearance of *A. tamiyavanichii* in the Seto Inland Sea

In the Seto Inland Sea, the first appearance of *A. tamiyavanichii* has been observed in middle and late August when water temperature rises to around 28°C, and the species has grown up to 30 cells mL^{-1} by late autumn (Yoshimatsu et al., 2000). Tropical species cannot survive at water temperatures lower than 15°C, and they die when temperatures drop below 15°C (Ogata et al., 1990; Nagai et al., 2008). Vegetative populations of this species are not found in middle December, therefore (Fig. 17). We speculate that this species produces durable resting cysts when growing in water columns as vegetative populations, perhaps in November-December when its abundance reaches its maximum, and resting cysts overwinters in surface sediments as seed populations between December and early June, during which it cannot survive as vegetative populations (<15°C). Accordingly, this life cycle characteristic enables this species to appear for 6–7 months a year in the water column. *A. tamiyavanichii* begins to germinate next in the middle of June, when the bottom water temperature exceeds 20°C, and swims out as a vegetative population in water columns. These characteristics strongly suggest that cysts play an important role in prolonged overwintering in surface sediments as a seed population in temperate Japanese coastal waters. Also, the fact that planozygotes have been observed in sea water samples collected from the Seto Inland Sea during *A. tamiyavanichii* blooms in 2001 and that appearances of this species have since been observed often not only in the Seto Inland Sea but also around Tsushima and Gotou Islands imply that they may have gained a niche and become settled in this coastal area. Moreover, *A. tamiyavanichii* might be transferred to other areas of Japan by natural and human-assisted dispersals, expanding its distribution.

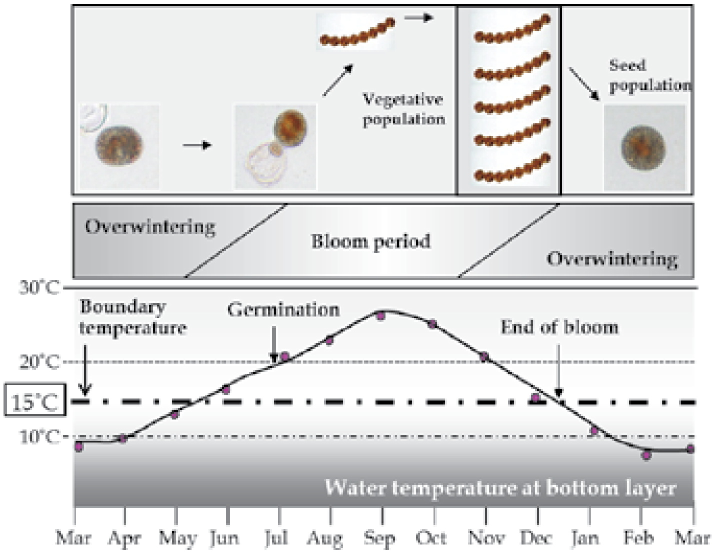


Fig. 17. A conceptual diagram showing the relationship between bottom water temperature and bloom mechanism in *Alexandrium tamiyavanichii* in the Seto Inland Sea. The solid line shows the change in water temperature in Hiroshima Bay (see Fig. 10).

But why does *A. tamiyavanichii* bloom during September–December and not during August–September in western Japan? We have investigated cyst abundance in the surface sediments collected from several locations in the Tokushima Prefecture region of the eastern Seto Inland Sea just after the dense bloom and carried out a germination experiment using 10 g of wet sediments with seawater under appropriate incubation conditions for germination and vegetative growth. No germinated cells were detected, however. We speculate, therefore, that *A. tamiyavanichii* is undetectable in July or August if the resting cysts germinate and begin blooming when the water temperature exceeds 20°C in mid-June (see Fig. 17), because cyst abundance is too low to grow to detectable levels in July-August. Occurrences of bloom in this species, resulting in PSP outbreaks in shellfish, are recognized as a new biological threat in western Japan. We have begun investigating the origin of the Japanese population of this species using highly polymorphic genetic markers (Nishitani et al., 2009).

3. Conclusion

The increase in atmospheric carbon dioxide concentrations caused by human activities has influenced the change of world's ocean environments such as increasing water temperature, decreasing sea ice, and causing acidification (Tadokoro et al., 2008). It has been suggested that enhanced stratification, caused by the increases in the surface layer temperature, is decreasing the nutrient supply from the subsurface layer hindering the primary productivity over a large area of the North Pacific Ocean, resulting in the changes of marine ecosystems in primary productivities and seasonal succession in phytoplankton (Ono et al., 2002), zooplanktons (Aoyama et al., 2008), fish (Tian et al., 2006; Shida et al., 2007; Masuda, 2008) and coral (Nojima & Okamoto, 2008). In this chapter, we demonstrated the influence of water temperatures on the changes of habitat of microalgal species or the Isoyake phenomena and the introduction of a toxic phytoplankton from tropical regions to Japanese coastal waters. Thus, effects of global warming on marine ecology have been studied with high research activities. In future, it is highly possible that the influence of global warming on marine ecosystems will be more prominent, therefore, continuous efforts for environmental and biological monitoring would be crucial.

4. Acknowledgement

We are grateful to Dr. T. Kamiyama, National Research Institute of Fisheries and Environment of Inland Sea, Fisheries Research Agency of Japan, for his useful suggestions and encouragement during this study. This work was supported in part by a grant from the Fisheries Research Agency of Japan.

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14

Vulnerability of South American Pinnipeds Under El Niño Southern Oscillation Events

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1. Introduction

The fur seal and sea lions, as well as other marine vertebrates along the Peruvian coast, were truly the eyewitness of cyclic events of global changes in the Pacific Ocean during *El Niño* Southern Oscillation (ENSO) events. In November 1997, the Punta San Juan Reserve (15°22'S, 75°12'W) concentrated with the National Reserve of *Paracas* (13°54'S) and Punta San Bernardo (15°09'S), over 90% of the Peruvian fur seal and sea lion populations (Majluf & Trillmich, 1981). The ENSO event developed unexpectedly and rapidly early in February of that year and became more intense than anticipated, with sea surface temperatures reaching up to 9°C in some locations along the Peruvian coast (Glantz, 2001). The 1997-98 ENSO was considered the "El Niño of the twentieth century", challenging the 1982-83 event in terms of intensity, marine mortality and economic loss.

The ENSO is a climatological phenomenon characterized by anomalous conditions in the atmosphere and ocean that are mainly related to warming of the sea surface temperature (SST) from 2°C to 9°C along the coast of Ecuador and Peru (Glantz, 1996). At intervals of two to seven years (Cane, 1983), the Humboldt Current upwelling system, which is the richest in the world (Cushing, 1982; Idyll, 1973), is affected by ENSO, with increased SST and reduced primary productivity which directly influences the depth distribution and abundance of Peruvian anchovy, *Engraulis ringens*, the most important prey of the South American sea lion, *Otaria flavescens*, and South American fur seal, *Arctocephalus australis*, in Peru (Arias-Schreiber, 2003; Idyll, 1973; Majluf, 1992). The South American sea lion and South American fur seal are distributed along the Atlantic and Pacific coasts of South America (from southern Brazil to northern Peru (Capozzo & Perrin, 2008; Rosas et al., 1994; Vaz-Ferreira, 1981, 1982). Nevertheless, the distribution of *O. flavescens* is larger and continuous, while that of *A. australis* has gaps mainly in the central coast of Chile and along the Argentinean coast (Guerra and Torres, 1987; Oliveira et al., 2008; Repenning et al., 1971). In the Peruvian territory these species are distributed among breeding colonies and haul-out areas on both the continent and islands. *O. flavescens* is the most abundant pinniped species with 118,220 individuals, followed by *A. australis* with 15,317 individuals (Imarpe, 2006). Both have a polygynic breeding system with very few males mating with many females (Capozzo & Perrin, 2008; Majluf 1987). These two species of South American seals were hunted intensively for several centuries, and Uruguay became the last country to prohibit hunting in 1991 (Vaz-Ferreira &Bianco, 1998). Nowadays the most important threat to the conservation of these species are the interactions with fishery activities (mainly in the case of *O. flavescens*), and mortality during ENSO events on the Pacific coast.

Starting in February instead of the usual December, this 1997-98 ENSO hit South American fur seals and sea lions at the time when they normally replenish their reserves for the upcoming breeding season in November-December and January-February, respectively (Majluf, 1998). Most of the female sea lions gave birth prematurely in December 1997 and their pups died within hours of birth, probably as a result of a bacterial infection. At the Punta San Juan colony over 2,000 sea lion pups died in a single week. In the same area all the few fur seal pups that were born died within a few weeks. Their mothers had to spend very long periods at the sea foraging (10-20 days) and the pups died of starvation. Adult fur seals and sea lions did not die significantly until January-February 1998, when sea temperature anomalies peaked at 7-8^{o} above normal (Majluf, 1998). As a final outcome, the Peruvian population of both species, sea lions and fur seals, declined roughly 81% and 72%, respectively (Arias-Schreiber & Rivas, 1998; Arias-Schreiber, 2000), as a result of low food availability due to the replacement of cold and nutrient rich waters of the upwelling system with warm, nutrient-deficient and low productivity waters (Majluf & Trillmich, 1981).

Throughout my field work at Peru I recovered hundreds of skulls and skeletons (Figure 1) of marine mammals in order to prepare a scientific collection for the project. All of the collected animals were a consequence of the remarkable mortality caused by this ENSO, and consisted mainly of adult fur seals of both sexes and adult female sea lions. In fact, the national census conducted by *Instituto del Mar del Perú* (IMARPE) along the Peruvian coast from 1996 to 1997 indicated that the sea lion population declined from 144,087 (Arias-Schreiber & Rivas, 1998) to 27,991 individuals in December 1998 (Imarpe, 2006) and the fur seals from 24,481 in December 1996 (Arias-Schereiber & Rivas, 1998) to 8,223 individuals in December 1999 (Arias-Schereiber, 2000). Due to the drastic population declines, the sea lions were classified as vulnerable (Decreto Supremo No. 034-2004-AG) and the fur seals as in danger of extinction along the Peruvian coast (Decreto Supremo No. 013-99-AG).

Trillmich & Ono (1991) comprehensively documented the consequences of the 1982-1983 ENSO event on many species of pinnipeds along the coasts of North, Central and South America in the book "Pinnipeds and El Niño – responses to Environmental stress." The biology of fur seals, sea lions and also elephant seals were deeply affected by this ENSO event. As a result, authors have reported an increase in pup and adult mortality, an increase in foraging trips, changes in migration movements, establishment of new breeding colonies and diminished reproductive success. Most of these conclusions were based on counting numbers before and after ENSO events.

In fact, the census population size (*N*) is usually the only information available for most threatened species. However, for evolutionary matters, the effective population size, not the census number, is the prime concern. The effective population size (*Ne*) is envisioned as the size of an ideal population that has the same rate of increase in homozygosity or gene frequency change as the actual population under consideration (Wright, 1931).

