EUROPEAN FOREST GENETIC RESOURCES PROGRAMME

EUFORGEN

Climate change and forest genetic diversity

Implications for sustainable forest management in Europe

J. Koskela, A. Buck and E. Teissier du Cros
editors

Bioversity International
IUFRO
Liberté • Égalité • Fraternité
République Française
Ministère de l'Agriculture et de la Pêche
MCPFE
Liaison Unit Warsaw
ENGREF

Climate change and forest genetic diversity

Implications for sustainable forest management in Europe

J. Koskela, A. Buck and E. Teissier du Cros
editors

Bioversity International is an independent international scientific organization that seeks to improve the well-being of present and future generations of people by enhancing conservation and the deployment of agricultural biodiversity on farms and in forests. It is one of 15 centres supported by the Consultative Group on International Agricultural Research (CGIAR), an association of public and private members who support efforts to mobilize cutting-edge science to reduce hunger and poverty, improve human nutrition and health, and protect the environment. Bioversity has its headquarters in Maccarese, near Rome, Italy, with offices in more than 20 other countries worldwide. The Institute operates through four programmes: Diversity for Livelihoods, Understanding and Managing Biodiversity, Global Partnerships, and Commodities for Livelihoods.

The international status of Bioversity is conferred under an Establishment Agreement which, by January 2007, had been signed by the Governments of Algeria, Australia, Belgium, Benin, Bolivia, Brazil, Burkina Faso, Cameroon, Chile, China, Congo, Costa Rica, Côte d'Ivoire, Cyprus, Czech Republic, Denmark, Ecuador, Egypt, Greece, Guinea, Hungary, India, Indonesia, Iran, Israel, Italy, Jordan, Kenya, Malaysia, Mali, Mauritania, Morocco, Norway, Pakistan, Panama, Peru, Poland, Portugal, Romania, Russia, Senegal, Slovakia, Sudan, Switzerland, Syria, Tunisia, Turkey, Uganda and Ukraine.

Financial support for Bioversity's research is provided by more than 150 donors, including governments, private foundations and international organizations. For details of donors and research activities please see Bioversity's Annual Reports, which are available in printed form on request from bioversity-publications@cgiar.org or from Bioversity's Web site (www.bioversityinternational.org).

European Forest Genetic Resources Programme (EUFORGEN) is a collaborative programme among European countries aimed at ensuring the effective conservation and the sustainable utilization of forest genetic resources in Europe. It was established in 1994 to implement Resolution 2 of the Strasbourg Ministerial Conference for the Protection of Forests in Europe. EUFORGEN is financed by participating countries and is coordinated by Bioversity International, in collaboration with the Forestry Department of FAO. It facilitates the dissemination of information and various collaborative initiatives. The Programme operates through Networks in which scientists, managers and policy-makers work together to analyse needs, exchange experiences and develop conservation methods for selected tree species. The Networks also contribute to the development of appropriate conservation strategies for the ecosystems to which these species belong and promote integration of gene conservation into sustainable forest management. Network members and other experts from the participating countries carry out an agreed workplan with their own resources as inputs in kind to the Programme. EUFORGEN is overseen by a Steering Committee composed of National Coordinators nominated by the member countries. Further information on EUFORGEN can be found from its Web site (www.euforgen.org).

Citation:
Koskela, J., Buck, A. and Teissier du Cros, E., editors. 2007. Climate change and forest genetic diversity: Implications for sustainable forest management in Europe. Bioversity International, Rome, Italy. 111 pp.

Cover illustrations:
A view over Lake Pielinen, Finland – J. Koskela
Diversity of fruits, strobili and seeds of forest tree species – M. Bozzano.

ISBN 978-92-9043-749-9

Bioversity International
Via dei Tre Denari, 472/a
00057 Maccarese
Rome, Italy

PREFACE

Climate change is increasingly recognized as one of the most important challenges faced globally by ecosystems and societies alike. According to the Intergovernmental Panel on Climate Change (IPCC), climate change could increase average temperatures by 2–4°C in Europe over the next 50 years and cause considerable changes in regional and seasonal patterns of precipitation. This will alter the environmental conditions to which forest trees in Europe are adapted and expose them to new pests and diseases. Climate change will thus create additional challenges for forest management, with consequent impacts on the economic and social benefits that societies and individuals derive from the forests, and on the biological diversity in forest ecosystems.

Sustainable forest management aims at using forests in such a way that their capacity to provide a vast array of products, socio-economic benefits and environmental services do not diminish over time. Long-term conservation of forest genetic diversity is therefore a cornerstone for sustainable forest management, especially under climate change. Genetic diversity ensures that forest trees can survive, adapt and evolve under changing environmental conditions. Genetic diversity is also needed to maintain the vitality of forests and to cope with pests and diseases. Ultimately, forest genetic diversity also has a crucial role in maintaining forest biological diversity at both species and ecosystem levels.

Forest genetic resources in Europe are still facing several threats, including habitat destruction, fragmentation, pollution, poor silvicultural practices and use of low quality or poorly adapted forest reproductive material. The threats and the distribution of forest genetic resources do not respect national borders, and thus countries are dependent on each other's forest genetic resources for practising sustainable forest management. This interdependence of countries in terms of forest genetic resources is likely to increase in the future due to climate change.

Because of the threats, the first Ministerial Conference on the Protection of Forests in Europe (MCPFE), held in Strasbourg in 1990, addressed the importance of conserving forest genetic resources (Strasbourg Resolution 2). This happened well before the United Nations Conference on Environment and Development (UNCED), organized in Rio de Janeiro in 1992, brought biodiversity into the global agenda. UNCED launched a new era in the international dialogue on forests and recognized, through the Convention on Biological Diversity (CBD), that countries have a sovereign right over their own genetic resources but also a responsibility to manage these resources sustainably.

In 2003, the fourth Ministerial Conference on the Protection of Forests in Europe addressed climate change and sustainable forest management in Europe (Vienna Resolution 5). Subsequently the new MCPFE Work Programme included a specific action to analyze the role of forest genetic diversity in improving the adaptability of forests and maintaining the productivity of forests under changing environmental conditions. Bioversity International and the International Union of Forest Research Organizations (IUFRO) were assigned the task of implementing this action.

Bioversity International coordinates the European Forest Genetic Resources Programme (EUFORGEN) in technical collaboration with the Food and Agriculture Organization of the United Nations (FAO). EUFORGEN was established in 1994 to implement Strasbourg Resolution 2 and to promote the conservation and sustainable use of forest genetic resources in Europe. Currently, more than 30 countries support and participate in EUFORGEN activities. EUFORGEN also contributes to the implementation of Vienna Resolution 4 (Conserving and enhancing forest biological diversity in Europe). Bioversity International is also actively involved in similar work on forest genetic resources in other regions.

Scientific collaboration within IUFRO covers multiple aspects of forest genetics. Division 2 ‘Physiology and Genetics’ includes research on the breeding and genetic resources of conifers and hardwoods, on quantitative and biological genetics of trees and tree populations, and on seed physiology and technology. Furthermore, a new IUFRO Task Force on Forests and Genetically Modified Trees was established in January 2006.

From 15 to 16 March 2006, Bioversity International and IUFRO organized a workshop on *Climate change and forest genetic diversity: Implications for sustainable forest management in Europe* in collaboration with the MCPFE Liaison Unit, Warsaw, as their contributions to the implementation of Vienna Resolution 5. The French Ministry of Agriculture and Fisheries hosted the workshop, and Ecole Nationale du Génie Rural, des Eaux et des Forêts (ENGREF) offered the meeting venue. EUFORGEN also provided significant financial inputs to the workshop.

The workshop brought together nearly 80 participants from 25 countries to discuss silvicultural practices, the use of forest reproductive materials, and regional and national strategies in the context of forest genetic diversity and climate change. The participants also included several representatives from all EUFORGEN Networks (Conifers; Scattered Broadleaves; Stand-forming Broadleaves; and Forest Management).

The workshop objectives were to: (1) present up-to-date reviews based on the current understanding on how forest trees will cope with and adapt to climate change; (2) discuss the implications for practising sustainable forest management in Europe; and (3) provide inputs and recommendations to the MCPFE process, for further action. This publication presents the papers of the invited speakers, the outputs of the working group discussions and the final workshop recommendations. The workshop recommendations were reported to the Round Table meeting of the MCPFE process in Wroclaw, Poland, on 24–25 April 2006, and they were further discussed during the MCPFE Expert Level meeting in Warsaw on 9–10 October 2006.

We are grateful to the French Ministry of Agriculture and Fisheries for hosting the workshop and to ENGREF for providing its facilities in Paris. We would like to express our gratitude to Mr Alain Chaudron at the Ministry for his support to the workshop. Our sincere thanks also go to Mr Pierre Bouillon at the same Ministry and Ms Lidwina Koop at Bioversity International for taking care of the practical arrangements for the workshop. We are also thankful to all workshop participants for their contributions during and after the workshop. Finally, we thank all those participants who helped us in capturing the comments made during the invited presentations, working group discussions and the final plenary session.

We hope that the papers presented in this publication and the workshop outcomes stimulate further action at national and international level to conserve forest genetic diversity and to use this diversity to ensure that forests and the European forest sector adapt to climate change.

Jarkko Koskela
EUFORGEN Coordinator
Bioversity International,
Rome, Italy

Alexander Buck
Deputy Executive Director
IUFRO
Vienna, Austria

Eric Teissier du Cros
Vice-President, Science
(2001–2005)
IUFRO
Erquy, France

CONTENTS

ACRONYMS USED IN THE TEXT

CBD	Convention on Biological Diversity
ENGREF	Ecole Nationale du Génie Rural, des Eaux et des Forêts
EUFORGEN	European Forest Genetic Resources Programme
FAO	Food and Agriculture Organization of the United Nations
FGR	forest genetic resources
IPCC	Intergovernmental Panel on Climate Change
IUFRO	International Union of Forest Research Organizations
MCPFE	Ministerial Conference on the Protection of Forests in Europe
NAS	national adaptation strateg(y/ies)
NBAP	national biodiversity action plan(s)
NFP	national forest programme(s)
NPFGR	national programme(s) on forest genetic resources
QTL	quantitative trait locus
UNCED	United Nations Conference on Environment and Development (Rio de Janeiro, 1992)
UNFCCC	United Nations Framework Convention on Climate Change

EXECUTIVE SUMMARY

Opening of the workshop

Ms Sylvie Alexandre (Deputy Director General, Forest and Rural Affairs, Ministry of Agriculture and Fisheries, France) delivered a welcome address on behalf of Mr Dominique Bussereau (then Minister of Agriculture and Fisheries, France). She stressed the commitment of France to the MCPFE work, and highlighted the ongoing work on the conservation and use of forest genetic resources in the country. She then informed the participants of a decision made by the Ministry of Agriculture and Fisheries in 2006 to make its forest genetic resources conservation policy a part of the national strategy for biodiversity. Mr Cyril Van Effenterre (Director, ENGREF) also welcomed the participants to the workshop.

The background and objectives of the workshop were introduced by Dr Jarkko Koskela (EUFORGEN Coordinator, Bioversity International) and Dr Eric Teissier du Cros (former Vice-President, Science, IUFRO). Dr Koskela summarized the EUFORGEN work in promoting conservation and management of forest genetic resources in Europe, and Dr Teissier du Cros highlighted IUFRO activities related to forest genetics and climate change.

The workshop continued with technical presentations by leading experts during three sessions that focused on (1) the regional policy context; (2) climate change and forest trees in Europe; and (3) the role of forest genetic diversity in forest management under climate change. The presentations and subsequent discussions are summarized below.