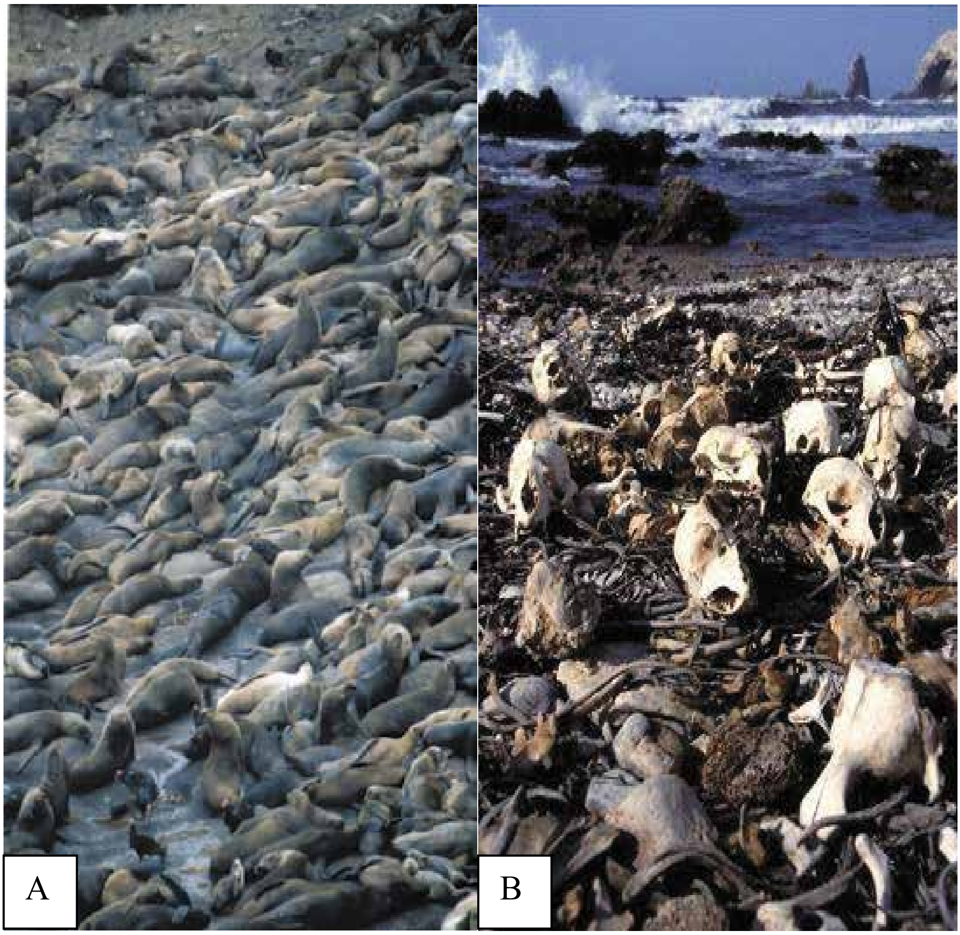

Fig. 1. South American sea lion (*Otaria flavescens*) breeding colony at Punta San Juan, Peru. **A**. during a non-ENSO period (Photo: Larissa Oliveira). **B.** during 1997-98 ENSO (Photo: Patricia Majluf).

An important application of N_e in conservation biology is the estimation of the minimum viable effective population size, particularly in cases like the Peruvian fur seals and sea lions that suffered significant declines after an environmental change due to ENSO. Adequate assessment of viability requires, in part, determining whether the population is large enough to avoid inbreeding or to maintain adaptive genetic variation (Vucetich & Waite, 1998). A population with a high N_e retains high levels of genetic diversity and reduces the probability of effects of inbreeding depression. In contrast, a population with a very low N_e is more susceptible to genetic drift and less able to respond to selection. This is because in small populations there is less genetic variation for natural selection to act upon, and there is a higher probability that beneficial alleles will not be maintained by selection and will instead be lost from the population because of random drift effects (Willi et al., 2007). Furthermore, the estimate of N_e reflects the number of individuals responsible for maintaining the genetic diversity of the species as well as its evolutionary potential. Since the goal is the conservation of species as dynamic entities capable of evolving to cope with environmental change, it is important that the species' evolutionary potential must be retained in order to respond to the current unpredictable climate change scenario (Frankham et al., 2002). The calculation of N_e numbers for the Peruvian coast fur seals and sea lions provide us with a quick insight into the ENSO effects and the short-term consequences of rapid changes in an ecosystem of large vertebrate species. It is important to mention that besides the ENSO effects, the Peruvian sea lions and fur seals also suffered local extinctions in the region due to indiscriminate commercial sealing for fur, meat and oil until 1946, when the hunting of both species of seals (*O. flavescens* and *A. australis*) was prohibited (Piazza, 1969; Tovar & Fuentes, 1984). The sealing was totally banned only in 1959 (Grimwood, 1969). Nevertheless, despite all the legal protection, seal poaching still occurs in order to supply the Asian aphrodisiac market (Lama, 2010).

Another important conservation problem that affects the Peruvian sea lions is the mortality due to interactions with fishery activities (Arias-Schreiber, 1993; Majluf et al., 2002), which have been documented throughout the species' range (Aguayo & Maturana, 1973; Dans et al., 2003; George-Nascimiento et al., 1985; Koen Alonso et al., 1999; Sepúlveda & Oliva, 2005; Szteren & Paez, 2002). The South American sea lion is an opportunistic predator that forages on the most abundant prey (Oliveira et al., 2008), including many benthic and pelagic fish that usually are economically important (Jefferson et al., 2008). As a result, many sea lions were incidentally captured or even intentionally killed by fishery and fish farming operations throughout their range (see Crespo et al., 2009 for a review).

The interactions with the fishery activities could be intensified during ENSO events and increase the mortality of sea lions during this period. In this sense the estimated N_e combined with the current ENSO events and fishery interactions are causes for great concern for the survival of the species. These concerns should be taken into account in future management plans in order to ensure the conservation and protection of this species on the Peruvian coast.

This chapter presents the estimated N_e of the Peruvian population of the South American sea lions and fur seals based on the effects of species polygyny and oscillations in population size in different generations, which includes the fluctuations caused by the most severe ENSO of the century (1997-1998). Also discussed is the importance of this value for the conservation of a population considered to be vulnerable and which faces environmental changes like ENSO events.

2. Effective population size of fur seals and sea lions

Estimated N_e is obtained by genetic (reviewed by Neigel, 1996; Nunney, 2002) and demographic methods (reviewed by Caballero, 1994; Husband & Barrett, 1992; Nunney, 1995; Oliveira et al., 2006; Traill et al., 2007, 2010). Perhaps the most important influence on N_e and a difficult factor to obtain is the temporal oscillation in population size based on long-term census (Vucetich et al., 1997). According to Nunney & Elam (1994), estimates based on data collected during a single season ignore the influence of temporal fluctuation and thus may represent gross overestimates of $N_{e.}$ Vucetich & Waite (1998) highlight the importance of long-term counts in order to improve the accuracy of the estimates of $N_{e.}$ Traill et al. (2010) also reinforce that conservationists working within developing nations rarely have the resources available to collect the long-term demographic and other data necessary to model viability for specific species or taxa. Fortunately, due to the systematic efforts of IMARPE for more than 25 years, results from a long-term census size are available for fur seals and sea lions along the Peruvian coast. Therefore I present and discuss data compiled and published by IMARPE staff (Arias-Schereiber, 2000; Oliveira et al., 2006 and Imarpe, 2006), taking into account the differences in the number of breeding males and females of South American fur seals and sea lions according to N_e calculations proposed by Hedrick (2000) (see below). I also comment on the consequences of this value for the conservation of bottlenecked populations.

For *O. flavescens* I used data from eight census (1984, 1993, 2000, 2002, 2003, 2004, 2005 and 2006 - IMARPE, 2006) (Table 1) and six censuses for *A. australis* (1984, 1992, 1996, 1999, 2005 and 2006 - Arias-Schereiber, 2000; IMARPE, 2006) (Table 2), both activities conducted by IMARPE including the census during 1999 (just after the 1997-1998 ENSO event, Arias-Schereiber, 2000) which covered 71 breeding colonies from South American sea lion and 46 from South American fur seal, from Los Órganos (04°10'S, 81°07'W) to Morro Sama (18°00'S, 70°53'W) and included the most important reproductive colonies of both species on the Peruvian coast (Isla Brava 11°22'S, 77°45'W, Islas Chincha 13°38'S 76°24'W, Punta Arquillo 13°54'S 76°19'W, Morro Quemado 14°20'S, 76°07'W, San Fernando 15°04'S 75°21'W, Tres Hermanas 15°26'S 75°04'W, Punta Atico 16°14'S 73°41'W and Punta Coles 17°42'S 71°23'W, Figure 2).

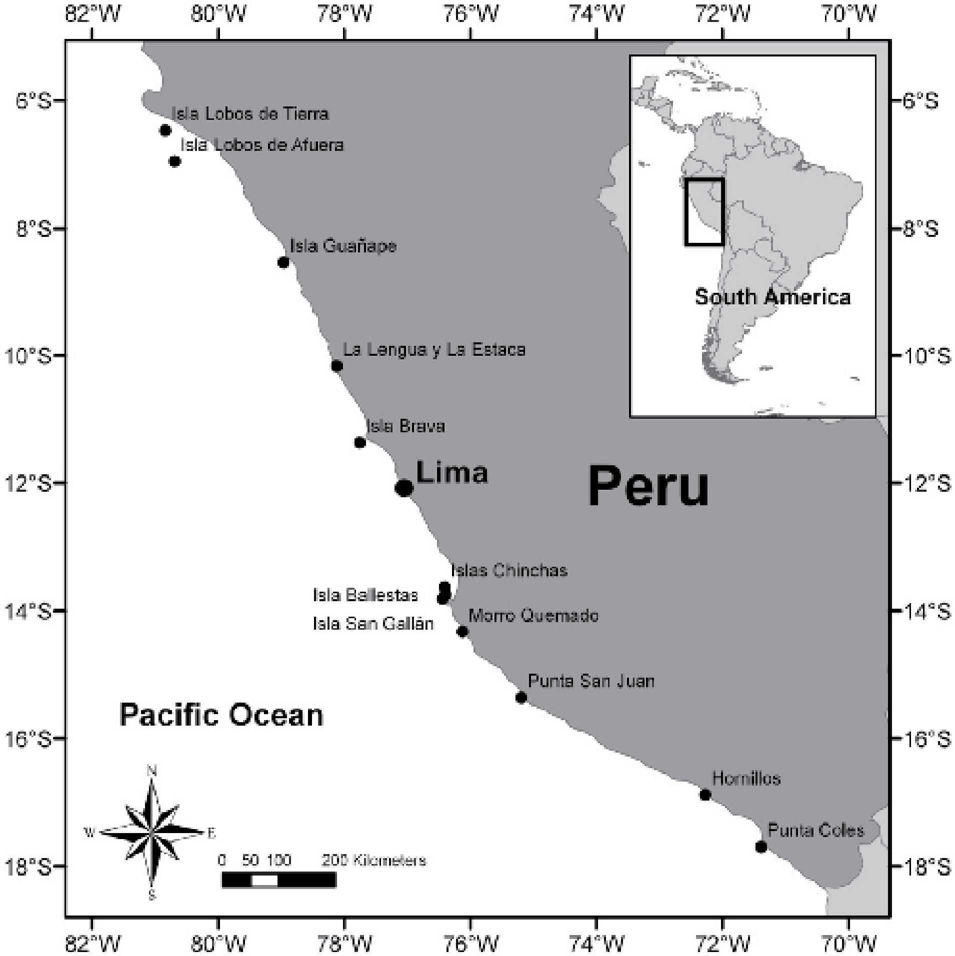

Fig. 2. Most important breeding sites and haul-out areas of South American sea lions (*Otaria flavescens*) and South American fur seals (*Arctocephalus australis*) along the Peruvian coast. These areas were censused between 1984 and 2006 by IMARPE (see text).

In order to estimates N_e we only used censuses that clearly identified adult breeding males and females (Oliveira et al., 2006). Breeding males, also called "territorial males", are considered all the males that copulate on the beach and assemble harems, while other males that are not in reproductive age and do not mate with females are counted as "subadult" males in the census (Imarpe, 2006).

The South American sea lion presents a polygynic breeding system with very few males being able to mate with many females (Capozzo & Perrin, 2008). The South American fur seal also presents a polygynic breeding system. However, it was modified from lekking to a territorial reproductive system on the Peruvian coast, following changes in population density and availability of space for male territories (Majluf 1987). In both systems, a small number of males are able to mate with many females, so the effective population size should be smaller than the actual population size (Crow and Kimura, 1970). The N_e equation that accounts for the effects of unequal sex-ratio is:

$$N_e = \frac{4N_f N_m}{N_f + N_m}$$

where N_f is the number of breeding females and Nm is the number of breeding males. In order to calculate the effect of changes in population size over time we estimated effective population sizes before and after the ENSO event for both species. To calculate the effective population size prior to the ENSO event for fur seals we used data collected for 1996-1997 by IMARPE (Arias-Schreiber & Rivas, 1998), with a census size of 24,481 individuals, among which 2,903 were reproductive males and 10,720 were reproductive females. For sea lions the census size was 76,349 individuals for the year 1993 (Imarpe, 2006), among which 6,435 were reproductive males and 45,080 were reproductive females.

The estimate of N_e for both species before and after the ENSO of 1997-1998 was then used to estimate an overall effective population size, which accounts for the variation in population size in different generations. The N_e for a population that varies in size over generations is given by the harmonic mean of the N_e in each generation (Hedrick, 2000):

$$N_e = \frac{t}{\sum 1/N_i}$$

where N_i is the effective population size in the ith generation and t is the number of generations considered.

The data obtained here was compared to the minimum viable population size (MVP), calculated by Reed et al. (2003), for 102 vertebrate species, including three pinnipeds. The MVP calculated was on average approximately 5,000 breeding age adults. The MVP can be defined as the smallest size required for a population or species to have a predetermined probability of persistence for a given length of time (Shaffer, 1981). All MVP estimates in the study of Reed et al. (2003) are for a 99% probability of persistence for 40 generations and the models for this estimate are comprehensive and include age-structure, the effect of demographic stochasticity, environmental stochasticity, and inbreeding depression (MacCarthy et al., 2001). The authors estimated MVP using three different criteria: the mean carrying capacity required for a 99% probability of persistence for 40 generations (MVPK), the minimum viable adult population size (MVPA), calculated by the software Vortex (Miller and Lacy, 1999) and the effective population size (MVPN_e). These three measures of

MVP all correlated very strongly with each other (r >0.93 in all comparisons) and the choice of measure does not qualitatively change the conclusions reached in any of the analysis.

3. Results and implications for conservation

The oscillations in census size and its respective effective population size by each year censused for *O. flavescens* and for *A. australis* are presented in tables 1 and 2, respectively. The N_e value that accounts for the effects of unequal sex-ratio for the Peruvian population of South American fur seal, *A. australis,* was 1,220 (year 1999) and the N_e prior to the 1997-98 ENSO was 9,138 for 1996. This yielded an overall effective population size of 2,153 which accounts for both the effects of the mating system and variation in population size. For South American sea lions, *O. flavescens,* the estimate N_e that accounts for the effects of unequal sex-ratio was 22,525 (year 1993) and 2,135 for the year 2000, which means that the N_e prior to the 1997-1998 ENSO was 10 times bigger than the N_e for the year 2000. Nevertheless, the overall effective population size given by the harmonic mean of the N_e in each generation was 7,715, which accounts for both the effects of the mating system and variation in population size. In all, the N_e values for the Peruvian population of *A. australis* and *O. flavescens* are 2,135 and 7,715 specimens respectively.

Year census	N	N_{em}	N_{ef}	N_e year
1984	33,816	5,887	18,872	17,948.94
1993	76,349	6,435	45,080	22,524.69
2000	48,088	558	12,323	2,135.31*
2002	62,840	3,166	29,676	11,443.18
2003	75,158	1,942	27,315	7,252.38
2004	59,399	2,665	19,508	9,378.76
2005	100,256	4,314	38,630	15,522.52
2006	118,220	3,786	40,737	13,856.23

*effective population size declined after 1997-1998 ENSO.

Table 1. Census size and effective population size for *Otaria flavescens* along the Peruvian coast.

Year census	N	N_{em}	N_{ef}	N_e year
1984	15,369	1,827	9,596	6,139.16
1992	27,219	2,557	15,670	8,793.15
1996	24,481	2,903	10,720	9,137.54
1999	8,223	3,215	337	1,220.11*
2005	14,320	716	4,725	2,487.12
2006	15,137	919	4,135	3,007.57

Table 2. Census size and effective population size for *Arctocephalus australis* along the Peruvian coast. *effective population size declined after 1997-1998 ENSO.

These results showed that even under the same conditions of ENSO and suffering similar selective pressures, both species presented highly different results, which is probably due to differences in original census size.

The South American sea lion is the most abundant pinniped species along the Peruvian coast, the last census from 2006 counted 118,220 individuals distributed on breeding colonies and haul-out areas on the continent as well as on islands (Imarpe, 2006). On the other hand, the South American fur seal population was estimated 15,317 individuals for the same year, after a fast recovery from the 6,257 remaining fur seals after 1997-98 ENSO (Imarpe, 2006). It is obvious that the census size population declined significantly for both species. However, are these remaining N_e critical for the conversation of both species along the Peruvian coast?

The calculated N_e for the Peruvian population of *A. australis* (N_e = 2,135) seems extremely large when compared with another pinniped species (14 Guadalupe fur seals (*Arctocephalus townsendi*) in 1954 (Hubbs, 1956); 20 Northern elephant seals (*Mirounga angustirostris*) in 1985 (Hedrick, 1985) and another 596 in 2003 (Reed et al., 2003); 3,249 Southern elephant seals (*M. leonina)*; 76 Hawaiian monk seals (*Monachus schauinslandi)* and 2,344 grey seals, *Halichoerus grypus,* (Reed et al., 2003)). However, according to Reed et al. (2003), for 102 vertebrate species, including three pinnipeds, the minimum viable population size (MVP) calculated was on average approximately 5,000 breeding age adults. The mean N_e estimated for 102 vertebrate species was 1,752 individuals (SD = 156) (Reed et al., 2003), which is a very close value to the 2,153 individuals estimated for the Peruvian population of *A. australis.* In this 23 sense the estimated N_e for the Peruvian population of fur seal represents a critical value, because it is significantly lower than the average MVP and close to the N_e values estimated for vertebrates.

Moreover, recently Oliveira et al. (2009) found that this population decline affected significantly the N_e, causing a genetic bottleneck. A direct consequence of short periods of small N_e (bottlenecks) or continued small population sizes is typically the loss of genetic diversity. The loss of genetic diversity in a bottlenecked population is a matter of concern because decreased polymorphism may reduce the evolutionary potential of a population to respond to a changing environment (Fisher, 1930). Furthermore, numerous studies have shown a direct correlation between genetic diversity and measures of fitness (*e.g.* Leary et al., 1983; Kohen et al., 1988; Soule, 1979), mainly related to inbreeding depression. The bottleneck found in the nuclear genes of South American fur seals could be an indirect result of the synergic effect between the repetitive ENSO events and the human impact in the past (sealing and overfishing) on the Pacific population of South American fur seals.

It is important to mention that a population bottleneck does not necessarily doom a species to immediate extinction (*e.g.* Northern elephant seal - Frankham et al., 2002; LeBoeuf & Bonnell, 1980). However, the loss of genetic diversity is likely to make it more prone to extinction due to the emergence of new diseases or environmental changes. Further, the population will be partially inbred, and is likely to have reduced reproductive fitness as a consequence. An important feature of such bottleneck events is the large chance element in the outcome. Some situations will be relatively harmless if few deleterious mutations are, by chance, present in the remaining population. In other cases, populations are not so lucky; deleterious mutations are fixed and the species may decline to extinction.

The estimated N_e of 2,153 combined with the apparently current increase in frequency of ENSO events are reasons of great concern for the survival of the species on the Peruvian coast. According to Majluf (1998), the ENSO event from 1997-1998 caused a high juvenile and pup mortality, as well as a high mortality of reproductive females, due to the need to spend very long periods foraging (10-20 days), suffering subsequently from physical stress and even starvation. Although the South American fur seal population on the Pacific side of its distribution most likely is well adapted to recurrent ENSO events, the already depleted current population may not be able to survive more events similar in magnitude to the 1997-1998 ENSO. Indeed, the continued viability of *A. australis* on the Peruvian coast may depend primarily on nongenetic factors, such as local availability of food resources during breeding seasons and its consequent effects on pup growth and survival. Global warming models predict stronger and more frequent ENSOs in the future (NCDC-NOOA, 2004). If a strong one were to hit the surviving adults in the near future, there would be few juveniles to replace them and the future generations may be compromised and in a much greater risk than ever imagined (Majluf, 1998).

On the other hand, I believe that the estimated N_e of 7,715 individuals for the Peruvian population of *O. flavescens* is not a critical value because it is higher than the mean minimum viable population for vertebrates (7000 breeding age adults, Reed et al., 2003). However, the viability of *O. flavescens* as well of *A. australis* on the Peruvian coast may depend primarily on local availability of food resources and its effects on pup growth and survival (Soto et al., 2004). The species faces the productive but unpredictable Peruvian upwelling ecosystem (Ryther, 1969), and is directly exposed to interannual and highly stochastic fluctuations in the distribution and abundance of its principal prey, *E. ringens* (Arias-Schreiber, 2003). According to Soto et al. (2006) there are strong linkages between maternal attendance patterns and the abundance of prey and oceanographic features close to the rookeries. Acute prey shortage during ENSO resulted in females increasing the length of their foraging trips and decreasing the time they spent onshore with their pups, which died due to starvation (Soto et al., 2004). Thus, stochastic fluctuations in the marine environment should directly affect the maternal behavior and possibly the reproductive success of this species.

ENSO year	Intensity of the event (based on SST)	Gap between events (years)
1877 - 1878	Strong	10
1888 - 1889	Moderate	7
1896 - 1897	Strong	2
1899	Strong	3
1902 - 1903	Strong	2
1905 - 1906	Strong	5
1911 - 1912	Strong	1
1913 - 1914	Moderate	4
1918 - 1919	Strong	4
1923	Moderate	2
1925 - 1926	Strong	6
1932	Moderate	7
1939 - 1941	Strong	5
1946 - 1947	Moderate	4
1951	Weak	2
1953	Weak	4
1957 - 1959	Strong	4
1963	Weak	2
1965 - 1966	Moderate	2
1968 - 1970	Moderate	2
1972 - 1973	Strong	3
1976 - 1977	Weak	1
1977 - 1978	Weak	1
1979 - 1980	Weak	2
1982 - 1983	Strong	3
1986 - 1988	Moderate	2
1990 - 1993	Strong	1
1994 - 1995	Moderate	2
1997 - 1998	Strong	4
2002 - 2003	Moderate	1
2004 - 2005	Weak	1
2006 - 2007	Weak	1

Table 3. ENSO events from 1877 - 2006 based on sea surface temperature (SST) reconstructions (Smith & Reynolds, 2004).

In this sense, the estimated N_e of 7,715 for *O. flavescens* should be considered as a value to be maintained in order to keep the population large enough to avoid inbreeding or to retain adaptive genetic variation to survive to future ENSO events. Moreover, this N_e result has an important application related to management decisions for the conservation of sea lions in Peruvian waters. This N_e value must be taken into account mainly during periods of suggestion of culling, based on the increasing competition between fishery activity and sea lions during ENSO events. In 1997 Peruvian fishermen called for a cull of sea lions to protect fisheries and the Peruvian Fisheries Ministry was considering a pilot program to kill up to 60 sea lions. However, as a result of the 1997-1998 ENSO event the numbers of sea lions onshore were drastically reduced and the program was abandoned (Seal Conservation Society, 2010; Lama, 2010).

The most important drawback of the estimate of N_e is the necessity of a data set from long term censuses that include temporal oscillations in population size (~20 years) (Vucetich et al., 1997). Nunney & Elam (1994) suggested that estimates based on data collected during a single season ignores the influence of temporal fluctuation and thus may represent gross overestimates of $N_{e.}$ This is why the data presented here are so important and unique in comparison to the information available on pinniped populations from other countries throughout South America. The long-term census size available for fur seals and sea lions along the Peruvian coast are results of the systematic efforts of IMARPE for more than 25 years.

Vucetich & Waite (1998) highlight the importance of long-term counts in order to improve the accuracy of the estimates of $N_{e.}$ Traill et al. (2010) also reinforce that conservationists working within developing nations rarely have the resources available to collect the long term demographic and other data necessary to model viability for specific species or taxa.

Global warming models predict stronger and more frequent ENSOs in the future (see table 3) (NCDC-NOOA, 2004). I recommend that conservation planners consider the estimated N_e for both species in future management strategies to ensure the conservation of the South American sea lions and fur seals on the Peruvian coast.