On the second day of the workshop, the participants formed three working groups to address the following issues: (1) silvicultural practices and forest genetic diversity; (2) forest reproductive materials; and (3) regional and national strategies for forest genetic diversity and climate change. The working groups reported the results of their discussions during a plenary session. The workshop recommendations were then developed and adopted based on the outputs of the working groups. The workshop recommendations are presented at the end of this Executive Summary.

Session 1: Regional policy context

Dr Roman Michalak (MCPFE Liaison Unit Warsaw) described the policy context of the workshop. He pointed out that the potential pressures arising from climate change had already been acknowledged at the first Ministerial Conference on the Protection of Forests in Europe, in Strasbourg in 1990. In 1993, the second Ministerial Conference, held in Helsinki, called for development of strategies to ensure long-term adaptation of European forests to climate change. The linkage between sustainable forest management and climate change was subsequently taken up at the fourth Ministerial Conference, in Vienna in 2003, where the ministers responsible for forests committed themselves to supporting research on the impacts of climate change on forests, and to develop policies to enhance adaptability of forests to climate change. Dr Michalak also presented briefly some forest-related issues of the United Nations Framework Convention on Climate Change (UNFCCC) and the work of the Intergovernmental Panel on Climate Change (IPCC). He communicated that the fifth Ministerial Conference was planned to be held in Poland in 2007, and that the present workshop was a good opportunity for providing inputs to the preparation of that Conference.

Session 2: Climate change and forest trees in Europe

In his presentation, Dr Antoine Kremer (INRA, France) focused on evolutionary processes, the rate of evolution and responses of forest trees to climate change. There is some evidence, based on long-term empirical data, that climate-change-induced evolution is already taking place and that trees have started to adapt to increasing atmospheric carbon dioxide concentrations, at both individual and population levels. According to Dr Kremer, evolution in forest trees can occur over a few generations or less than 200 hundred years. In some cases, even one generation is enough for local adaptation, as demonstrated by the transfer of a Norway spruce (*Picea abies*) provenance from Germany to Norway as part of a provenance experiment.

Dr Kremer remarked that most climate models predict a dramatic shift in the range of forest trees, but they assume that the climatic envelopes of the species will not change. However, this assumption is unlikely to be valid as the climatic envelopes will probably change due to evolutionary processes. The climatic envelope of a species refers to the range of climatic variation within which the species can persist, provided its non-climatic environmental requirements are met. Dr Kremer concluded that it is unlikely that the widely-occurring tree species will face extinction at species level due to climate change. However, local extinctions of tree populations may occur as a result of fragmentation and lack of reproduction. Human interventions, such as transfer of forest reproductive material, may thus in particular be needed to enhance local adaptation of rare and scattered tree species.

Dr Outi Savolainen (University of Oulu, Finland) emphasized that natural tree populations adapt as a result of selection and migration based on total fitness, not just growth. These processes are likely to be slow in comparison with the rate of the predicted climate change. She further pointed out that landscapes are very fragmented in most of Europe, making migration of forest trees even more difficult. Dr Savolainen highlighted that climate change will affect tree populations very differently in southern Europe compared with northern Europe. For example, in higher latitudes, Scots pine (*Pinus sylvestris*) populations can migrate northwards under climate change, but at the southern edge of the species' distribution range, the species is likely to withdraw to more suitable sites. Furthermore, large and diverse tree populations have higher probable potential to adapt to new climatic conditions than have fragmented tree populations. She concluded that a cautious transfer of forest reproductive material has a role in facilitating migration of tree species and increasing the intensity of selection. She also stressed the need to integrate ecology and genetics in further experiments, as currently there is limited data available on the fitness of tree species facing simultaneously competition from evolving species.

Session 3: The role of forest genetic diversity in forest management under climate change

Dr Marcus Lindner (European Forest Institute, Finland) pointed out that future climate projections still include a considerable degree of uncertainty and that this creates a big challenge when designing adaptation strategies in forest management. However, what seems more obvious is that the frequency of extreme weather events is increasing and that such events are likely to be the most important drivers of ecosystem change. While the productivity of forests is likely to increase in northern Europe, it is expected to decrease in southern Europe due to more severe drought periods. Subsequently, forest fires will become an even more serious problem in southern Europe. Furthermore, storms may become more frequent also in the northern and central parts of Europe, and new pests and diseases are likely to spread northwards. Dr Lindner highlighted that different tree species respond differently to extreme weather events, such as drought. Overall, mixed forests are likely to withstand better a broad range of climatic conditions, and broadleaved species are more susceptible to disturbances. Dr Lindner concluded that diversification of adaptation strategies leaves more options to cope with uncertain future climatic conditions. No single adaptation strategy is the best one. Thus, he recommended diversifying species, forest types, forest management practices, forest products and services.

Dr Koen Kramer (ALTERRA, Netherlands) focused on the concepts of equilibrium, non-equilibrium and resilience. He noted that traditional thinking is largely based on the concept of equilibrium, i.e. that species coexistence is due to niche differentiation and that species' distribution areas are in equilibrium with climate. Due to climate change, however, species are in disequilibrium with the prevailing climate.

Moreover, the future equilibrium states of species composition in a forest and of species' distribution areas are essentially unknown. Forest management guidelines and policies based on the restoration of a historic pre-disturbance reference are not necessarily still attainable. A non-equilibrium approach is therefore needed, focusing on setting conditions so that the system can adapt to environmental changes. Resilience is then defined as the rate of return to the stable state, i.e. how well a system can absorb disturbances and environmental stress and still persist. Hence, Dr Kramer proposed that the concept of resilience be made operational by quantifying both genetic and ecological aspects of diversity at the stand, landscape and regional scales. He then presented the DYNABEECH project as an example where genetics, ecophysiology and silviculture were successfully integrated to formulate forest management practices that optimize the adaptive capacity, as measure of non-equilibrium resilience, of beech (*Fagus sylvatica*) stands.

Professor Csaba Mátyás (University of West Hungary) reviewed results of various field trials and stressed the need to use quantitative genetic knowledge in forecasting adaptive responses of forest trees to climate change, formulating mitigation strategies and in supporting adaptation of trees by human interventions. He stated that results of field trials show a remarkable range of adaptability in forest trees even to dramatic changes in thermal and moisture conditions. However, he emphasized that there are genetically set limits to adaptation and that some tree populations are seriously threatened by climate change. He emphasized that tree populations at the xeric limits, such as the Mediterranean region and continental Europe, are the most threatened ones. Concerning the role of spontaneous migration in adaptation of forest trees to climate change, Prof. Mátyás expressed his doubt that spontaneous migration could occur in most parts of Europe. This is mainly because fragmented and intensively managed landscapes pose considerable obstacles to migration. He therefore considered that human interference is necessary to facilitate the adaptation of forest trees to climate change. He then recommended the development of flexible pan-European guidelines for the use of forest reproductive material, and the incorporation of climate change and adaptation issues into national forest programmes.

Dr Bo Jellesmark Thorsen (Royal Veterinary and Agricultural University, Denmark) discussed the role of forest genetic diversity in maintaining the supply of numerous benefits derived from forests. In addition to supporting supply of many marketable forest products, forest genetic diversity also contributes indirectly to securing the long-term health of forest ecosystems and the services they provide. He underlined that climate change implies increased uncertainty, which is a key factor in economic considerations. He further highlighted two economic aspects of uncertainty. Firstly, uncertainty can be perceived as risk and handled by diversification. Secondly, with uncertainty ahead, we may benefit from strategies that retain options open for later adjustment. The time horizon of the implications of the climate change may be of little importance to an individual forest owner, but of great importance for society pursuing sustainable development. He recommended that forest owners and policymakers pursue flexible strategies and decisions on forest genetic diversity, as these are likely to increase both the private value and social values of the forests. He also emphasized that diversification through increased use of forest genetic diversity is a recommendable risk-reduction strategy for an individual forest owner.

Ms Mari Rusanen (Finnish Forest Research Institute) provided an overview of Finland's National Strategy for Adaptation to Climate Change. The strategy was prepared in a collaborative effort of all relevant sectors and was finalized in 2005. It identifies actions and measures for each sector (including forestry), and also takes into account changes occurring outside Finland (transboundary effects). Furthermore, the strategy places special emphasis on cross-cutting adaptation, such as public sector capabilities (e.g. risk assessments, environmental impact assessment and management systems), observation and warning systems, research and development, communication and information sharing. The strategy highlights the role of the National Forest Programme as a planning and implementation tool for the adoption of specific adaptation measures for the forest sector. Also, it addresses the need to conserve forest genetic resources and the new challenges for tree breeding and seed production. Regarding forest management, the strategy proposes actions such as revision of silvicultural guidelines, rapid harvesting of forests destroyed by storms, control of pests and diseases, and better maintenance of forest roads. Ms Rusanen summarized that the lessons learned were that key elements of the comprehensive strategy involved integration of mitigation and adaptation measures and implementation through specific sectors. The strategy will be reviewed within 6 to 8 years.

Dr François Lefèvre (INRA, France) gave an overview of the institutional framework for the conservation of forest genetic resources in France, and analyzed the effects of climate change on gene conservation strategies. He stated that 11 *in situ* or *ex situ* networks of gene conservation units have been established throughout the country for different tree species. All units are located in public forests and gene conservation is incorporated into the management plans of these forests. Dr Lefèvre observed that there is a need to re-evaluate and improve the existing gene conservation networks in the context of climate change. The objectives of the gene conservation networks should not only focus on genetic diversity per se, but also on plasticity, adaptation and migration potential of tree species. Subsequently, process-based rather than diversity-based criteria and indicators should be developed for the management of the gene conservation units. The robustness of the existing gene conservation networks to extreme weather events should be assessed and monitored, as there are already examples of such events destroying particular units. He stressed that there is a need for better coordination between habitat and gene conservation programmes. Gene conservation efforts for several scattered tree species should also be managed on a larger scale than that of the stand.

Working group discussions

Working Group 1: Silvicultural practices and forest genetic diversity

The working group recognized that there is still considerable uncertainty in the future climate projections based on different models. However, it is likely that climate variability and the frequency of extreme weather events will increase, bringing storms and extended drought periods. Furthermore, there may well be combined effects of climate change, pests and diseases on forests. It was also emphasized in the discussion that there are regions where forests are facing high risks (e.g. southern Europe) due to climate change, while forests in other regions are likely to have lower risks. Furthermore, the working group agreed that specific silvicultural and gene conservation measures should be taken to protect species that are endangered or of special interest.

The working group stressed that silviculture should help forest ecosystems to regenerate and thus evolve under climate change. In this regard, an important question is the balance between natural and artificial regeneration, i.e. to what extent promote natural regeneration and when to encourage planting of seedlings, possibly originating from different climatic conditions. The occurrence of frequent natural regeneration is fundamental for continuous natural selection in forest ecosystems, thus maintaining the evolutionary process of forest trees. Artificial regeneration is needed to complement natural regeneration and, in some cases, to accelerate the adaptation of forest trees to climate change. The working group concluded that forest genetics can play an important role in identifying the most feasible regeneration methods in terms of adaptation to climate change.

Working Group 2: Forest reproductive materials

The working group highlighted that knowledge-based use and transfer of well-documented and characterized forest reproductive material can be an effective tool to ensure that forests are able to cope with climate change. Existing networks of provenance trials of various tree species and the research results already available provide plenty of information and a solid basis for the assessment of provenance regions. The working group recognized that climate change is likely to alter the existing provenance regions in most countries. Consequently, there is a need to revise the delineation of the present provenance regions of forest trees in most countries, and to modify these regions according to the predicted climate change scenarios. The working group also underlined that new strategies and guidelines were needed at pan-European level to support and promote appropriate use of forest reproductive material.