4. Acknowledgments

The author would like to thank Patricia Majluf for opening the doors of the Punta San Juan Project and providing all of the knowledge about the Peruvian fur seals and sea lions. To the Instituto del Mar del Perú (IMARPE), that kindly provided information related to Peruvian studies. To the research team of the Punta San Juan Project (1997 and 2003): Nora Rueda, Gabriela Battistini, Rosana Paredes, Carlos Zavalaga, Diana and Juan Cervantes-Sanchez, Milena Roca, Susana Cárdenas, Armando Valdés, Marco Cardeña, Walter Diaz, Manuel Apaza and Pedro Llerena for their assistance in the field work in Peru. To Nathalia dos Santos Freitas for supply important references, to Adriano Duarte, who kindly prepared Figure 2. This study was Gemars contribution n. 37.

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15

A Review of Sea-Level Rise Effect on Mangrove Forest Species: Anatomical and Morphological Modifications

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1. Introduction

Mangrove forests are among the most productive and biologically important ecosystems of the world, because they provide important and unique ecosystem goods and services to human society and coastal and marine systems, as stabilizing shorelines and reducing the devastating impact of natural disasters, providing breeding and nursing grounds for marine species, and food, medicine, fuel and building materials (Tomlinson, 1986; Giri et al., 2011).

Mangroves are taxonomically diverse trees and shrubs that have evolved independently through convergence (Hogarth, 1999). The principal genera are *Avicennia* (Avicenniaceae), *Laguncularia* and *Lumnitzera* (Combretaceae), *Nypa* (Palmae), *Bruguiera, Ceriops, Kandelia* and *Rhizophora* (Rhizophoraceae), and *Sonneratia* (Sonneratiaceae) (Tomlinson, 1986). These plants have developed complex physiological, morphological and anatomical adaptations allowing survival and success in the high stress habitat where they inhabit (Hogarth, 1999). They can tolerate the stress of waterlogging and salinity prevailing in coastal environments influenced by tides and have adapted to wide salinity levels, may be influenced by local hydrology and episodic disturbance events (Doyle, 2003). The maximum concentration of soil water salinity that mangrove species can tolerate is suggested up to 155 ‰ with annual averages of 100 ‰ (Tomlinson, 1986).

Mangrove forests are generally distributed along tropical coastlines of America, Africa and Asia between 25° N and 25° S, although this range extends beyond due to the movement of unusually warm waters from the equator, including the east coast of Africa, Australia, and New Zealand (Hogarth, 1999; McLeod & Salm, 2006).

Nevertheless, sea-level rise in the future could be the biggest threat to mangrove ecosystems as climate change consequence (Giri et al., 2011). In the last century, sea-level has risen 10-20 cm mainly due to thermal expansion of the oceans and melting of glacial ice caused by global warming, with climate models predicting an accelerated rate of sea-level rise over coming decades from 0.09 to 0.88 m (McLeod & Salm, 2006). This will generate salinity concentration, along with rising CO_2, and temperature, determining future species distributions, abundances, and viability (Kareiva et al., 1993; Yáñez-Arancibia et al., 1998), concerning worldwide from both scientific and policy perspectives (Alongi, 2008; Gilman et al., 2008; Semeniuk, 1994).

Increased surface temperature is expected to affect mangrove forests (Field, 1995). However, it is uncertain the effect of rising temperature when the interactive effects of changes in precipitation and other weather-related factors are considered (Alongi, 2008). In addition, temperature change in the tropics may not be as great as in boreal and temperate regions (Beaumont et al., 2011; Solomon et al., 2007). Responses of mangroves to rising temperature depend on reactions of individual plants, but such responses have not been addressed experimentally.

The chapter approach involve a review of worldwide studies regarding the association of mangroves morphological and anatomical traits variation with local and regional environmental factors, analyzing their stem, leaves, roots and growth, allowing to infer the effect of potential impacts of sea-level rise on their structure.

2. Morphological and anatomical adaptations of mangrove forest species to environmental factors

Mangrove species anatomical and morphological adaptations are relevant from ecological point of view, due to the particular environment where they inhabit, frequently flooded and highly saline (Tomlinson, 1986) (Fig. 1).

Fig. 1. Mangrove *Avicennia germinans* (L.) Stearn (Avicenniaceae) trees in the coastal lagoon "La Mancha", Veracruz, in the Gulf of Mexico (photo by Jorge López-Portillo).

There is in addition a group of species described as mangrove associates that comprises a large number of species typically occurring on the landward margin of the forest or non-mangrove habitats like salt marsh or lowland fresh water swamps that are completely or partially flood tolerant (Hogarth, 1999) (Fig. 2). There is a long list of mangrove associates like *Hibiscus* and *Pavonia* (Malvaceae), *Amoora* (Meliaceae), *Ardisia* and *Myrsine* (Myrsinaceae), *Calamus* and *Phoenix* (Arecaeae), *Pandanus* (Pandanaceae), *Pouteria* (Sapotaceae), *Pachira* (Bombacaceae), *Ficus (*Moraceae), *Tabebuia* (Bignoniaceae), *Achrosticum* (Pteridaceae), *Annona* (Annonaceae), and others (Tomlinson, 1986).

The most typical adaptations of mangrove species are the aerial roots, stilt-roots, pneumatophores, root knees, and plank roots that have a higher proportion of gas space when waterlogged, mechanisms of salt exclusion by the roots, tolerance of high tissue salt concentrations and excretion of salt excess from leaves, vivipary or the development of the embryo in seed plants before they are dispersed, and seeds and propagules have different morphological adaptations that facilitate flotation (Baskin & Baskin, 2001; Hogarth, 1999; Tomlinson, 1986).

Fig. 2. Mangrove associate *Annona glabra* L. (Annonaceae) trees showing massive root system in the Everglades, Florida.

Trees vascular system has strong influence on leaves structure and function, carbon gain, nutrient use efficiency and growth rate. Diverse studies have revealed that mangroves show great plasticity in wood, bark and leaves structure as an adaptation to a wide gradient of water salinity, flooding level and waterlogging period. These modifications are important to account and understand the possible effects of the predicted sea-level rise as a consequence of global warming, because as all mangrove forests occur between high and low tide marks it is evident that they will be drastically influenced by any changes in sea-level.

3. Modifications of wood structure in response to environmental factors

Several studies have demonstrated that mangroves like *Bruguiera*, *Rhizophora, Laguncularia* and *Avicennia* trees stem vascular system, particularly wood anatomical traits as vessel density, grouping, diameter and length, as well as fiber wall thickness, are affected by variations on salinity and flooding level. (Table 1).

Anatomical traits	Species	Environmental factors	Reference
Vessel density	*Annona glabra* *Laguncularia racemosa* *Rhizophora mangle*	Salinity Flooding level Soil texture	Yáñez-Espinosa et al., 2001
	Laguncularia racemosa	Salinity Flooding level	Yáñez-Espinosa et al., 2004
	Rhizophora mucronata	Salinity	Schmitz et al., 2006
	Avicennia marina *Rhizophora mucronata*	Salinity	Robert et al., 2009
	Avicennia germinans	Salinity Flooding period	Yáñez-Espinosa et al., 2009
	Bruguiera gymnorrhiza	Flooding period	Xiao et al., 2010
Vessel diameter	*Rhizophora mangle*	Salinity Flooding level	Yáñez-Espinosa et al., 2001
	Avicennia marina *Rhizophora mucronata*	Salinity	Robert et al., 2009
	Avicennia marina	Flooding period	Xiao et al., 2009
	Rhizophora mucronata	Salinity	Schmitz et al., 2006
Vessel grouping	*Annona glabra*	Salinity Flooding level Soil texture	Yáñez-Espinosa et al., 2001
	Avicennia marina *Rhizophora mucronata*	Salinity	Robert et al., 2009
Vessel length	*Avicennia marina* *Rhizophora mucronata*	Salinity	Robert et al., 2009
	Laguncularia racemosa	Salinity Flooding level	Yáñez-Espinosa et al., 2004
Fiber wall thickness	*Laguncularia racemosa*	Salinity	Yáñez-Espinosa et al., 2004
	Avicennia germinans	Salinity Flooding period	Yáñez-Espinosa et al., 2009
	Bruguiera gymnorrhiza	Flooding period	Xiao et al., 2010

Table 1. Mangrove and mangrove associate species wood anatomical characters affected by different environmental variables.

Vessel density increases from low- to high-salinity areas in all species, from high- to low-flooding level in most of them, and from temporal- to prolonged flooding period. Increasing vessel density with salinity can be explained by an interference with nutrient uptake and auxin physiology with higher soil water salinity (Schmitz et al., 2006).

Numerous vessels promote protection against cavitation in stressed environments, avoiding cavitation damage when flooding level is higher, because a sporadic drought could occur (Yáñez-Espinosa et al., 2004).

The concentration of salinity effects on vessel density could be observed in the relationship of *Rhizophora mucronata* 23–30 vessels mm$^{-2,}$ and *Avicennia marina* 78-68 vessels mm$^{-2,}$ ranging from 26.4–49.2‰ in Gazi Bay, Kenya (Robert et al., 2009; Schmitz et al., 2006); *Avicennia* *germinans* 30 – 52 vessels mm^{-2}, ranging from 3.2 – 30‰ of soil water in La Mancha lagoon, México (Yáñez-Espinosa et al., 2009); *Laguncularia racemosa* 7-16 vessels mm$^{-2,}$ ranging from 6–9‰ in an estuarine river in Nayarit, México (Yáñez-Espinosa et al., 2004).

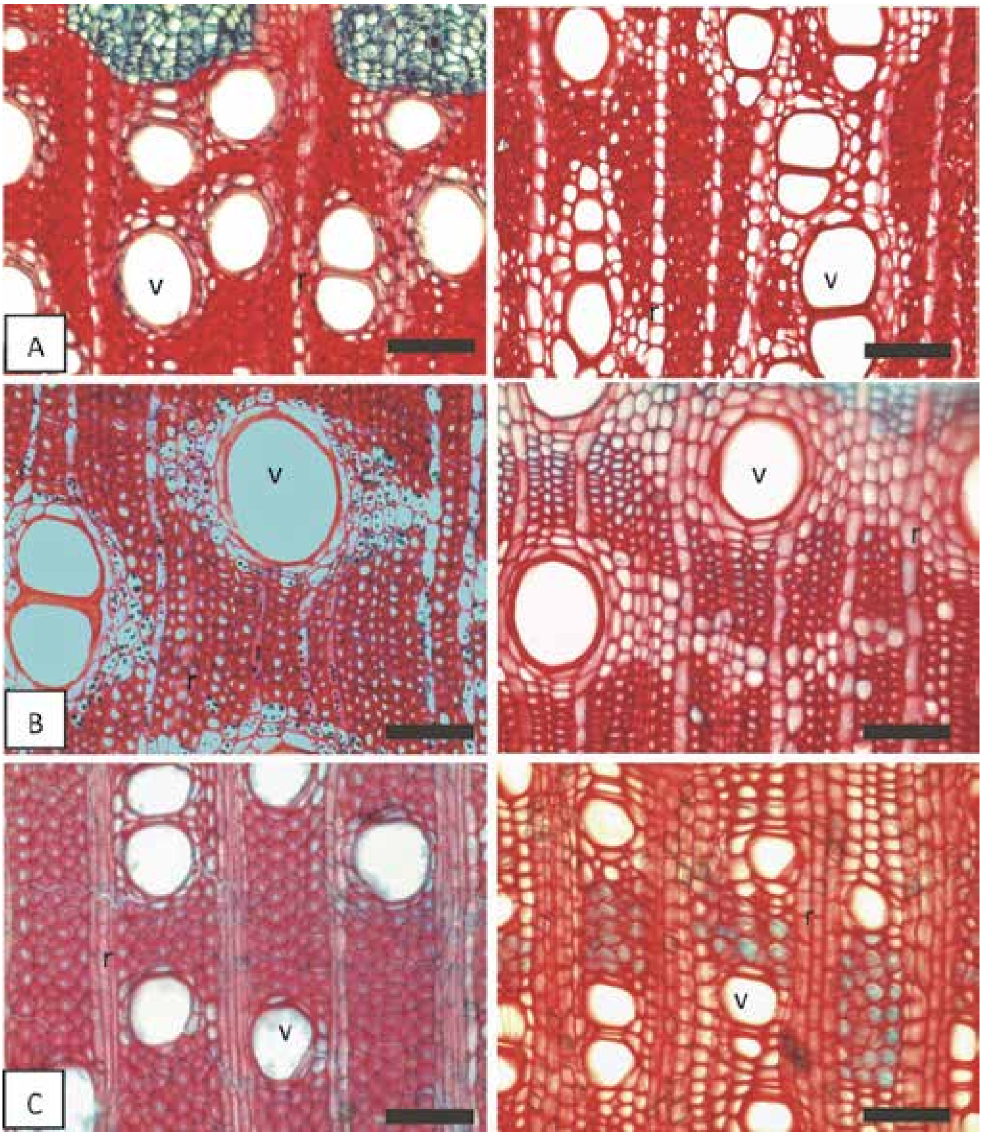

Fig. 3. *Avicennia germinans* (A), *Laguncularia racemosa* (B), and (C) *Rhizophora mangle* wood of trees growing in sites with lower (left) and higher (right) salinity. Differences in vessel density and diameter are present. Light microscope micrograph. Transverse section. v = vessel; r = wood ray; bar = 100 µm.

The stem water transport system consisting of a high vessel density, a high vessel grouping, small vessel diameters and short vessel elements in *Avicennia* and *Laguncularia* species, is contrasting with the water transport system of *Rhizophor*a species, suggesting to be safer based on a physiological interpretation of the observed characteristics (Fig. 3). Structure modifications of *Bruguiera gymnorrhiza* seedlings of fiber wall thickness and length, and vessel diameter were reduced as flooding prolonged, suggesting distinct strategies for maintaining a balance between growth, conductive capacity, conductive safety and mechanical strength (Xiao et al., 2010). Lovelock et al. (2006a) suggest that over a range of species and sites, hydraulic conductivity in mangroves is constrained by salinity, with a variable relationship due to species differences (*Avicennia germinans* [2.13 kg m^{-1} s^{-1} $MPa^{-1} \cdot 10^{-4}$]; *L. racemosa* [0.81 kg m^{-1} s^{-1} $MPa^{-1} \cdot 10^{-4}$]), and to variation in nutrient availability.

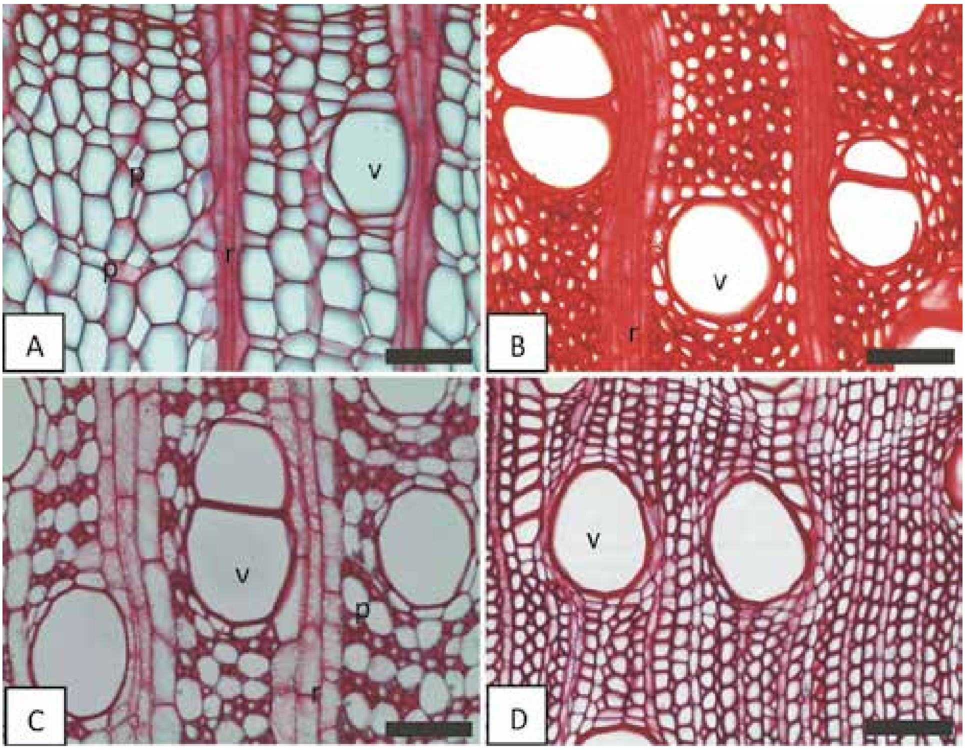

Fig. 4. The mangrove associate species *Annona glabra* (A), *Hibiscus tiliaceus* (B), *Pachira aquatica* (C), and *Rhabdadenia biflora* (D), showing vessels with wider tangential diameter than mangrove species. Light microscope micrograph. Transverse section. v = vessel; p = axial parenchyma; r = wood ray; bar = 100 µm.

Numerous mangrove associate species are more susceptible to modifications in flooding regime and salinity concentration, increasing vessel density like *Annona glabra*, from 4 to 7 vessels mm^{-2}. In general, vessel tangential diameter of mangrove associates is wider than those of mangrove species, suggesting an increment in vulnerability based on a physiological interpretation (Yáñez-Espinosa & Terrazas, 2001) (Fig. 4) (Table 2).

Nevertheless, abundant axial and radial parenchyma cells may be storing water in the stem, like *Annona*, *Pachira* and *Hibiscus* species. This mechanism would compensate the effects of increased axial resistance on leaf water status, extracting water from storage in the stem and then sap flow would increase more slowly during the morning (Stratton et al., 2000).The mangrove associate vine, *Rhabdadenia biflora*, growing on *Avicennia germinans* mangrove tree has scarce axial and radial parenchyma cells, however fiber diameter is wider like the other associate mangrove species.

Mangrove	Vessel tangential diameter (μm)	Mangrove associate	Vessel tangential diameter (μm)
Avicennia germinans	70	*Annona glabra*	93
Laguncularia racemosa	96	*Hibiscus tiliaceus*	122
Rhizophora mangle	73	*Pachira aquatica*	130
Conocarpus erectus	68	*Phyllanthus elsiae*	74
		Rhabdadenia biflora	93

Table 2. Comparison of average vessel tangential diameter from mangrove and mangrove associate species growing in Mexican mangrove forests (unpublished data).

Analysis of wood traits plasticity in some studies has identified hydraulic properties of trees as more plastic than those of leaf structural and physiological characters, concluding that hydraulic properties explain growth control.

The wide tolerance of mangroves wood traits to environmental gradient of salinity, soil texture and flooding conditions suggests that even if increases in relative sea level will eventually raise saturation and salinity conditions at ecotonal boundaries, mangroves are capable to advance or invade inland into freshwater marsh and swamp habitats (Doyle, 2003), modifying distribution and composition of the mangrove.

4. Modifications of bark structure in response to environmental factors

Prolonged flooding also affects bark anatomy of mangrove species, modifying the secondary phloem, rhytidome and periderm tissues, suggesting that prolonged flooding modifies vascular cambium and phellogen differently (Yáñez-Espinosa et al., 2008). Typical structural responses include formation of hypertrophied lenticels and adventitious root (Fig. 5), and increased aerenchyma development in the bark (Table 3).

Species	Rhytidome	Aerenchyma in rhytidome	Aerenchyma in collapsed phloem	Ray dilatation	Hypertrophied lenticels	Adventitious roots
*Annona glabra**	++	++	++	++	++	++
*Hibiscus tiliaceus**	++	++	++	++	++	--
*Phyllanthus elsiae**	--	--	++	++	++	++
*Avicennia germinans**	--	--	--	--	++	--
*Laguncularia racemosa**	++	++	--	±±	++	±±
Conocarpus erectus•	++	++	--	±±	++	--
Pachira aquatica•	--	--	++	++	++	++

Table 3. Mangrove and mangrove associate species bark anatomical characters. ++ = present; -- = abscent; ±± = slightly present. * Data from Yáñez-Espinosa et al., 2008; • = Unpublished data.

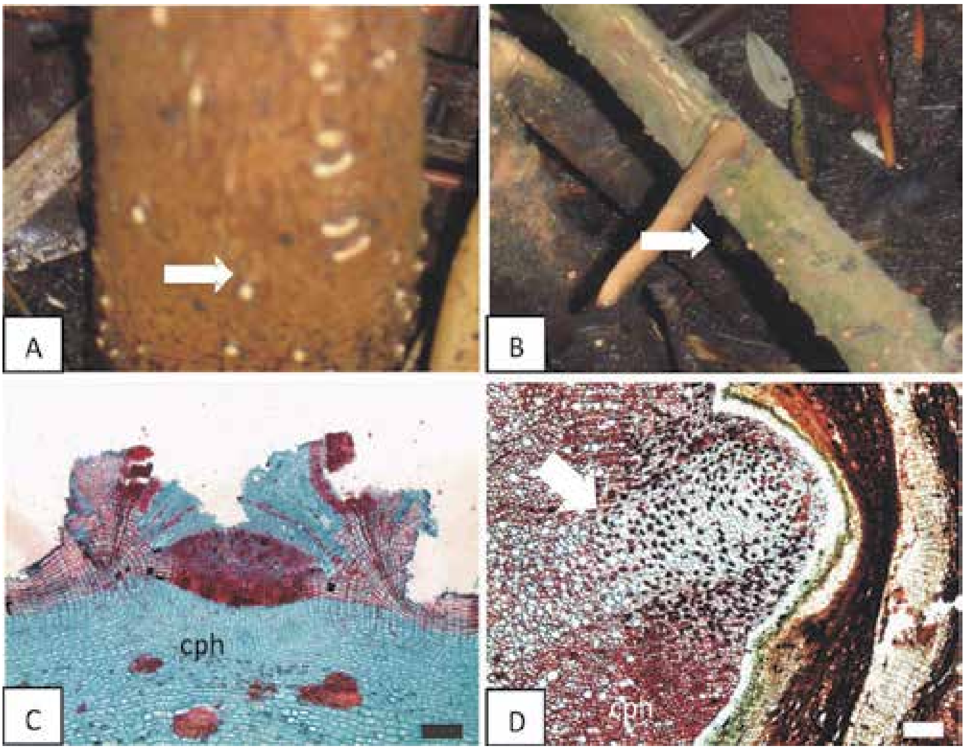

Fig. 5. Hypertrophied lenticels in the immersed portion of the stem of *Avicennia agerminans* (arrow) (A); and in the immersed stilt root of *Rhizophora mangle* (arrow) (B) macroscopic appearance; Light microscope micrograph. Transverse section. *Phyllanthus elsieae* hypertrophied lenticel in the immersed portion of the stem (C); *Annona glabra* adventitious root (arrow) in the immersed portion of the stem (D). p = periderm; cph = collapsed phloem; f = filling tissue; bar = 100 µm.

Mangrove species develop hypertrophied lenticels in the immersed portion of the stem, as well as mangrove associates tolerant to flooding, like *Annona glabra* (Mielke et al., 2005), excepting *Phyllanthus elsiae* (Euphorbiaceae), which develops hypertrophied lenticels above and below flooding level (Yáñez-Espinosa et al., 2008). Adventitious roots were present in the mangrove associate species *Annona glabra*, *Hibiscus tiliaceus*, *Pachira aquatica* and *Phyllanthus elsiae* (Mielke et al., 2005; Yáñez Espinosa et al., 2008). These species have not specialized roots like stilt roots or pneumatophores, then aeration depends on abundant hypertrophied lenticels and adventitious roots to tolerate prolonged or permanent flooding.

The importance of aerenchyma in the development of a continuous interconnected series of intercellular spaces is the most important adaptation to flooding in plants (Lambers et al., 1998). Trees without cork aerenchyma in their barks might develop larger air spaces in the phloem parenchyma, phelloderm or primary cortex (Roth, 1981), like *Rhizophora mangle* develops aerenchyma in phloem axial and radial parenchyma of collapsed region (Yáñez-Espinosa, unpublished data).