The working group welcomed that most European countries have implemented the EC Regulations on the marketing of forest reproductive material (1999/105/EC) in their legislation, but pointed out that there is still a need to promote the use of high quality and well adapted material. It was noted that long-term economic analyses confirm the benefits of using high quality reproductive material. The working group also urged European countries to keep better records on the transfer and use of forest reproductive material so that the origin of a forest stand could later be verified, even after a long period. This would enable future analyses of the long-term performance and economic aspects of natural versus artificial regeneration under climate change.

Working Group 3: Regional and national strategies for forest genetic diversity and climate change

The working group acknowledged that most European countries have national forest programmes (NFP), national biodiversity action plans (NBAP) or similar processes in place. However, only about one third of the countries have well-established national programmes on forest genetic resources (NPFGR) or related strategies, as revealed by a EUFORGEN survey in 2002. Furthermore, the discussions demonstrated that very few countries have initiated the development of national adaptation strategies (NAS), which aim at increasing the capacity of the whole of society to adapt to climate change. The working group considered NAS as a useful approach to tackle and coordinate mitigation efforts at national level.

The working group welcomed the efforts of the MCPFE process in promoting cross-sectoral coordination and implementation of sustainable forest management through NFP in Europe. It is important to include NAS and climate change considerations in NFP as these remain the mechanism through which various strategies are actually implemented in the forest sector in a country. The working group noted that the existing examples of NAS highlight the role of forest genetic diversity in mitigating the impacts of climate change. However, in many countries, the linkages between NFP and NPFGR remain weak, and the management of forest genetic resources is not incorporated well enough into NFP. The working group concluded that it is necessary to strengthen the linkage and collaboration between NFP and other relevant national processes, in particular NPFGR and NAS.

Workshop recommendations

Climate change may have substantial impacts on the European forest sector as well as conservation of forest biodiversity. The genetic diversity of forest trees plays a key role in maintaining the resilience of forests to the threats and in taking advantage of the opportunities. The wise use of this genetic diversity also provides flexibility with respect to forest management and adaptation strategies for climate change. The workshop made the following recommendations for further action:

Recommendation 1: Policy-makers in Europe should recognize the importance of forest genetic diversity in mitigating the impacts of climate change on the forest sector by expressing a commitment at pan-European level to incorporate the management of this diversity into national forest programmes and other relevant policies, programmes and strategies.

Recommendation 2: Policy-makers in Europe should promote forest management practices that maintain evolutionary processes of forest trees and support natural regeneration of forests, especially in areas where long-term natural regeneration is self-sustainable despite climate change.

Recommendation 3: Policy-makers in Europe should take into account the potential for accelerating adaptation of forest trees to climate change through tree breeding and transfer of potentially suitable forest reproductive material by endorsing the development of pan-European guidelines for the transfer of forest reproductive material in Europe on the basis of scientific knowledge.

Recommendation 4: The European forest research community should, with the support of policy-makers, carry out more interdisciplinary studies (e.g. tree physiology, forest genetics, pests and diseases, forest management and economics, and modelling) on the impacts of climate change on forests.

MCPFE COMMITMENTS ON FORESTS AND CLIMATE CHANGE

Roman Michalak

MCPFE Liaison Unit, Warsaw, Poland

Summary

From the very beginning, the Ministerial Conferences on the Protection of Forests in Europe (MCPFE) have recognized the need for consideration of climate change aspects in their commitments. General awareness about forest stability, vitality and regeneration as well as adaptive capacity lay at the origin of the Process. The ministerial declaration and resolutions adopted during the first Ministerial Conference, held in Strasbourg in 1990, addressed climate change aspects by establishing a series of scientific and monitoring activities, the objective of which was to provide knowledge on interrelations between forests and the environment. The majority of these activities have been successfully continued. One visible example of the scientific and technical collaboration is the European Forest Genetic Resources Programme (EUFORGEN) that directly contributes to the implementation of Strasbourg Resolution 2.

Multidimensional significance of climatic factors for forests and possible implications of climate change impacts on forest management were shown during the second Ministerial Conference, convened in Helsinki in 1993. The importance of these topics was addressed in the General Guidelines for the Sustainable Management of Forests in Europe, and in Helsinki Resolution 4, by which the ministers committed themselves to support appropriate measures for the mitigation of climate change and the limitation of greenhouse gas emissions. The General Guidelines were reaffirmed and further developed at the third Ministerial Conference, in Lisbon in 1998, particularly by endorsing the Pan-European Criteria and Indicators for Sustainable Forest Management and the Pan-European Operational Level Guidelines for Sustainable Forest Management. The role of European forests in the global carbon cycle and threats posed to forests by human-induced climate change were addressed again in Vienna Resolution 5 during the fourth Ministerial Conference, in Vienna in 2003. The ministers responsible for forests committed themselves to further contribute to the ongoing work under the United Nations Framework Convention on Cli-

---

Michalak, R. 2007. MCPFE commitments on forests and climate change. In: Koskela, J., Buck, A. and Teissier du Cros, E., editors. Climate change and forest genetic diversity: Implications for sustainable forest management in Europe. Bioversity International, Rome, Italy. pp 1–2.

mate Change (UNFCCC) as well as to share experiences at pan-European level on forest-related national and regional strategies for mitigation of and adaptation to climate change.

The pan-European actions for the implementation of Vienna Resolution 5 and the related commitments in the Vienna Declaration aim at enhancing the contribution of forests to reduce greenhouse gas emissions, and encouraging forest management practices in carbon sequestration measures, as well as further improving the adaptability of forests to climate change. Besides this workshop on the role of forest genetic diversity in improving the adaptability of forests to climate change, other implementation actions include a workshop on resource mobilization and comprehensive wood utilization strategies in support of sustainable forest management, as well as the elaboration of pan-European recommendations for afforestation and reforestation in the context of UNFCCC. The main purpose of these actions is to assist countries in achieving the MCPFE goals through practical implementation of the commitments undertaken.

HOW WELL CAN EXISTING FORESTS WITHSTAND CLIMATE CHANGE?

Antoine Kremer

INRA, UMR Biodiversity Genes & Communities, Cestas, France

Introduction

There is widespread concern that forest tree species may not be able to cope with future environmental changes. Such concern arises from the discrepancy between the generation period of trees and the time span of climate change, in addition to the general assumption that, according to palaeoecological data, the rate of evolution is slower than the rate of present climate change (Davis et al. 2005). Expected temperature increases are far higher than those that occurred during the interglacial periods of the Quaternary. The concern also stems from the growing body of papers predicting extinctions in plants and animals as a result of climate change (Thomas et al. 2004; Thuiller et al. 2005). This debate was further strengthened by the publication of forecast distribution maps for forest trees at the end of the current century that clearly indicate that major changes, if not local extinction, may be expected (Thuiller 2003; Badeau et al. 2005). However, none of these papers have considered the various responses that tree species may adopt and the evolutionary changes that populations may undergo. For example, the niche-based models that are used to predict future distribution of species are based on the conservation of species' climatic envelopes, ignoring the capacity of populations to modify their ecological niche (Thuiller et al. 2006). In this paper, I will challenge these views by confronting these perspectives with recent results obtained in population genetics of forest trees, and expectations based on evolutionary processes.

'How fast will a tree population respond to climate change?' remains one of the main questions. Monitoring evolutionary changes in trees is a challenging task, as only diachronic approaches can be used; hence, there is a dramatic lack of experimental data to answer this question. There are, however, various sources of information that can be assembled to provide arguments as to how trees may be able to cope with the ongoing climate change: results of provenance tests, quaternary palaeoecological records of evolutionary changes, and artificial transfer of populations from cool to milder climates.

Kremer, A. 2007. How well can existing forests withstand climate change? In: Koskela, J., Buck, A. and Teissier du Cros, E., editors. Climate change and forest genetic diversity: Implications for sustainable forest management in Europe. Bioversity International, Rome, Italy. pp. 3–17.

I will review the results from these sources and proceed in four steps. The first part will be devoted to the description of the genetic mechanisms that are likely to promote evolutionary changes in response to climate change. These mechanisms will be described at individual, population and species level. I will then examine the time scales at which these mechanisms are acting. The third part addresses the essential argument concerning evolutionary rates in trees: 'How fast do trees evolve?' and 'What records of evolutionary change are available?' The final part tackles the potential responses of tree populations in terms of risks of extinction, local adaptation and migration.

Evolutionary mechanisms

Evolutionary mechanisms contributing to the adaptation of a given species may be acting at different levels: individuals, populations and species. I will review some of these processes, and concentrate on those that have been at least partly documented in the forestry literature.

Evolutionary mechanisms at the individual level

Adaptive mechanisms of individual trees have been gathered under the generic term *plasticity*, but they may actually cover different processes, acting separately or in combination.

Individual heterozygosity

There is a wide body of literature on the distribution of individual heterozygosity in tree populations, based on isozyme investigations (see Bush and Smouse (1992) for a review). Older stands exhibit usually higher heterozygosity than younger stands. Interpretation of these results is still controversial, as some authors advocate that increased heterozygosity was the mechanistic consequence of elimination of inbred genotypes, due to correlation between homozygosity and inbreeding depression (Ledig 1986). Others have claimed that heterozygosity at the specific study loci (overdominance) contributes to higher fitness (Mitton and Grant 1984) or that heterozygous individuals exhibit greater buffering capacity towards environmental change (Mitton 1997). Whatever the evolutionary significance of heterozygosity might be, there are examples where individual heterozygosity has been correlated (surrogate or cause?) to adaptation to strong environmental changes. This is illustrated by the comparative analysis of heterozygosity in sensitive versus tolerant beech populations in heavily polluted areas during the late 1970s in Germany (Müller-Starck 1988). In this example, the observed heterozygosity of each tolerant beech population was greater than the heterozygosity of sensitive populations wherever the comparison was made, and the difference was larger at higher altitudes where pollution was stronger.

Acclimation

Acclimation is the phenotypic change of a single individual to gradual environmental modification, i.e. it is a reversible process. The premature leaf fall of some trees during dry summers is an example of rapid acclimation. A well illustrated case of acclimation response over the lifetime of a tree is the gradual decrease of leaf stomatal density on a single birch tree that was observed over 50 years (Wagner et al. 1997) as a response to the steadily increasing atmospheric CO_2 concentration. The genetic basis of such phenotypic response has not been elucidated, and to date it is considered to probably be a physiological adaptation to environmental change. However, a recent investigation in quantitative trait loci (QTL) detection of ecophysiological traits in seedlings of forest trees has indicated that the number and contributions of QTLs might vary substantially according to the CO_2 concentration (Torti 2005).

Epigenetic response

Many epigenetic responses have been documented in plants as a response to temporary, severe environmental or biotic stresses (Madlung and Comai 2004). This review indicates that changes in gene expression may be generated by structural changes (e.g. quantitative modification of repetitive DNA; insertion or deletion of transposable elements) or by change in DNA methylation. Epigenetic effects under milder environmental changes have not received as much experimental support, with the exception of the modifications in chromatin of target loci on vernalization in plants (Sung and Amasino 2005).