Although studies realized on bark rays show no statistical differences from short- to long-flooding period, mangrove species *Laguncularia racemosa*, *Avicennia germinans* and *Rhizophora mangle*, present shorter phloem rays under longer flooding period, may be associated with the effect of prolonged flooding similar to that of drought. But mangrove associate *Annona glabra* tend to have lower rays under short-flooding period, may be due to anoxic conditions caused by prolonged flooding (Yáñez- Espinosa et al., 2001).

Increments in rays are related to enlargement of cells that could mobilize a higher oxygen volume and more photosynthates (Kozlowski et al., 1991). The intercellular space system of ray tissue is essential, because ray cells have indefinite viability and require gas exchange for metabolic activity (Carlquist, 1988) (Fig. 6).

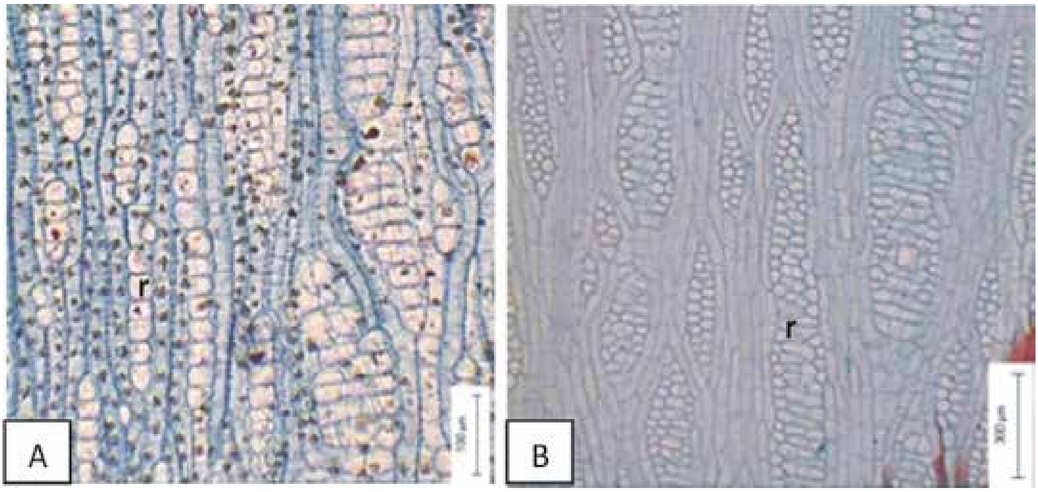

Fig. 6. Secondary phloem rays of *Laguncularia racemosa* (A) and *Annona glabra* (B) close to vascular cambium, showing a slightly dilatation. Light microscope micrograph. Tangential section. r = phloem ray.

Annona glabra, *Pachira aquatica* and *Hibiscus tiliaceus* develop aerenchyma in the rhytidome, phelloderm, and phloem parenchyma, which suggests a greater volume for aeration, particularly in the immersed portion of the stem. *Laguncularia racemosa* and *Conocarpus erectus* (Combretaceae) axial and radial parenchyma cells in the collapsed phloem region dilate slightly close to periderm, but develop abundant aerenchyma in the rhytidome. *Avicennia germinans* only develops rhytidome in the immersed portion of the stem and presents an aerenchymatous cork that may be the path connecting the aerial atmosphere with the immersed tissues (Fig. 7).

Even though aerenchyma and hypertrophy are the most common events related to flooding, each type of tissue responded differently, depending on the species. The mangrove and mangrove associate species respond to different flooding periods and then cohabit on a wide environmental gradient, suggesting that accelerated sea-level rise caused by global warming, would affect distribution of the species according to their particular tolerance.

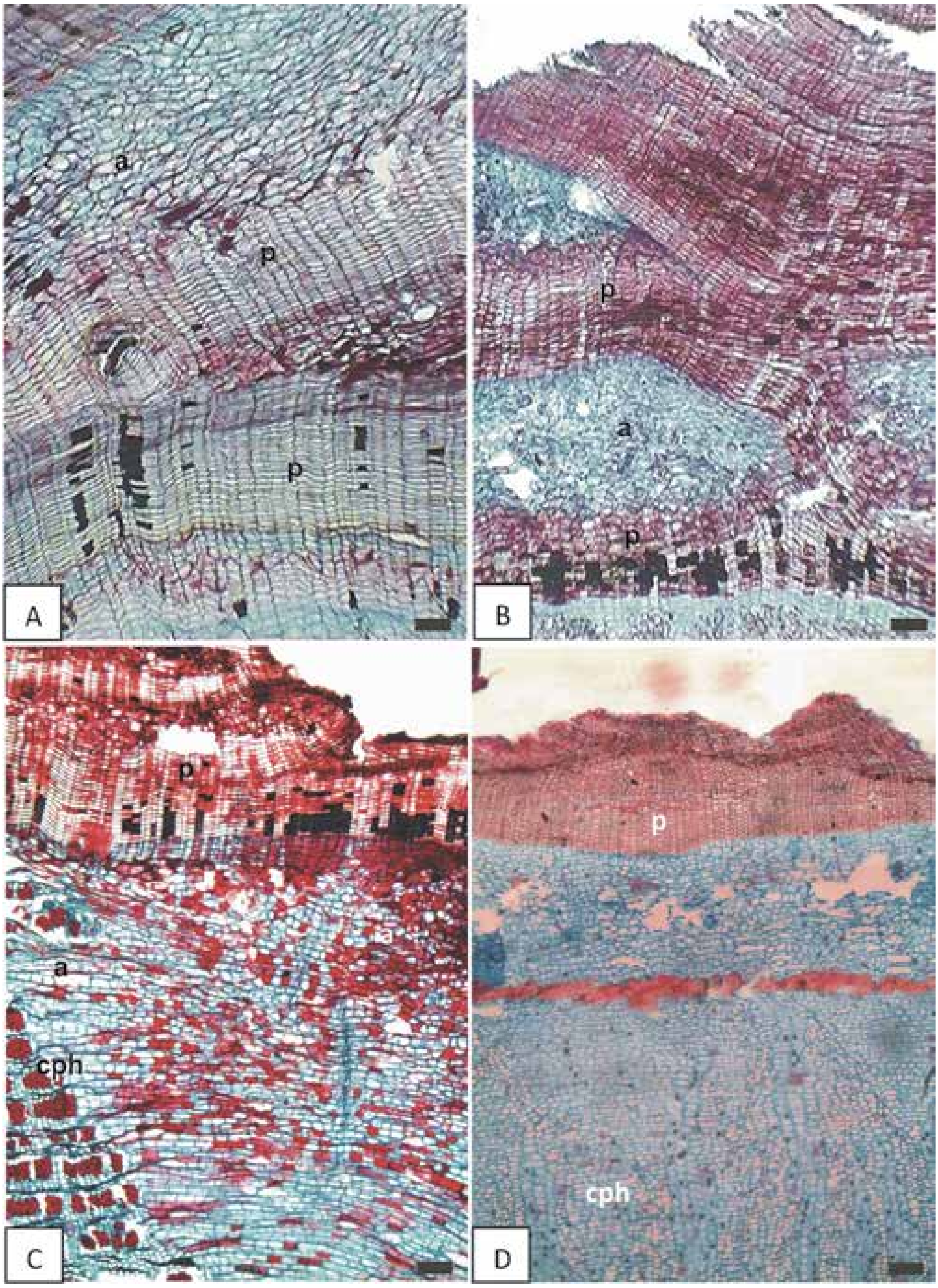

Fig. 7. *Annona glabra* aerenchyma in rhytidome of immersed portion of the stem (A), *Avicennia germinans* aerenchyma in rhytidome of immersed portion of the stem (B), bar = 200 µm; *Hibiscus tiliaceus* axial and radial parenchyma dilatation close to periderm (C), *Rhizophora mangle* aerenchyma close to periderm and dilatation of axial and radial parenchyma in collapsed phloem region (D). Light microscope micrograph. Transverse section. a = aerenchyma; p = periderm; cph = collapsed phloem; bar = 100 µm.

5. Modifications of leaf structure in response to environmental factors

Mangroves show many xerophytic adaptations that are evident in their leaves. Leaves are dorsiventral (Fig. 8), excepting *Lumnitzera racemosa*, where they are isobilateral and amphistomatic; the cells of the lower epidermis are larger than those of the upper surface, and water storage tissue is present in all the species, except *Aegialitis rotundifolia* (Seshavatharam & Srivalli, 1989; Tomlinson, 1986).

Experimental studies point to mangrove species-specific responses to increases in atmospheric CO_2 concentration. Increase in atmospheric CO_2 can be expected to improve mangrove tree growth, *i.e.* leaf area ratio increased with a decrease in humidity when *R. stylosa* was grown under elevated CO_2 (700 cm^3 m^{-3}) (Ball et al. 1997). However, elevated CO_2 (until 700 μll^{-1}) did not affect leaf area of *Rhizophora mangle* seedlings (Farnsworth *et al.* 1996). In addition, increased CO_2 until 700 cm^3 m^{-3} did not affect leaf area of *Rhizophora apiculata* limited by high salinity, but did enhance leaf area when the plants were limited by humidity (Ball et al. 1997).

Responses of mangrove to sea-levels rise depend on reactions of individual plants, and some evidence exists on modifications of leaf structure in response to increasing flooding or waterlogging. *Bruguiera gymnorrhiza* and *Rhizophora stylosa* seedlings decreased leaf area intensely with decreasing tidal elevation (from 30-40 cm) in Yingluo Bay, a core zone within the Shankou Mangrove Reserve of Guangxi, China. Inversely, *Aegiceras corniculatum* and *Avicennia marina* seedlings increased leaf area with decreasing tidal elevation, at 10, 0, and - 30 cm (He et al. 2007).

Fig. 8. Leaves with xerophytic adaptations of *Avicennia germinans* (A), *Bruguiera* sp. (B), *Rhizophora mangle* (C), *Laguncularia racemosa* (D).

In addition, leaf area of adult individuals from *Laguncularia racemosa*, *Rhizophora mangle*, *R. racemosa*, *R. harrisonii*, and *Avicennia germinans* was generally significantly larger for species growing in wet (dry season lesser than 1 month) than in dry sites (dry season of seven months) in the Caribbean coast of Venezuela (Medina & Francisco, 1997). Similarly, *Rhizophora mangle* seedlings in Belize decreased leaf area in plants under water (Ellison & Farnsworth, 1997). However, there are some species with leaf area unaffected by tidal flooding, like *Xylocarpus granatum* seedlings in the Federated States of Micronesia (Allen et al. 2003), as well as *Aegiceras corniculatum* and *Avicenia marina* seedlings in Yingluo Bay, China (He et al. 2007), and *Annona glabra* after 56 days of flooding showed no symptoms of stress, and there were no changes in total leaf area (2.20 m^2) (Mielke et al., 2005).

Mangrove leaf anatomy is very uniform matched by a suite of features common to most mangrove species, including the colorless "water storage" tissue, the short tracheids terminating vein endings, the marked absence of sclerotic vein sheaths, presence of sclereids, thickened outer epidermal wall strongly cutinized, thick mesophyll including the adaxial hypodermis layers, palisade parenchyma layers and spongy parenchyma (Tomlinson, 1986) (Fig. 9).