In a series of repeated experiments on offspring originating from the same parents but with the mothers raised under different weather conditions, it has been shown that the climate during sexual reproduction influences the development of seedlings (Skrøppa et al. 1994; Johnsen and Skrøppa 1997). It has been clearly shown that the timing of bud break in spring, leader shoot cessation in summer, bud set in autumn and the lignification of the annual ring are all processes that will be advanced or delayed according to temperature during female reproduction. Temperature-induced regulation of the level of gene expression (through methylation) in the developing embryos is supposed to last in the progenies as an ‘epigenetic memory’ (Johnsen et al. 2005).

Evolutionary mechanisms at the population level

Natural selection has driven population differentiation throughout the natural distribution of forest trees. The response is a continuous shift in gene frequencies or phenotypic values of traits. There is ample evidence of the efficiency of natural selection shown by the large body of literature on provenance tests (see Wright (1976) and Morgenstern (1996) for reviews in North American species, and König (2005) for a review in European species). In almost any tree species for which provenance tests have been established, significant variation between populations has been observed for fitness-related traits. There are several clinal patterns of geographical variation that are congruent across species living in different continents, suggesting that these patterns result more probably from directional selection pressures than from stochastic, demographic or historical effects. For example, bud burst shows a clear latitudinal variation in all conifers, with northern provenances flushing earlier and setting bud earlier than southern populations (Wright 1976). Other evidence that selection is the most likely evolutionary force responsible for provenance variation is given by the comparative analysis of 'historical' versus 'geographical' factors of variation. In oaks, it was shown that extant populations stemming from the same source (refugial) of glacial origin but growing today in different ecological sites exhibit strong phenotypic differentiation for fitness-related traits, while the populations are not differentiated for neutral genetic markers (Le Corre et al. 1997; Kremer et al. 2002).

Evolutionary mechanisms at the species level

Besides the processes acting at the individual or population level, there are also important processes acting at the metapopulation level of a species. These may contribute to increasing the fitness of a given population that encounters severe selective pressures. Migration of alien genes through gene flow will change the genetic composition of the receiving population. Subsequent changes might be unfavourable or favourable, depending on the source population (Lenormand 2002). If the migrating gene has a positive effect on fitness, it will rapidly increase its frequency in the receiving population. The dynamics of migrating genes (migration rates, subsequent frequency variation and change in population fitness) have never been monitored in forest tree populations, but deserve to receive more attention within the focus of climate change. Clearly, a species that has a continuous distribution across contrasting ecological sites might be able to 'import' genes contributing to higher fitness in areas exposed to severe stress. However, a species having a scattered and disrupted distribution may not be able to benefit from alien genes. Extensive research has been done on gene flow in forest trees at a rather narrow spatial scale (Smouse and Sork 2004; Austerlitz et al. 2004). Most of these theoretical and experimental studies have shown that gene dispersion has both local and large-distance components, as revealed by the existence of the 'fat tails' of the dispersion curve. The second component is, of course, more relevant in the context of climate change, as drier sites where potentially favourable genes are likely to exist, may be separated by rather long distances from the sink population that would benefit from the imported gene. Dispersion from the source to the sink populations may take one or more generations, depending on the spatial connectivity between the two.

Time scales of evolutionary mechanisms

The time scales where these mechanisms may act should be separated into two components (single or multiple generations), depending on whether their effects are cumulative over generations or not.

Mechanisms acting at the individual level will of course take place during the lifetime of a tree. However, they may not be cumulative over successive generations in a directional pattern. Individual heterozygosity would be cancelled out after each generation as meiosis and random mating will disrupt allelic associations in diploid organisms. Acclimation or epigenetic responses may also be erased when passing to the next generation, depending on their inheritance. The genetic basis of methylation or other epigenetic sources of change is not fully understood, and their inheritance remains speculative at this stage.

Natural selection would induce recurrent and cumulative directional evolutionary change over successive generations. Significant effects can already be expected within one single generation. Genetic change within one generation depends on the level of genetic variation (selection differential), and the further cumulative change over generations results from the combined effects of genetic variation and heritability (selection response) (Falconer 1989; Conner and Hartl 2004). Investigations in quantitative genetics of forest trees have shown that there is large genetic (additive) variance for most traits studied so far (e.g. growth, form, wood quality) but rather low heritability (except for wood physical properties and phenology) (Cornelius 1994; Kremer 1994). Hence, genetic variation, rather than heritability, is the most important driving factor of evolutionary change. Unfortunately, fitness-related traits have not been studied in such detail and the amount of genetic variation for these traits is less known. Nevertheless, based on the data on other traits and the additional results obtained with gene markers, one might also expect a high level of genetic variation. Significant evolutionary changes can therefore be expected within one generation, as a result of the predominant role of genetic variation versus heritability. These speculations are actually supported by the results observed in artificial selection programmes. They show that rather moderate selection rates can lead to important genetic change in the very early generations of selection (Anonymous 2005).

Migration over long distances connecting source populations where genes of interest exist and sink population where they might increase fitness may require a few generations to take place. This remains to be investigated in more detail. Gene flow studies have usually been undertaken at two extreme time scales: (1) instantaneous gene dispersion within one generation, conducted by parentage analysis; and (2) cumulative estimations over long historical time scales, derived from genetic differentiation measures. The research that is required in the frame of climate change is the estimation of dispersion distances over a very few successive generations at the landscape scale.

Evolutionary rates due to environmental change

Evolutionary rates measure the genetic change of a population over time. Change is monitored from the 'ancestral' source population to the extant population (allochronic monitoring, Hendry and Kinnison 1999) and this requires three sources of information: source population, time period and extant population. Allochronic approaches cannot be implemented in trees, as the source population can hardly be accessible. Therefore synchronic approaches have been preferred, which consist of comparing different extant populations that have diverged from a common source population. While allochronic approaches measure evolutionary rates, synchronic approaches measure differentiation rates. Even if there can be strong discrepancies between both rates (Hendry and Kinnison 1999), large differentiation among existing populations bears witness of past evolution. Focusing on differentiation for obtaining indirect estimates of evolutionary rates makes provenance tests of forest trees very attractive. However, an important component lacking in provenance research is the time scale that separated the ancestral from the extant provenances. An additional difficulty in using provenance tests is that our interest in evolutionary rates related to global change is to address only directional changes generated by environmental modifications. However, differentiation results from the contribution of very different evolutionary factors. In addition to the processes mentioned in the previous paragraph, additional demographic and historical trajectories may have influenced population differentiation.

Below, I will provide a few examples where indirect estimates of evolutionary rates were available in forest trees. The results are extracted from provenance tests that were screened for two additional criteria: (1) indication of time scales separating extant provenances from the source populations, and (2) indirect evidence that population differentiation is only due to directional selection generated by environmental change.

Differentiation between 'recently' established populations in Europe

Norway spruce (*Picea abies*) has colonized southern Scandinavia during the last 2000 years by natural spreading or through human-mediated dispersion (Bradshaw et al. 2000; Bradshaw and Lindbladh 2005). This is probably the most recent documented spreading of a European tree species. Provenance tests established with seeds originating from

Scandinavia or North Baltic regions (Hannerz and Westin 2000; Danusevicius and Gabrilavicius 2001) showed evidence of population differentiation for all traits investigated, and particularly for phenological traits. Moreover, the trend of geographic variation follows a clinal latitudinal pattern in each study, suggesting that natural selection occurring during the past 2000 years was the main evolutionary driver of population divergence.

For other European tree species, where colonization was achieved over a longer period, population differentiation is of less interest because the time scale for divergence was expanded over much longer periods. For example, pedunculate oak (*Quercus robur*) and sessile oak (*Q. petraea*) have occupied their extant range in Central Europe since 8000–6000 years ago (Brewer et al. 2002), and they have also diverged extensively for phenological traits (Ducousso et al. 1996). It was further demonstrated that the observed provenance variation in a provenance test was generated by diversifying selection due to different environmental conditions occurring at the original sites of the provenances (Kremer et al. 2002) rather than historical factors.

Differentiation between source and transferred populations (European species)

Seed of forest trees have been transferred by man in many different directions in Europe. In a very few cases, the geographical origin of an introduced population is documented, and today's comparisons of the source and transferred population offers an interesting opportunity to estimate evolutionary rates. As an example, Norway spruce has been transferred from the Harz Mountains in Germany (latitude 52°N) to central Norway (64°N), and provenance tests were established with three sources of material: seeds collected from the native stands (in the Harz Mountains); the introduced stands in Norway; and Norwegian local populations grown at the same latitude as the introduced stands (Skrøppa and Kohlmann 1997; Saxe et al. 2001). The results showed that offspring of the introduced stands set bud at the same time as offspring of the local autochthonous populations and earlier than offspring of the native source population from Harz (Skrøppa and Kohlmann 1997). The time scales for population divergence is, in this example, one generation. Significant shifts in one generation were also found for frost resistance in Maritime pine (*Pinus pinaster*), in which provenances from the Atlantic coast were transferred inland to the Massif Central of France. After one generation, seedlings originating from the Massif Central stands exhibited higher frost resistance than provenances from the Atlantic coast (Bouvarel 1960).

Differentiation between source and transferred populations (exotic tree species)

Exotic tree species, mainly originating from North America, have been widely introduced to Europe during the past centuries. Lodgepole pine (*Pinus contorta*) and Sitka spruce (*Picea sitchensis*) in Nordic countries and Douglas fir (*Pseudotsuga menziesii*) and red oaks (*Quercus* spp.) in central Europe are among the well known introduction success stories. Interestingly, in some cases the change in distribution corresponded to a change of climate, mimicking the future predicted climate change in Europe. Similarly to autochthonous tree species that were transferred to other regions, exotic tree species offer unique case studies permitting evaluation of their divergence since their introduction. Northern red oak (*Q. rubra*) is a well documented case. The species was introduced shortly after the French revolution (Timbal et al. 1984) and today it is widespread in Europe. A genetic survey based on cpDNA (chloroplast DNA) showed that introduced populations harbour the same haplotypes as populations from the natural distribution, suggesting that the introduced gene pool is a representative sample of the original germplasm (Magni Diaz 2004). A large-scale provenance test was established in south-western France, and the collection included progenies collected from introduced European stands. Interestingly, the introduced populations, as a whole, exhibited a clear shift in bud burst and leaf coloration from the populations of the natural range (Daubree and Kremer 1993). As the time scale is at most 200 years, these results also provide clear evidence for rapid evolution in Northern red oak.

Other examples illustrating the divergence of exotic species have been reported in Saxe et al. (2001), and are best known by practitioners for formation of landraces in forest trees. The differentiation of landraces might, however, originate from three different causes: (1) directional shifts due to different selection pressures existing in the natural and introduced range; (2) changes in the genetic structures of introduced and natural stands; (3) stochastic shifts due to foundation events or genetic drift effects due to the limited amount of seed introduced. Results should therefore be interpreted with caution, as our focus (in relation to global change) is mainly on directional shifts generated by new selection pressures.

These examples clearly suggest that evolutionary rates might be quite substantial, despite the long generation intervals of trees. Forest tree populations may exhibit significant differentiation in a very few generations. Rapid evolution may result from the contribution of different evolutionary processes acting at the individual, population or species level. An important motor of evolution is obviously the level of diversity that resides within tree populations. There is also a more mechanistic interpretation that derives from the complex genetic architecture of adaptive traits. For a trait that is controlled by a large number of genes, differentiation builds up not only from the differences in allelic frequencies at the different genes, but also from the complementary contribution of alleles at different genes. As the number of genes increases, so will the number of favourable associations, and they will be captured right at the beginning by diversifying selection (Le Corre and Kremer 2003).