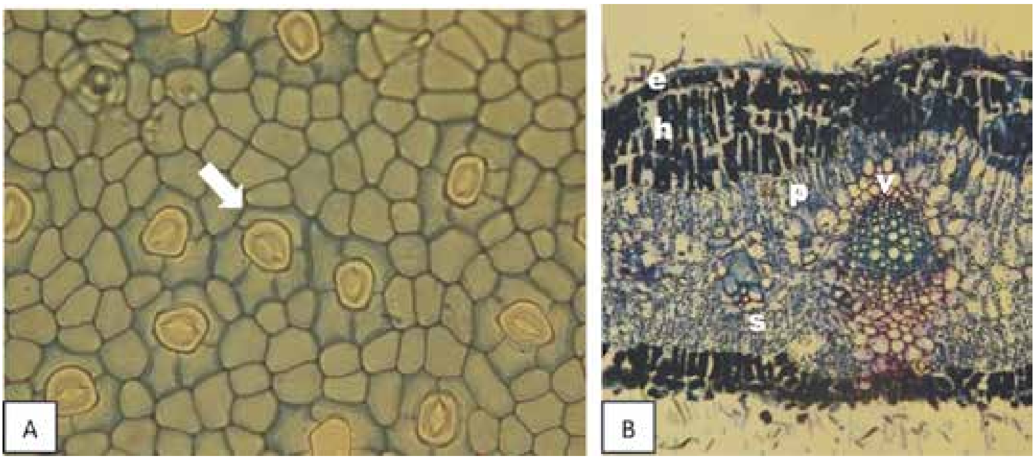

Fig. 9. *Conocarpus erectus L. (Combretaceae)* leaf epidermis showing stomata (arrow) (A), and showing dorsiventral structure: epidermis, adaxial hypodermis with two distinct layers, assimilating tissue below, and a vascular bundle. Light microscope micrograph .Paradermal (A) and transverse (B) section, by Guillermo Angeles. e = epidermis; h = hypodermis; p = palisade parenchyma; s = spongy parenchyma; v = vascular bundle.

Nevertheless, studies of modifications on leaf anatomical features under experimental conditions are scarce. Changes of *Avicennia marina* seedlings under experimental conditions were expressed in the progressive increase of upper and lower epidermis thickness to leaf thickness ratio and mesophyll to leaf thickness ratio with prolonged waterlogging duration, but prolonged waterlogging duration have negative effects on hypodermis thickness, leaf thickness, mesophyll thickness, palisade parenchyma thickness, palisade–spongy ratio, tangential vessel diameter and vessel wall thickness in leaf tissue (Xiao et al., 2009), contrary to *Bruguiera gymnorrhiza* seedlings grown under experimental conditions of simulated semidiurnal tides with salinities of 15‰, after 12 h treatments, that showed declination in leaf thickness, palisade parenchyma thickness, spongy parenchyma thickness, xylem length of the vascular system and number of vessels and vessel lines, up to 67.1%, compared with the 0 h treatments. However, the upper and lower epidermis and stomatal density of 12 h treatments showed increases of up to 104.3% over the 0 h treatments. The cuticle and percentage of intercellular spaces in spongy tissue decreased significantly with waterlogging duration at first and then increased. These results suggest that modifications in the anatomical features of *B. gymnorrhiza* as a result of periods of immersion longer than 2 h, would result in a reduction of photosynthesis and water transport (Wang et al., 2007). However, anatomical characters of *Rhizophora mangle* leaves did not differ when Ellison & Farnsworth (1997) simulated a 16 cm decrease and increase of sea-level.

There are many studies indicating the importance of salinity for mangrove species as well as evidence that various mangroves may have different tolerances and optimal salinity (Ball et al., 1997; Ball, 2002). The physiology of their ability to survive in saline environment may shed light on the evolution of mangroves from terrestrial species (Parani et al. 1998).

Leaf structure traits reflect the long-term adaptive strategy successfully (Cunningham et al., 1999; Wang et al,. 2003; Wright et al., 2004). Salinity affects ion accumulation in leaves, thereby membrane permeability and chlorophyll synthesis (Cram et al., 2002). In addition, with increase in salinity, carbon allocation to roots increases at the expense of leaf area (Ball 1988). Leaf area decreased at higher salinity concentrations (47-92‰) for *Laguncularia racemosa* in the Sontecomapan lagoon in Veracruz, Mexico (Medina et al., 1995), and for *Sonneratia alba* at 100‰ sea water and *S. lanceolata* seedlings at 50‰ sea water, in northern Australia (Ball & Pidsley 1995). The average leaf area of *Rhizophora apiculata* and *R. stylosa* propagules in the Northern Territory of Australia decreased with an increase in salinity from 125 to 350 mol m^{-3} NaCl, with *R. apiculata* being the more sensitive (Ball et al. 1997). For *Bruguiera parviflora* in Bhitarakanika mangrove forest, Orissa, India, leaf area was significantly less at 400 mM NaCl as compared to 0 mM NaCl (Parida et al., 2004), for *Laguncularia racemosa* in Sepetiba Bay, Rio de Janeiro, Brazil, which showed significant lower leaf area in salt marsh plants with high soil salinity and low nutrient input, than in riverside plants with daily tidal fluxes and consequently high nutrient input, that can be associated with environmental restrictions of their habitat (Lira-Medeiros et al., 2010), and for *Rhizophora mucronata* seedlings in the 45 PSU in South Africa (Hoppe-Speer et al., 2011).

In some species, leaf area is unaffected by salinity concentrations, *i.e. Rhizophora mangle*, which had similar leaf area in plants from El Real (at 47-92 ‰) and from La Boca (at 0-22 ‰) in the Sontecomapan lagoon in Veracruz, Mexico (Medina et al., 1995), and *Xylocarpus granatum* seedlings at 0.5 and 23 ‰ salinity in the Federated States of Micronesia (Allen et al,. 2003).

Increasing flood level and salinity due to sea-level rise, may result in mangrove leaves morphology and anatomy modifications, considering that extant studies show perceptible modifications, although not all species are affected (i.e. *Rhizophora* and *Xylocarpus)*. Modifications include increasing stomatal density, reduction of leaf area and thickness, palisade parenchyma thickness, number of vessels and vessel diameter in leaf tissue, whose may generate the reduction of transpiration, photosynthesis and water transport.

6. Modifications of root structure in response to environmental factors

The anatomy of mangrove roots has been extensively studied in relation to development and function (Tomlinson, 1986). Prolonged flooding alters soil physical and chemical properties, as well as bacterial composition, directly affecting species roots (Rajaniemia &

Allison, 2009). Root vascular system affects stem vascular system and leaves structure of mangrove species, even when there are present modified roots like pneumatophores, cable, knee and stilt roots (Visser & Pierik, 2007).

Pneumatophores arise vertically from cable roots and have evolved independently in at least five mangrove families and genera: *Laguncularia* (Combretaceae), *Avicennia* (Avicenniaceae), *Bruguiera* (Rhizophoraceae), *Xylocarpus* (Meliaceae), and *Sonneratia* (Sonneratiaceae) (Tomlinson 1986). They have abundant lenticels, and aerenchyma may account for up to 70% of root volume (Hogarth, 1999) (Fig. 10).

The normal pneumatophores of *Sonneratia* and *Avicennia* are slender and cone shaped, standing erect and aligned on the cable root, of 1-20 m or more in length, which spread horizontally in the soil. *Sonneratia alba* trees in Ranong and Phang-nga Bay, Thailand, produce pneumatophores 25-35 cm long, 4–6 cm thick at the base, with a regular conical shape. However, pneumatophores of *S. caseolaris* may become 1.2 m tall and 12 cm thick at the base. The cable roots morphology and length are more related to soil structure and tidal regime than tree variables, as well as pneumatophores that may be deformed due to massive waves, sediments deposition, and other environmental changes (Nakamura et al., 2004).

Avicennia marina in Kenya has the ability to adapt its pneumatophores to micro-topographical irregularities in the regularly sloping intertidal zone. Significantly higher pneumatophore densities and total pneumatophore lengths are present in the center of the landward depression, and significantly lower lengths in the center of the seaward depression (Dahdouh-Guebas et al., 2007), suggesting that cable roots and pneumatophores morphology, density and length may be affected by sea-level rise. *Rhizophhora mangle* underground roots are in permanently hypoxic or anoxic environment, and then vertical roots have the role of supplying oxygen to underground roots, reaching adequate gas exchange at low tide. Air passes through aerenchyma tissue, constituted by air spaces running longitudinally the root axis (Hogarth, 1999) (Fig. 10).

Experiments with *Avicennia marina* have demonstrated that oxygen concentrations decrease from 16 to less than 2% within one hour after exposure to hypoxic conditions. The roots increased then the capacity for alcoholic fermentation, although ethanol concentration was low in intact and hypoxic roots, but may have diffused from the roots into the surrounding substrate (McKee & Mendelssohn, 1987). *Avicennia germinans* roots, commonly found in anaerobic substrate, create oxidized rhizospheres substantially larger, but when air cannot enter the root system through the pneumatophores, the rhizospheres become as reduced as nearby non-vegetated soil. *Rhizophora mangle* have no effect on the oxidation state of surrounding anaerobic soils (Thibodeau & Nickerson, 1986).

Studies realized in *Laguncularia racemosa* cable roots and pneumatophores showed that cable roots are very efficient for water transport, and that this occurs mainly through the external vessels of the secondary xylem (Angeles et al., 2002). The development of a massive root system under soil flooding conditions in *Annona glabra* can be a mechanism to compensate for the high resistance to water flow in the roots (Mielke et al., 2005). However, more studies on mangrove root water transport are necessary to understand hydraulic properties of the whole plant system.

Sea-level rise caused by global warming may affect mangrove roots in different ways, depending of different functional root types (McLeod & Salm, 2006). Lenticels in the aerial roots have the role of supplying oxygen to underground roots, then if a rapid increment of sea-level occurs, pneumatophores of *Sonneratia* and *Avicennia* may have not the capacity of increase pneumatophore density and length fast enough to avoid oxygen concentration decrease, producing death of the plant. However, *Rhizophora* aerial roots could not be affected, because lenticels would remain above sea-level.

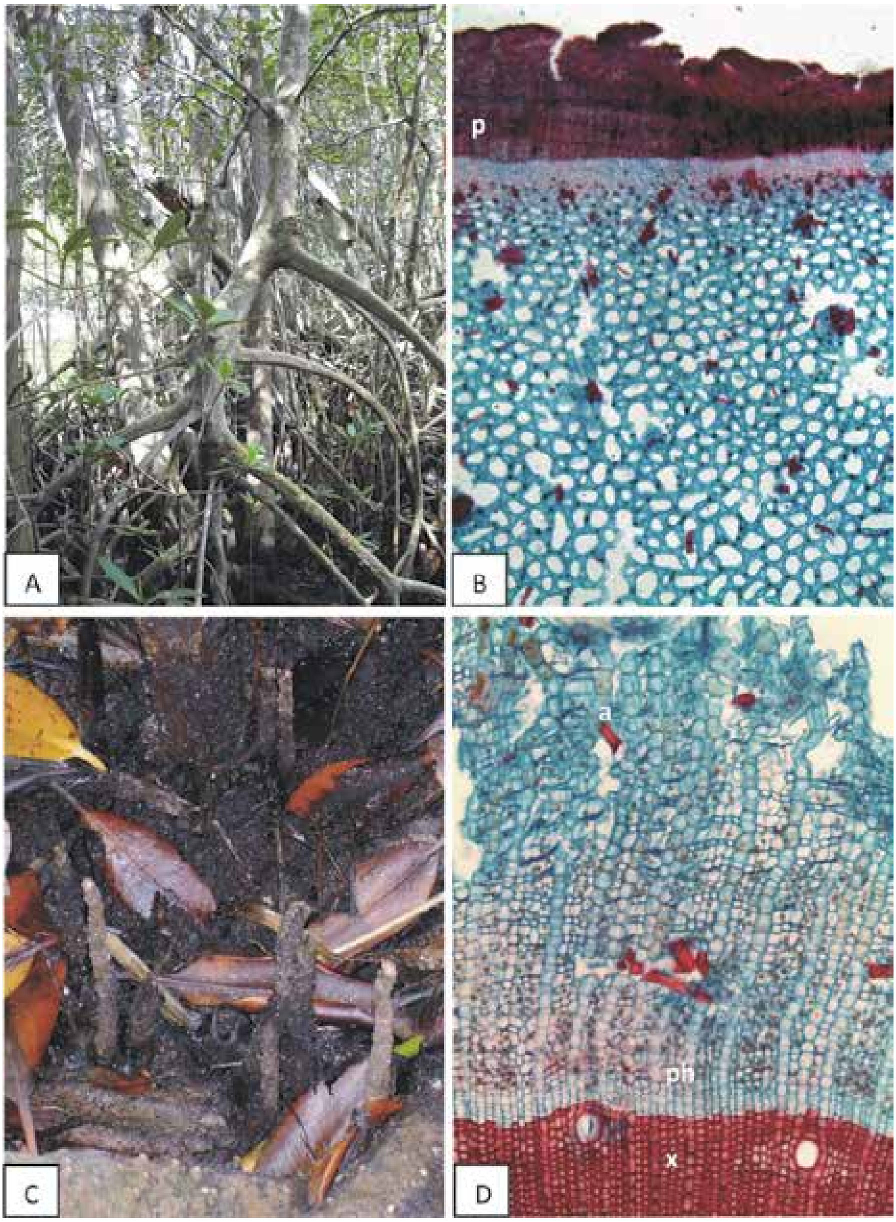

Fig. 10. *Rhizophora mangle* stilt roots (A); Light microscope micrograph of aerenchyma tissue close to periderm in a *R. mangle* aerial root (B); *Avicennia germinans* pneumatophores (C); Light microscope micrograph of dilated parenchyma tissue in *Laguncularia racemosa* pneumatophore (D). p = periderm; a = aerenchyma; x =secondary xylem; ph = secondary phloem; bar = 100 μm.