Expected responses to environmental change

Climatic projections for the end of the 21st century predict that today's climatic envelopes of forest tree species will be shifted northwards and eastwards, on average, by a few hundred kilometres (Thuiller 2003; Badeau et al. 2005). In these predictions, the future tree distributions are projected on the assumption that current envelopes reflect species' environmental preferences, which are assumed to remain the same under climate change. To illustrate these predictions in the case of sessile oak and beech (*Fagus sylvatica*), France will be out of their new climatic envelope, whereas central Finland is likely to be included within the envelope. Although strictly based on a 'copy-and-paste' approach of constant climatic envelopes, these projections raise in concrete terms the issues that forest trees are facing. What will happen at the western and southern limits that are likely to be out of the climatic envelope? Will there be a progressive decline of the species and extinctions? Will local populations adapt to the new conditions? What will happen at the eastern and northern limit, where new areas will be included in the climatic envelope? Will trees be able to migrate at such distances to cope with the shift of the climatic envelope? Species will most likely respond differently to these challenges, depending on their ecology, demographic and genetic structures, and biotic interactions with other species. Additional reasoning on how trees will respond should take into account evolutionary processes leading to changes in their climatic envelope over time. We are lacking experiments to answer these questions, as evolutionary change would need to be monitored over successive generations. However, two sources of information can help to understand and predict future responses:

- lessons of past evolution of trees in response to climate change occurring over longer time scales; and
- results from multi-site provenance tests.

By assembling elements from these sources of information, one can make some speculations on the risks of extinction, migration potential of the species to cope with the shift of the climatic envelope, and adaptation to environmental change.

Risks of extinction

During the past two million years (Quaternary era), forest trees have been confronted with successive glacial periods (lasting from 70 000 to 100 000 years), alternating with interglacial periods (lasting from 10 000 to 20 000 years). More than fifteen periods generated by orbital oscillations of Earth (so called Milankovitch oscillations) occurred successively during the entire Quaternary era (Hays et al. 1976). These repeated drastic environmental changes were followed by important alternating retractions and expansions of tree species distributions, placing them in different habitats over time and space, and preventing them from specialization. It is thought that repeated climatic oscillations selected species for their dispersability and low specialization (Dynesius and Jansson 2000). Indeed, extinctions of European forest trees occurred between 2.4 to 1. 7 million years ago, during the early severe glacial cycles of Quaternary. Many species that existed in Europe at the end of Tertiary, based on fossil evidence, disappeared and are nowadays only present in North America and Asia (e.g. species belonging to *Magnolia, Liriodendron, Nissa, Taxodium* and *Sequoia*) (Skelton 1993). Periodic climate changes during the Quaternary period resulted in important extinction rates during the earlier oscillations, but selected species with reduced specialization and efficient dispersability, mitigating extinction in the long term. It is intriguing to notice that there has been no tree species extinction during the most recent periods, despite the occurrence of very rapid climate changes (Dansgaard-Oeschger events). Indeed, rapid warming episodes occurred during the last glacial periods every 1500 years, followed by gradual cooling over longer periods (Alley 2000). During Dansgaard-Oeschger events temperature increased by from 5° to 10°C over a few decades. These rates are of the same magnitude as the future predicted changes, but the warming occurred during the glacial periods. No extinction of tree species has been reported from the investigations of those periods. Quaternary evolutionary history suggests that past climate changes have selected species able to prevent extinction, thanks to their rapid dispersion and colonization of contrasting habitats. Natural selection induced by climate changes therefore produced, in particular, species with large distributions in northern latitudes (Dynesius and Jansson 2000). One might conclude from these speculations that extinction risks under the present climate change are lower for those species, whereas highly specialized species occurring at lower latitudes may be exposed to higher risks.

Migration potential

Postglacial history of forest trees provides additional information on the dispersal capacity of trees. Since trees were major components of past European landscapes, they produced large quantities of pollen that survive in fossil remains (Huntley and Birks 1983). Migration rates were inferred from historical species ranges reconstructed using pollen fossil data for several European tree species (Birks 1989) in the British Isles and on a continental scale in oaks (Brewer et al. 2002) and beech (Magri et al. 2006). The average rate of spreading varied between 100 and 700 metres per year, depending on species and the periods of colonization. Earlier dispersion rates (11 000 to 9000 BP) were usually higher and strongly correlated with climate change, whereas more recent rates (6000 to 4000 BP) were lower, as competition between species constrained their spread (Birks 1989). Despite the limitation of migration rates derived from pollen data (McLachlan and Clark 2004), these figures could be used to provide some rough estimates predicting future natural dispersion. At maximum, trees would be able to shift their range from 10 to 70 km during the next coming hundred years, not taking into account that land fragmentation and agriculture would actually reduce migration. This is far less than the shifts of range predicted for oak or beech based on the climatic envelope projections, which amounts to a few hundred kilometres (Thuiller 2003; Badeau et al. 2005). Hence, natural dispersion would need to be assisted by artificial seed transfer to cope with the shifting climatic envelopes.

Short-term adaptation

Predictions of the potential adaptation of trees to climate change can be made from provenance tests that were established under various environmental conditions. When a given provenance is planted in many different environments, the response function of a measured trait can be constructed if the mean value of trait is plotted as a function of any environmental variable of the testing site. Unfortunately, most provenance tests were established on a limited number of sites and thus do not allow the construction of these functions. There are, however, a few cases where large scale provenance test were established (Rehfeldt et al. 2002 for Scots pine (*Pinus sylvestris*); Rehfeldt et al. 1999 for Lodgepole pine). Rehfeldt and co-workers constructed response curves for two surrogates of tree fitness: survival and height growth as a function of mean temperature of the testing site. These two case studies provided convergent results that can be summarized in three points:

The response curve usually follows a parabolic function, although the maximum of the function is not a peak. The curve reaches a plateau extending over a few Celsius degrees. The plateau indicates, therefore, substantial plasticity in the provenances.

When compared to the temperature where the provenance reaches the maximum value for the fitness surrogate, the temperature of the site where the provenance originates is, on average, lower. The difference being on average 2.8°C in Lodgepole pine (Table 8 in Rehfeldt et al. 1999) and 2.6°C in Scots pine (Page 921 in Rehfeldt et al. 2002) for height growth.

The temperature difference between the inhabited climate and the optimum climate is related to population latitude. Northern provenances tend to be native to cooler climates than their optimum whereas southern provenances tend to originate from climates near their optimum (Figure 6 in Rehfeldt et al. 2002 for Scots pine; Figure 10 in Rehfeldt et al. 1999 for Lodgepole pine).

These observations suggest that the predicted temperature increase for the next century would still fall within the optimal region of the response curve. These preliminary optimistic results should, however, be taken with caution as they rely only on surrogates of fitness (height growth and survival). Secondly, they concern widespread tree species of northern latitude, which have actually been selected for generalism and plasticity, as described earlier (Dynesius and Jansson 2000). Responses of other tree species of southern latitude and with scattered distributions or highly specific habitats also need to be studied.

Conclusion and recommendations

There is a growing body of evidence stemming from different sources of information (Quaternary evolutionary history; lessons from population and species transfers; provenance experiments) that trees may have resources and mechanisms to respond to climate change. Overall, the pieces of evidence are fragmentary and refer to separate case studies in different time and space settings. It remains an open research field as to how strong and how prevalent these mechanisms will be in the evolutionary setting of future climate change. Unfortunately, such investigations would need long-term experiments and would not be able to answer short-term concerns. In the meantime, however, a few recommendations can be made for further research that could lead to practical short-term implementations.

Construction of response functions in provenance tests

Provenance tests have been widely established during the past 50 years in Europe, either through national or international initiatives. For most economically important species, the data sets are, however, scattered among different research institutions, limiting their compilation for the construction of response curves. In-depth exploitation of the data—in a similar manner to the Rehfeldt studies—requires assembling the different data sets, and remains undone. Full exploitation may be limited by the heterogeneity of sampling strategies or experimental designs used. Nevertheless, the results of these investigations would provide some clues regarding the transferability of forest reproductive material. A strong recommendation is the assessment of different complementary surrogates of fitness, and particularly sexual reproduction.

Monitoring of evolutionary change in transferred tree populations

There are many historical examples of artificial transfers of tree populations or species (in the case of exotics). In some cases, these transfers mimicked climate change, e.g. transfer from cooler to milder climate. A review of these scenarios and their final outcome (success or failure) should be made. Of particular interest is the estimation of the evolutionary changes –and particularly adaptation—that was associated with these transfers. Introduction scenarios, including tracking of source populations by molecular fingerprints, could be reconstructed and evolutionary change monitored. These investigations would ideally complement the provenance test analysis, as a few generations have usually elapsed since introduction, whereas provenance tests only reveal changes after one generation. Additionally, transferred populations or species have usually been implemented over larger areas than provenance tests and the transferred material has been tested in a real forestry context, rather than an experimental plantation.

References

Alley, R.B. 2000. Ice core evidence of abrupt climatic change. *Proceedings of the National Academy of Sciences of the United States of America*, 97: 1331–1334.

Anonymous. 2005. Genetic breeding of the maritime in Aquitaine. Gis Pin Maritime du Futur, INRA, Pierroton, France.

Austerlitz, F., Dick, C.W., Dutech, C., Klein, E., Oddou-Muratorio, S., Smouse, P.E. & Sork, V.L. 2004. Using genetic markers to estimate the pollen dispersal curve. *Molecular Ecology*, 13(4): 937–954.

Badeau, V., Dupouey, J.L., Cluzeau, C. & Drapier, J. 2005. Aires potentielles de répartition des essences forestières d'ici 2100. *Forêt Entreprise*, 162: 25–29.

Birks, H.J.B. 1989. Holocene isochrone maps and patterns of tree spreading in the British Isles. *Journal of Biogeography*, 16: 503–540.

Bouvarel, P. 1960. Note sur la résistance au froid de quelques provenances de Pin Maritime. *Revue Forestière Française*, 7: 495–508.

Bradshaw, R.H.W., Holmqvist, B.H. & Cowling, S.A. 2000. The effects of climate change on the distribution and management of *Picea abies* in southern Scandinavia. *Canadian Journal of Forest Research*, 30: 1992–1998.

Bradshaw, R.H.W. & Lindbladh, M. 2005. Regional spread and stand-scale establishment of *Fagus silvatica* and *Picea abies* in Scandinavia. *Ecology*, 86(7): 1679–1686.

Brewer, S., Cheddadi, R., De Beaulieu, J.L. & Reille, M. 2002. The spread of deciduous *Quercus* throughout Europe since the last glacial period. *Forest Ecology and Management*, 156: 27–48.

Bush, R.M. & Smouse, P.E. 1992. Evidence for the adaptive significance of allozymes in forest trees. *New Forests* 6: 179–186.

Conner, J.K. & Hartl, D.L. 2004. *A primer of Ecological Genetics*. Sinauer Associates, Sunderland, MA, USA. 304 p.

Cornelius, J. 1994. Heritabilities and additive genetic coefficients of variation in forest trees. *Canadian Journal of Forest Research*, 24: 372–379.

Danusevicius, D. & Gabrilavicius, R. 2001. Variation in juvenile growth rhythm among *Picea abies* provenances from the Baltic states and the adjacent regions. *Scandinavian Journal of Forest Research*, 16: 305–317.

Daubree, J.B. & Kremer, A. 1993. Genetic and phenological differentiation between introduced and natural populations of *Quercus rubra* L. *Annales des Sciences Forestières*, 50(Suppl. 1): 271s–280s.

Davis, M.E., Shaw, R.G. & Etterson, J.R. 2005. Evolutionary responses to climate change. *Ecology*, 86: 1704–1714.

Ducousso, A., Guyon, J.P. & Kremer, A. 1996. Latitudinal and altitudinal variation of bud burst in western populations of sessile oak (*Quercus petraea* (Matt.) Liebl.). *Annales des Sciences Forestières*, 53(2/3): 775–782.

Dynesius, M. & Jansson, R. 2000. Evolutionary consequences of changes in species geographical distributions driven by Milankovitch climate oscillations. *Proceedings of the National Academy of Sciences of the United States of America*, 97: 9115–9120.

Falconer, D.S. 1989. *Introduction to quantitative genetics*. Third edition. Longman, Harlow, England, UK. 438 p.

Hannerz, M. & Westin, J. 2000. Growth cessation and autumn-frost hardiness in one-year-old *Picea abies* progenies from seed orchards and natural stands. *Scandinavian Journal of Forest Research*, 15: 309–317.

Hays, J.D., Imbrie, J. & Shackleton, N.J. 1976. Variations in the Earth's orbit: pacemaker of the ice ages. *Science*, 194: 1121–1132.

Hendry, A.P. & Kinnison, M.T. 1999. Perspective: the pace of modern life: measuring rates of contemporary microevolution. *Evolution*, 53(6): 1637–1652.

Huntley, B. & Birks, H.J.B. 1983. *An atlas of past and present pollen maps for Europe 0–13 000 years ago.* Cambridge University Press, Cambridge, UK. 667 p.

Johnsen, O, & Skrøppa, T. 1997. Parents of Norway spruce adjust the performance of their progeny according to changes in climate and weather conditions during female flowering, a review. pp. 159–163, *in:* G.M.J. Mohren, K. Kramer and S. Sabaté (editors). *Impacts of global change on tree physiology and forest ecosystems.* Proceedings of the International Conference on Impacts of Global Change on Tree Physiology and Forest Ecosystems, Wageningen, The Netherlands, 26–29 November 1996. Kluwer Academic Publishers, Dordecht, The Netherlands. Published as *Forestry Sciences*, Vol. 52. 388 p.

Johnsen, O., Fossdal, C.G., Nagy, N., Molmann, J., Daehlen, O.G. & Skrøppa, T. 2005. Climatic adaptation in *Picea abies* progenies is affected by the temperature during zygotic embryogenesis and seed maturation. *Plant, Cell and Environment*, 28:–1090–1102.

König, A.O. 2005. Provenance research: evaluating the spatial pattern of genetic variation. pp. 275–328, *in:* Th. Geburek and J. Turok (editors). *Conservation and Management of Forest genetic Resources in Europe.* Arbora Publishers, Zvolen, Slovakia.

Kremer, A. 1994. Diversité génétique et variabilité des caractères phénotypiques chez les arbres forestiers. *Génétique Sélection Evolution*, 26(Supplement 1): 105–123.

Kremer, A., Kleinschmit, J., Cottrell, J., Cundall, E.P., Deans, J.D., Ducousso, A. et al. 2002. Is there a correlation between chloroplastic and nuclear divergence, or what are the roles of history and selection on genetic diversity in European oaks? *Forest Ecology and Management*, 156(1–3): 75–87.

Magni Diaz, C.R. 2005. Reconstitution de l'introduction de *Quercus rubra* L. en Europe et conséquences génétiques dans les populations allochtones. PhDF Thesis, ENGREF, Paris, France. 419 p.

Le Corre, V., Dumolin-Lapègue, S. & Kremer, A. 1997. Genetic variation at allozyme and RAPD loci in sessile oak *Quercus petraea* (Matt.) Liebl.: the role of history and geography. *Molecular Ecology,* 6(6): 519–529.

Le Corre, V. & Kremer, A. 2003. Genetic variability at neutral markers, quantitative trait loci and trait in a subdivided population under selection. *Genetics*, 164: 2005–2019.

Ledig, F.T. 1986. Heterozygosity, heterosis, and fitness in outbreeding plants. pp. 77–104, *in:* M.E. Soulé (editor). *Conservation Biology. The science of scarcity and diversity.* Sinauer Associates, Sunderland, MA, USA.

Lenormand, T. 2002. Gene flow and the limits to natural selection. *Trends in Ecology and Evolution,* 17: 183–189.

Magri, D., Vendramin, G.G. Comps, B. Dupanloup, I. Geburek, T. Gömöry, D. et al. 2006. A new scenario for the Quaternary history of European beech populations: palaeobotanical evidence and genetic consequences. *New Phytologist,* 171: 199–221.

Madlung, A. & Comai, L. 2004. The effect of stress on genome regulation and structure. *Annals of Botany,* 94: 481–495.

McLachlan, J.S. & Clark, J.S. 2004. Reconstructing historical ranges with fossil data at continental scales. *Forest Ecology and Management*, 197: 139–147.

Mitton, J.B. 1997. *Selection in natural populations.* Oxford University Press, Oxford, UK.

Mitton, J.B. & Grant, M.C. 1984. Association between protein heterozygosity, growth rate, and developmental homeostasis. *Annual Review of Ecology and Systematics*, 15: 479–499.

Müller-Starck, G. 1988. Genetic implications of environmental stress in adult forest stands. pp. 127–142, *in:* F. Scholz, H.R. Gregorius and D. Rudin (editors). *Genetic effects of air pollutants in forest tree populations.* Springer Verlag, Berlin, Germany.

Morgenstern, E.K. 1996. *Geographic variation in forest trees.* University of British Columbia Press, Vancouver, Canada. 209 p.

Rehfeldt, G.E., Ying, C.C., Spittehouse, D.L. & Hamilton, D.A. 1999. Genetic responses to climate in *Pinus contorta*: niche breadth, climate change and reforestation. *Ecological Monographs*, 69: 375–407.

Rehfeldt, G.E, Tchebakova, N.M., Parfenova, Y.I., Wykoff, W.R., Kuzmina, N.A. & Milyutin, L.I. 2002. Intraspecific response to climate in *Pinus sylvestris*. *Global Change Biology*, 8: 912–929.

Saxe, H., Cannell, M.G.R., Johnsen, O., Ryan, M.G. & Vourlitis, G. 2001. Tree and forest functioning in response to global warming. *New Phytologist*, 149: 369–400.

Skelton, P. 1993. Evolution. A biological and palaeontological approach. Addison-Wesley Publishing Co., Boston, MA, USA. 1051 p.

Skrøppa, T., Nikkanen, T. Ruotsalainen, S. & Johnsen, O. 1994. Effects of sexual reproduction at different latitudes on performance of the progeny of *Picea abies*. *Silvae Genetica*, 43: 297–303.

Skrøppa, T. & Kohlmann, K. 1997. Adaptation to local conditions after one generation in Norway spruce. *Forest Genetics*, 4(3): 171–177.

Smouse, P.E. & Sork, V.L. 2004. Measuring pollen flow in forest trees: an exposition of alternative approaches. *Forest Ecology and Management*, 197: 21–38.

Sung, S. & Amasino, R.M. 2005. Remembering winter: toward a molecular understanding of vernalization. *Annual Review of Plant Biology*, 56: 491–508.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C. et al. 2004. Extinction risk from climate change. *Nature,* 427: 145–148.

Thuiller, W. 2003. BIOMOD. Optimizing predictions of species distributions and projecting potential future shifts under global change. *Global Change Biology*, 9:1353–1362.

Thuiller, W., Lavorel, S., Araujo, M.B., Sykes, M.T. & Prentice, J.C. 2005. Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences of the United States of America,* 102: 8245–8250.

Thuiller, W., Lavorel, S., Sykes, M.T. & Araújo, M.B. 2006. Using niche-based modelling to assess the impact of climate change on tree functional diversity in Europe? *Diversity and Distributions,* 12: 49–60.

Timbal, J., Kremer, A., Le Goff, N. & Nepveu, G. (editors). 1984. *Le chêne rouge d'Amérique*. Editions de l'INRA, Paris, France. 564 p.

Torti, X. 2005. Variabilité génétique de la réponse du métabolisme carboné du chêne pédonculé (*Quercus robur* L.) à des teneurs croissantes en CO_2. PhD Thesis, Université Henri Poincaré, Nancy I, France. 130 p.

Wagner, F., Below, R., de Klerk, P., Dilcher, D.L., Joosten, H., Kürschner, W.M. & Visscher, H. 1997. A natural experiment on plant acclimation: lifetime stomatal frequency response of an individual tree to annual atmospheric CO_2 increase. Proceedings of the National Academy of Sciences of the United States of America, 93: 11705–11708.

Wright, J.W. 1976. *Introduction to forest genetics.* Academic Press, New York, NY, USA.

ADAPTATION OF FOREST TREES TO CLIMATE CHANGE

Outi Savolainen,[1] Folmer Bokma,[3] Timo Knürr,[1,2] Katri Kärkkäinen,[2] Tanja Pyhäjärvi[1] and Witold Wachowiak[1,4]

1. Department of Biology, University of Oulu, Finland
2. Finnish Forest Research Institute, Vantaa Research Centre, Finland
3. Department of Ecology, University of Umeå, Sweden
4. Polish Academy of Science, Institute of Dendrology, Kórnik, Poland

Introduction

As the environment changes, trees and other plants can respond in different ways. They may have high phenotypic plasticity and the existing genotypes or populations can simply tolerate the environmental change. Alternatively, they may become extinct due to lack of ability to cope with the abiotic changes. About 10% (8750) of the nearly 100 000 tree species are on the endangered species list, for many different reasons (Oldfield et al. 1998). Further, following changes in the abiotic environment, trees can migrate through seed movement to more suitable areas and thus maintain their 'climatic envelope'. Range extension has been historically a very important way of migration (Bradshaw and McNeilly 1991). Historically, trees have been able to spread fast, largely based on events of long-distance dispersal (Clark 1998). The dispersal rates in general are between 10 and 100 m per year, or a maximum of 100 km per 100 years. These are nevertheless short distances, compared with what is required by current climate change (Malcolm et al. 2002). Range extension is currently occurring. For instance, the Scots pine (*Pinus sylvestris*) forest limit in northern Finland moved 6 km to the north between 1935 and 1995 (Sirén 1998).

The above-mentioned possibilities have been extensively considered as responses to the current human-induced climate change, but populations may also be able to evolve and genetically adapt to new conditions. This was suggested early by Bradshaw and McNeilly (1991). More recently, Davis and colleagues have examined the potential for evolutionary responses (Lynch 1996; Davis and Shaw 2001; Davis et al. 2005). The genetic structure of many tree populations demonstrates that, in addition to migrating to different areas with changing climate, a common response of tree populations has historically also been to evolve through genetic differentiation

---

Savolainen,O., Bokma, F., Knürr, T., Kärkkäinen, K., Pyhäjärvi, T. and Wachowiak, W. 2007. Adaptation of forest trees to climate change. In: Koskela, J., Buck, A. and Teissier du Cros, E., editors. Climate change and forest genetic diversity: Implications for sustainable forest management in Europe. Bioversity International, Rome, Italy. pp. 19–30.

with respect to the geographically varying climatic conditions. Thus, this possibility deserves attention.

In this paper, we discuss the extent of local genetic adaptation in trees, the evolutionary forces that generate this differentiation, and then evaluate possibilities for trees to adapt to the changing climate, in both natural populations and under silvicultural conditions. We use Scots pine as a special case study, but aim to make some general conclusions on the adaptation of forest trees to climate change. We especially consider northern Europe.