7. Modifications of growth in response to environmental factors

Growth of a plant is the increment in dry mass, volume, area or length as a result of division, expansion and differentiation of cells, determined by the interaction of photosynthesis, long-distance transport, respiration, water relations, and mineral nutrition (Lambers et al., 1998). Total above-ground biomass varies widely being highest at low latitude and declining northward and southwards from the equator. Undisturbed *Rhizophora* forests in northern Australia may reach up to 700 t ha^{-1} dry weight, but in old mangrove forests of South-east Asia range from 500 to 550 t ha^{-1} dry weight (Hogarth, 1999). However, the growth rate of mangroves is critically related to the availability of water to the trees and this is reflected in the soil water content and soil salinity (Field, 1995).

7.1 Biomass

The relative growth rate of *Bruguiera gymnorrhiza* decreased significantly with waterlogged time, with the highest value found for drained plants and the lowest in plants less than 12 weeks waterlogging. On the contrary, no significant difference was found between waterlogged and drained *Kandelia candel* plants. The shoot to root biomass ratio of *K. candel* increased when subjected to 8 or 12 weeks waterlogging but little change was recorded in *B. gymnorrhiza*, indicating a shift in biomass allocation from roots to shoots in *K. candel* under prolonged waterlogging but not in *B. gymnorrhiza*. Chlorophyll contents of *K. candel* increased more rapidly in response to waterlogging than *B. gymnorrhiza*. These physiological indicators supported the hypothesis that *K. candel* is more tolerant to waterlogging than *B. gymnorrhiza (*Ye et al., 2003*)*. In mangrove associate *Annona glabra* seedlings, the high survival and growth rates are directly related to the capacity to develop a massive root system and maintain a high stomatal conductance and net photosynthesis under soil flooding. In most flood-tolerant species the initial decrease in stomatal conductance is followed by recovery, like in *A. glabra* seedlings under flooding treatment, where stomatal conductance was reduced to 65% of control levels with four days of flooding, but reached 152% at day 56. Significant increases in root, stem and total plant biomass and in collar diameter were observed. These results suggest that *A. glabra* is highly adapted to both periodic and permanent flooding (Mielke et al., 2005).

The effect of salinity on the growth of *Avicennia germinans* propagules collected in Cuman´a, Venezuela, was experimentally determined comparing the relative growth rates (RGR) after 27 weeks, reaching a maximum 10.4 mg g^{-1} d^{-1} in 170 mol m^{-3} NaCl, followed by the 0 and 430 mol m^{-3} NaCl treatments (8.4 and 7.9 mg g^{-1} d^{-1} respectively). At the same period the RGR of plants grown in 680 and 940 mol m^{-3} NaCl were 47 and 44% lower than that of plants grown in 170 mol m^{-3} NaCl. Higher salt tolerance of *A. germinans* in relation to other mangrove species might be due to low relative growth rates and high water-use efficiency over a wide salinity range. The decline in RGR with increasing salinity was clearly associated with a decrease in net assimilation rate (Suárez & Medina, 2005).

Also nutrient deficiency is relevant, when comparing dwarf and taller fringing tree forms of *Rhizophora mangle* in Belize, allow identifying trait plasticity in hydraulic properties of trees as more plastic than those of leaf structural and physiological characteristics, implying that hydraulic properties are significant in controlling growth in mangroves. Improvement of P deficiency reduced the structural and functional distinctions between dwarf and taller fringing tree forms, releasing trees from hydraulic limitations (Lovelock et al., 2006b).

Topography would be relevant if tidal effect would change. In one experiment, seven mangrove species *Rhizophora mucronata, R. apiculata, Bruguiera cylindrica, Ceriops tagal, Sonneratia alba, Avicennia officinalis* and *Xylocarpus granatum*, were planted at various topographic sites in an intertidal zone of Phang Nga, Thailand. The experimental plots were on a slope and showed a maximal elevation difference of 1.8 m, submerged with 2-3% saline water twice a day. Survival and growth performance of seedlings were measured differing and showing increasing tolerance to higher tidal inundations in the order: *R. mucronata, S. alba, R. apiculata, A. officinalis, C. tagal, B. cylindrica* and *X. granatum* (Kitaya et al., 2002).

7.2 Growth rings

Secondary growth, or secondary tissues added lateral to stems and roots increasing their thickness, are produced by the vascular cambium. In secondary xylem or wood, growth rings may be produced during one season, and usually they are delimited by growth boundaries (Beck, 2010) (Fig. 11). In mangroves, the highly dynamic intertidal environment and the overriding ecological drivers difficult the existence of growth rings. Nevertheless, climatic conditions that result in a range of soil water salinity experienced over the year are a prerequisite for the formation of growth ring (Robert et al., 2011).

Recently, annual growth rings were discovered in *Rhizophora mucronata* in Kenya, but the ring boundaries are indistinct and growth ring consists of a low vessel density earlywood, produced during the rainy seasons, and a high vessel density latewood, produced during the dry season. Intra-annual differences in the vessel features revealed a trade-off between hydraulic efficiency (large vessels) during the rainy season and hydraulic safety (small vessels) during the dry season (Verheyden et al., 2005).

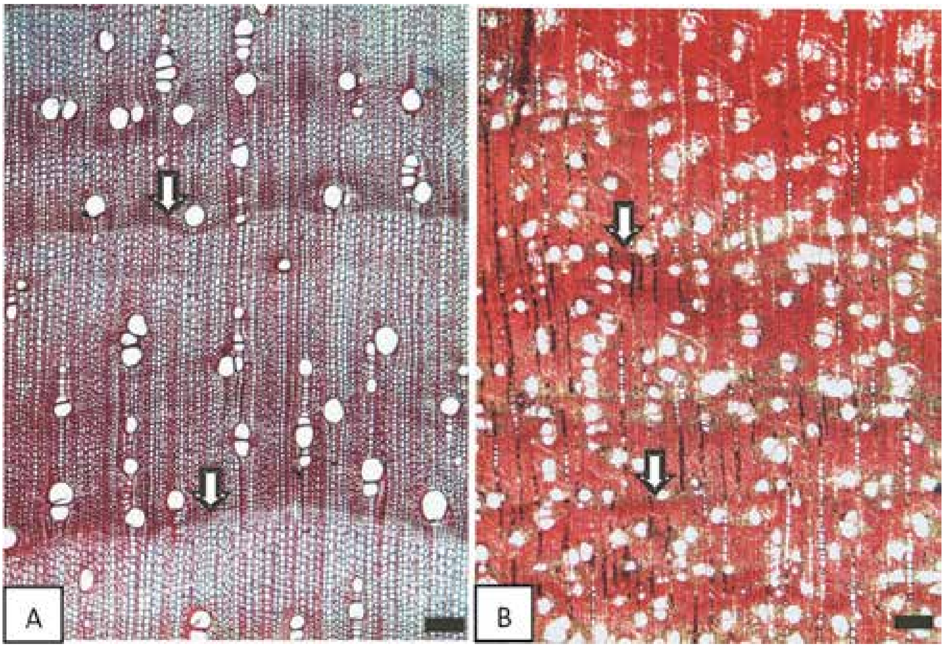

Fig. 11. Light microscope micrograph growth boundaries (arrows) distinct in *Pachira aquatica* (A), slightly defined in *Conocarpus erectus* (B). bar = 100 µm.

Laguncularia racemosa from Rio de Janeiro, Brazil, also present distinguishable growth rings macroscopically, with alternating early wood formed between spring and autumn and consists of layers with abundant paratracheal axial parenchyma, while late wood is formed in winter and consists of narrower dark layers which are basically fibrous zones with scarce paratracheal axial parenchyma. The occurrence of a dry season in winter could be the seasonal factor determining the formation of annual rings (Duque Estrada et al., 2008). These results are relevant because a factor that may be important for the future of mangrove ecosystems is any change in precipitation (Field, 1995).

Sea-level rise might reduce survival and growth performance of mangroves seedlings, expressed as biomass decrement due to variation in flooding and salinity. However, initial decrease is followed by recovery, suggesting that mangrove species are adapted to both periodic and permanent flooding, and high salinity levels. Secondary growth apparently is determined by seasonal precipitation, expressed by the formation of growth rings. Considering that precipitation rates are predicted to increase by about 25% by 2050 in response to global warming (McLeod & Salm, 2006), changes in precipitation patterns may affects at local scale the patterns of freshwater inflow, diminishing salinity concentration in consequence, and affecting mangroves growth and their distribution.

8. Conclusions

Modification of anatomical and morphological patterns of wood, bark, leaf and root of mangrove and mangrove associate species are predictable as result of sea-level rise caused by global warming. Sea-level rise will alter environmental conditions, increasing salinity, flooding level, and altering the rate of deposition of sediment. These species show a wide plasticity in structural and physiological patterns, allowing them to survive and prosper in this ecosystem exposed to a dynamic environment, and occasionally subjected to extreme events, like hurricanes and massive waves. General tendencies suggest a strong association between structure patterns and environmental gradient (salinity, flooding level and periodicity, and soil structure). Cell and organ size decrease while salinity and flooding or waterlogging increases.

Nevertheless, each species has its specific tolerance range, allowing to success along different zones of the mangrove ecosystem with particular geomorphology and environmental conditions, causing a change in forest species composition and dominance, allowing expanding distribution of more tolerant species and limiting or suppressing those less tolerant, particularly in places where sedimentation rates are low. Some studies suggest that mangroves can adapt to sea-level rise if it occurs slowly, there are sufficient space for distribution expansion, and the other environmental factors are tolerable. They may adapt growing inland on more elevated areas, probably increasing their distribution, but if these not occur fast, mangroves adaptation to stressing factors will result in smaller trees until disappearing.

9. Acknowledgments

We thank the financial support of CONACYT (L.Y.E. scholarship no. 112170), Colegio de Postgraduados (M.Sc.), and Instituto de Ecología, A.C. (postdoctoral research), to develop the research projects on mangrove forests from the Pacific and Gulf of Mexico; National Tropical Botanical Garden (Kenan Fellowship for College Professors) to visit and photograph the mangrove forests in Florida, USA; Idea Wild (2007) and PROMEP 103.5/07/2574 (2008) for the acquisition of the digital camera and the light microscope. Thanks to Teresa Terrazas (Universidad Nacional Autónoma de México), Guillermo Ángeles and Jorge López-Portillo (Instituto de Ecología, A.C.), for the time we have dedicated to understand the ecoanatomy of mangroves.

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Edited by Stefano Casalegno

This book addresses the theme of the impacts of global warming on different specific fields, ranging from the regional and global economy, to agriculture, human health, urban areas, land vegetation, marine areas and mangroves. Despite the volume of scientific work that has been undertaken in relation to each of each of these issues, the study of the impacts of global warming upon them is a relatively recent and unexplored topic. The chapters of this book offer a broad overview of potential applications of global warming science. As this science continues to evolve, confirm and reject study hypotheses, it is hoped that this book will stimulate further developments in relation to the impacts of changes in the global climate.

ISBN 978-953-51-4423-6

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