By definition, locally adapted populations have the highest fitness when compared with other populations at their growing site (Kawecki and Ebert 2004). At other sites, they will have lower fitness than the local populations (Figure 1). Thus, the appropriate test of local adaptation is the ranking (against other populations) of lifetime fitness at the local site. This does not mean that the locally adapted population would not grow better elsewhere, just that they are best at home. This kind of full information is not available for forest trees, but is it needed? Tree breeders are of course not directly interested in this evolutionary definition of local adaptation, because growth and survival in different environments are of more immediate interest. However, it can be important to also consider reproduction or competitive

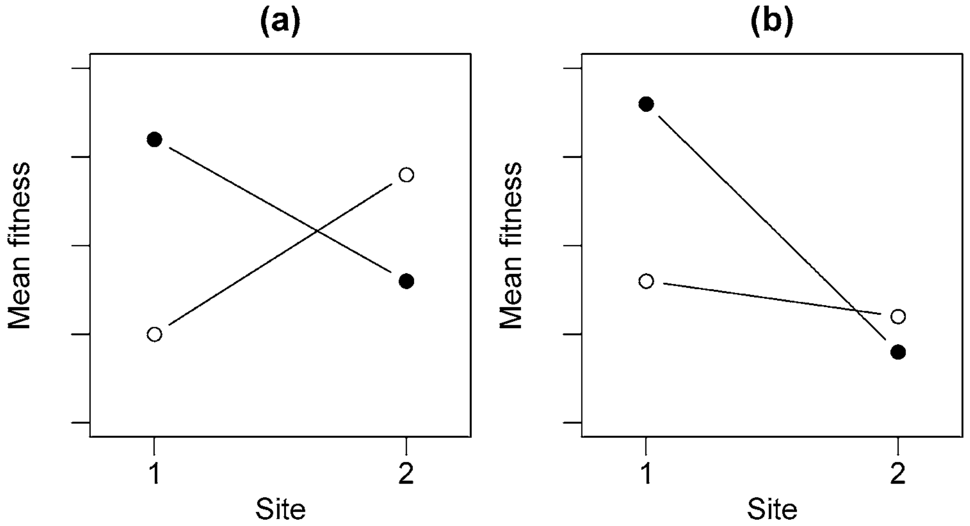

Figure 1. Schematic presentation of local adaptation. Locally adapted populations have higher fitness than other populations at their site of origin. Population A (solid circles) originates from site 1, population B (open circles) from site 2. In Figure 1 (a), each population has highest fitness at its home site; in Figure 1 (b), although population B performs better at site 1 than in site 2, local population A does even better at site 1.

ability in intra- and interspecific competition. During climate change, economically important tree populations may be intensively managed with silviculture to directions decided by humans but other, natural tree populations will follow the rules of natural evolution. Thus it will also be important to understand the evolution of local climatic adaptation and to take both natural and human directed evolution into account.

Trees have evolved through local adaptation: evidence from provenance trials and clines

Results on local adaptation in trees come from two sources: provenance trials and patterns of clinal variation. Provenance trials of forest trees differ from classical local adaptation experiments of other plants in many ways (Clausen et al. 1948). Seedlings are planted as plots of seedlings of the same origin, in spaced plantings, where both intraspecific and interspecific competition are avoided, or at least reduced. Not surprisingly, reproductive fitness is practically never studied in such trials. Thus, two important fitness components, early survival in competitive conditions and reproductive ability, are not included.

Provenance trials are generally not designed to test for local adaptation, but for finding genetic materials that could be used to increase productivity. Eiche (1966) and Eriksson et al. (1980) found in large Scots pine experiments that seedlings transferred southward [in the northern hemisphere] had increased survival. Beuker (1994) also found that volume production of northern provenances increased upon transfer to the south. The results of a very large Scots pine provenance trial (Shutyaev and Giertych 1997) were used by Rehfeldt et al. (2002) to assess Scots pine response to climate change. Again, northern provenances transferred south to warmer climates had higher growth than at their original location. Thus the northern populations are likely to benefit from the warming climate. However, this large-scale study also predicted that the southernmost populations in the northern hemisphere are likely to suffer from the warming climate. This suggests that the limiting factors of Scots pine populations differ in the different parts of the range. Findings of increased (radial) growth upon climate change in the expected elevated temperatures have also been made in experimental studies (Kilpeläinen et al. 2005).

Note that compared with the above definition, the studies do not address the issue of whether forest trees are locally adapted. The northern populations transferred to the south may grow better than at home, but worse than the southern populations at those sites. But is the local population best in fitness? Wu and Ying (2004) analyzed provenance trial data of Lodgepole pine (*Pinus contorta*). They used height growth as a surrogate for fitness, and found that, in a large part of the range, the local population was optimal for height growth. The large study of Scots pine also found evidence of local adaptation (Shutyaev and Giertych 1997). Very northern and very southern materials in the northern hemisphere were not found silviculturally interesting, because they were inferior in growth performance to those from more central latitudes, except locally. This finding of local superiority is evidence of local adaptation. Thus, even when just using height as a fitness surrogate, provenance trials do show evidence of local adaptation.

We also know that Scots pine has limits to its adaptation. In northern Scandinavia, the distribution range ends without any geographical barrier. While survival is high in areas of temperature sums of more than 800 day degrees, in colder areas (e.g. northern Sweden, about 67°N at low altitudes) survival rapidly decreases (Eiche 1966). Likewise, northern populations in areas with temperature sums less than 1000 day degrees show poor adaptation in terms of seed maturation (Harju et al. 1996). Thus, it seems the populations may not be able to fully adapt to the severe conditions. The existence of genetically determined clinal variation in adaptive traits along environmental gradients is also evidence of local adaptation, especially if neutral markers in the genome show no corresponding differentiation (Prout and Barker 1993; Merilä and Crnokrak 2001; McKay and Latta 2002). Evidence of such clines is abundant in forest trees, For instance, in common garden experiments in the northern hemisphere, Scots pines of northern origin set their terminal buds before the southern ones (Mikola 1982; Hurme et al. 1997; García-Gil et al. 2003). Figure 2 shows an example of such a cline over the Scandinavian latitudinal range for timing of bud set of one-year-old Scots pine seedling, grown in common garden conditions (as described earlier, e.g. by García-Gil et al. (2003)). In the same range, the divergence at neutral markers is much lower (Karhu et al. 1996; García-Gil et al. 2003). Similar variation patterns that are concordant with climate variation have been found in many forest trees, such as Norway spruce (*Picea abies*) and Lodgepole pine (Lagercrantz and Ryman 1990; Yang et al. 1996). Cold hardiness also shows such patterns of variation in Scots pine (Aho 1994; Hurme et al. 1997) and in many North American conifers (as reviewed by Howe et al. 2003). In sessile oak (*Quercus petraea*), there is a longitudinal cline in timing of bud flush (Kremer et al. 1997). The latitudinal ecotypes of other woody perennials, including species of willows (*Salix* spp.), also show photoperiod-dependent variation in cessation of growth (Junttila 1982). Furthermore, populations of forest tree species show differences in adaptation to drought. In the Mediterranean region, summer drought is a major factor limiting plant distribution and growth. Variability in

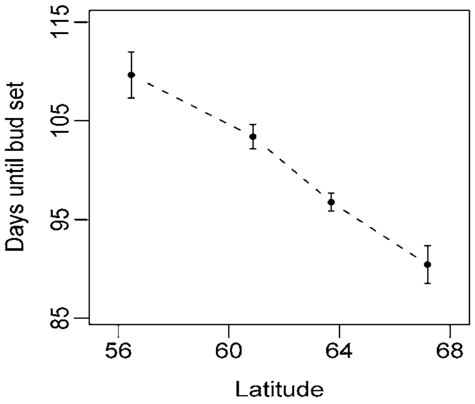

Figure 2. Timing of bud set in first-year seedlings of Scots pine (*Pinus silvestris*) in a common garden environment in the northern hemisphere. Northern populations set their buds much before more southern ones (T. Knürr, K. Kärkkäinen and O. Savolainen, personal communication). For methods, see García-Gil et al. (2003).

ecophysiological response to drought is found among geographical races of maritime pine (*Pinus pinaster*) (Fernandez et al. 1999). Adaptation to different soil water conditions may also be due to structural rather than physiological variation, as was found in Scots pine (Palmroth et al. 1999).

In most of these cases, there is little differentiation at neutral markers. The steepness of the clines and the degree of differentiation depends on the balance between gene flow through seeds and pollen, as well as natural selection (Ennos 1994; Barton 1999). The low differentiation of marker genes reflects high migration rates. In the oak clines, traces of history have been eliminated, as shown by Kremer et al. (2002). In Norway spruce, the quantitative trait differentiation is partly also reflected at marker genes, suggesting that history is also reflected in patterns of quantitative variation, in addition to selection (Lagercrantz and Ryman 1990).

Potential for adaptation

The genetic response to selection depends on the heritability of the trait and on the intensity of selection. The familiar breeder's equation states that $R = h^2S$, where R is response, h^2 is heritability and S the selection differential. Forest trees are highly variable in most quantitative traits. Much of this variation is genetic, giving rise to moderate and high heritabilities (Cornelius 1994). Specifically, this has also been found to hold true for timing of bud set in Scots pine, where heritabilities in two populations were 0.33 to 0.67 (Savolainen et al. 2004). Also, cold tolerance is found to be heritable, with more variable results, as reviewed by Howe et al. (2003). The real potential for evolutionary response is measured by additive genetic variance. A high heritability does not guarantee an evolutionary response if both additive genetics variance and total phenotypic variance are low (Houle 1992). Selection in tree populations can be strong, as mortality can be high. Thus, there is considerable capacity for high selection differentials. The populations are large, and there is much gene flow, so that genetic drift is expected to be a minor factor. The conditions for a selective response are therefore favourable.

In simple situations that correspond to the model, there can be very rapid genetic change. Introduced plant populations sometimes adapt rapidly to the local climatic conditions. Introduction of exotic tree species or provenances has quickly produced new landraces under the combination effect of natural and artificial selection (Eldridge et al. 1993; Hahl 1978). Large-scale provenance transfers of Douglas fir (*Pseudotsuga menziesii*) to Europe have resulted in locally adapted populations (Kleinschmidt and Bastien 1992). Evolution in natural conditions can also be relatively rapid. Novel photoperiodic genotypes adapted to the very long days of northern Scandinavia evolved in silver birch (*Betula pendula*) during colonization after the last glacial maximum, taking only a few thousand years (Viherä-Aarnio et al. 2005).

Gene flow influences the process of adaptation. When new areas are colonized, seed migration is especially important (Austerlitz et al. 2000). In the later stages, pollen flow is especially effective. This is reflected in the lack of differentiation for most of the genome. Gene flow can hamper adaptation in marginal populations, but it also provides more genetic variability for selection to act upon. These general features of forest trees show that selection is likely to be powerful. This has led some authors to conclude that forest trees will be able to adapt to the current climate change without problems.

Evolving in the changing climate is a complex process

Evolution during the current climate change is a more complicated situation than colonization and adaptation after the ice age. The present environmental changes are taking place rapidly. In northern Europe, temperature is expected to increase by at least 4° to 6°C within the next hundred years (Houghton et al. 2001). The landscape is not empty but filled with existing plant species. This will make colonization of new areas much more difficult for many trees (Malcolm et al. 2002). For some species, such as Scots pine, interspecific competition is predicted to be more intense, as climate change is likely favour other species, such as birch (Kellomäki et al. 2001). Ecologists have thus predicted that Scots pine will decline, while tree breeders have suggested that it will do very well in the northern areas under the warming climate (Kellomäki et al. 2001).

As the biological situation is quite complex, we used simulations to evaluate the potential of trees to adapt genetically to a new environment, through local selection and through gene flow, mostly by pollen (Savolainen et al. 2004). The basic assumption is that the genetic composition of the population, with respect to timing of growth (or cessation of growth), should follow the 'climatic envelope'. The temperature sum at latitude 68°N is expected to be approximately like the temperature sum at latitude

61°N currently. Thus, the population at 68°N should evolve to have the timing of growth characteristics of the population currently found at latitude 61°N.

We simulated adaptation of 10 Scots pine populations equally spaced along a latitudinal climate gradient, all consisting of 1000 individuals that reached maturity at 20 years and a maximum age at 150 years. Vacancies left by individuals that reached the maximum age were filled by the best adapted (see below) of 20 seedlings, the mothers of which were sampled at random from the population where the vacancy occurred, while the fathers were sampled from a randomly sampled population. This reflects that dispersal in Scots pine is mainly by pollen. Paternal populations were sampled from a normal distribution with zero mean and unit variance, which translates into pollen dispersal distances that make the 10 populations correspond approximately to the latitudinal range of Scots pine in Finland.

Contrary to adult trees, seedlings (i.e. individuals younger than 20 years) may die due to frost damage. We assumed that the autumn onset of frost varies linearly from south (late onset, long growing season) to north (early onset, short growing season). Seedlings must set bud (and become frost hardy) before the onset of frost, otherwise they die. Timing of bud set was modelled as a quantitative trait with 50% heritability, governed by 5 additively acting loci on different chromosomes, with two alleles per locus. Seedlings that set bud after the onset of frost quickly die in the simulations. In contrast, seedlings that set bud too early remain small due to their short period of growth. They are therefore likely to lose the competition for space. We assumed that competition for space takes place dominantly during the seedling stage. Therefore, the 'best' seedling, that fills a vacancy, is the largest of the 20 seedlings that did not die due to frost damage. There is thus a stabilizing selection, with frost selecting against late bud set and competition against early bud set. As the onset of frost varies clinally, so the point towards which selection acts differs clinally between populations.

From random initial genotypes and age distribution, the populations were set to adapt to a stable (but clinally varying) climate for 5000 years. Then climate change began, with the onset of autumn frost changing by equal increments each year and in every population for a period of a hundred years. The magnitude of change is such that the northernmost populations experience the climate of the southernmost after 100 years. That corresponds to the prediction from climate change models that, in a hundred years, northern Finland will have the climate that is currently found in southern Finland. The magnitude of change depends in this way only on the steepness of the initial cline. After 100 years of climate change, the response of the populations was monitored for another

400 years, during which no further climate change took place.

After having grown adapted to a stable, clinally varying climate, the simulated Scots pine populations are clearly locally adapted, as population average bud set date closely follows the cline in onset of frost (not shown), with early bud set in the north and late in the south. Climate change evokes a response in the clinally adapted Scots pine populations. The change in the mean of the overall populations (including all age classes) is shown in Figure 3. Because adult trees do not die due to frost damage or competition, the response of the populations to changing climate is much slower than the climate change itself. Thus, these simulations that are based on the biology of the species, suggest that the genetic change in Scots pine will be very small during the next 100 years. In northern Europe, the existing trees will survive for a long period under the warmer climate and there will be few sites available for the new, genetically more adapted seedlings. At the same time, the surviving trees will act as a buffer against an immediate population decline.

Change was achieved through new individuals that enter the population only when vacancies occur, which happens relatively rarely in a long-lived species like Scots pine. Under climate warming, pollen migration from the south can increase the rate of adaptation (within reasonable values). Genetic and phenotypic change of the pine populations still continues after climate change has ceased. Only 500 years after the onset of climate change, that is 400 years after the climate has stopped changing, do

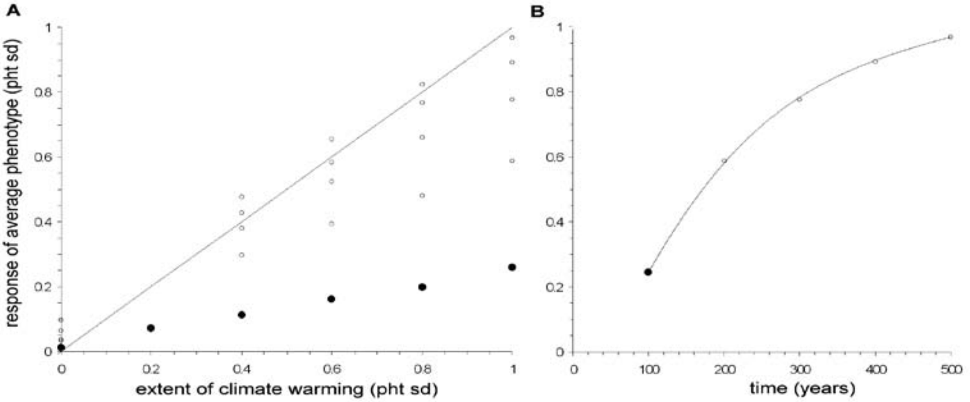

Figure 3. Response of clinal Scots pine (*Pinus silvestris*) populations to climate warming.
A. The relation between phenotypic response and intensity of climate change. Climate change and response are measured in phenotypic standard deviations (pht sd).
B. Phenotypic response over time when the intensity of climate change is -0.25.
For both panels: closed dots represent average change over 10 populations in the average phenotype after 100 years of climate change. Open dots represent the subsequent averages after intervals of 100 years. The straight line in panel A is x=y.

phenotypic and genetic change in the populations cease. Interestingly, that period does not depend on the intensity of climate change: if the initial cline is shallow, and consequently climate change is less intensive, the response of populations is also smaller, but it continues about as long. In all simulations, irrespective of the intensity and direction of climate change, it takes approximately 500 years before genotypic and phenotypic response is complete.

Rehfeldt et al. (2002) considered how long it would take for local populations to evolve to a new optimum, using the simple models. They suggested about 13 generations, which in Scots pine could be much longer than the time that we predict here. The difference is at least partly accounted for by considering migration.

Evolution may be slowed down by various factors. Etterson and Shaw (2001) found that negative genetic correlation may slow down the response. Also note that, in our case, migration from the south contributes to speeding the response to climate change. However, the southern populations will not experience any migration from the south, and migration from populations in the north will have the opposite effect, preventing adaptation. Rehfeldt et al. (2002) predicted that some southern populations might become extinct if they are not able to evolve. Lynch (1996) reviewed the theoretical results of quantitative genetics. Initial responses of populations with high genetic variability can be very large for many generations, accompanied by high mortality. However, the long-term sustainable response within individual populations per generation is only a few percent of the phenotypic standard deviation.

Competition between species may have very important effects. In the southern part of the distribution range, the situation may be quite different due to different selective agents (i.e. drought stress instead of adaptation to cold). Sabaté et al. (2002) studied impact of climate change on growth of five forest tree species (*Quercus ilex, Pinus halepensis, P. pinaster, P. sylvestris, Fagus sylvatica*) at seven Mediterranean sites representing different environmental conditions, with a broad range of elevation, latitude, rainfall and temperature patterns. The simulations show that increased temperature and rainfall in the region, together with increased atmospheric CO_2, will have positive effects on forest growth and wood production. However, the response of different tree species may differ.

Conclusions and recommendations

The effects of changes in interspecific competition and reproductive potential should be included when considering climate change effects. The adaptation of trees can be aided by appropriate moving of forest reproductive materials, taking into consideration seasonal adaptation. High genetic variability and much opportunity for selection allow natural selection to result in adaptation. Research work on short-lived model species can also help in understanding climate change consequences. The potential changes in the growth rhythm of trees in a changing temperature environment but current photoperiodic conditions need to be examined more closely. More detailed information on the genetic basis of growth rhythm would help us to build more reliable models of possible processes.

References

Aho, M.-L. 1994. Autumn frost hardening of one-year-old *Pinus sylvestris* (L.) seedlings: effect of origin and parent trees. *Scandinavian Journal of Forest Research*, 9: 17–24.

Austerlitz, F., Mariette, S., Machon, N., Gouyon, P.-H. & Godelle, B. 2000. Effects of colonization processes on genetic diversity: differences between annual plants and tree species. *Genetics*, 154: 1309–1321.

Barton, N.H. 1999. Clines in polygenic traits. *Genetic Research*, 74: 223–236.

Beuker, E. 1994. Long-term effects of temperature on the wood production of *Pinus sylvestris* L. and of *Picea abies* (L.) in old provenance experiments. *Scandinavian Journal of Forestry Research*, 9: 34–45.

Bradshaw, A. D. & McNeilly, T. 1991. Evolutionary response to global climate change. *Annals of Botany*, 67: 5–14 Suppl. 1.

Clausen, J., Keck, D.D. & Hiesey, W.M. 1948. *Experimental studies on the nature of species. III. Environmental responses of climatic races of* Achillea. Carnegie Institute Washington Publications, 581: 1–189.

Clark, J.S. 1998. Why trees migrate so fast: confronting theory with dispersal biology and the paleorecord. *American Naturalist*, 152: 204–224.

Cornelius, J. 1994. Heritabilities and additive genetic coefficients of variation in forest trees. *Canadian Journal of Forest Research*, 24: 372–379.

Davis, M.B. & Shaw, R.G. 2001. Range shifts and adaptive responses to Quaternary climate changes. *Science*, 292: 673–679.

Davis, M.B., Shaw, R.G. & Etterson, J.R. 2005. Evolutionary responses to changing climate. *Ecology*, 86: 1704–1714.

Eiche, V. 1966. Cold damage and plant mortality in experimental provenance plantations with Scots pine in northern Sweden. *Studia Forestalia Suecica*, 36: 1–218.

Eldridge, K., Davidson, J., Hardwood, C. & van Wyk, G. 1993. *Eucalypt Domestication and Breeding*. Oxford Science Publications, USA.

Ennos, R.A. 1994. Estimating relative rates of pollen and seed migration among plant populations. *Heredity*, 72: 250–259.

Eriksson, G., Andersson, S., Eiche, V., Ifver, J. & Persson, A. 1980. Severity index and transfer effects on survival and volume production of Pinus sylvestris in northern Sweden. *Studia Forestalia Suecica*, 156: 1–32.

Etterson, J.R. & Shaw, R.G. 2001. Constraint to adaptive evolution in response to global warming. *Science*, 294: 151–154.

Fernandez, M., Gil, L. & Pardos, J.A. 1999. Response of *Pinus pinaster* Ait. provenances at early age to water supply. I. Water relation parameters. *Annals of Forest Science*, 56(2): 179–187.

García-Gil, M.R., Mikkonen, M. & Savolainen, O. 2003. Nucleotide diversity at two phytochrome loci along a latitudinal cline in Pinus sylvestris. *Molecular Ecology*, 12: 1195–1206.

Hahl, J. 1978. *Results from an eight-year-old provenance trial of lodgepole pine* (Pinus contorta *Dougl.*). The Foundation of Forest Tree Breeding in Finland, Information.

Harju, A., Kärkkäinen, K. & Ruotsalainen, S. 1996. Phenotypic and genetic variation in the seed maturity of Scots pine. *Silvae Genetica*, 45: 205–211.

Houghton, J.T., Ding, Y., Griggs, D.J., Noguer, M., van der Linden, P.J., Dai, X., Maskell, K. & Johnson, C.A. (editors). 2001. *Climate Change 2001: The scientific basis.* Cambridge University Press, Cambridge, UK.

Houle, D. 1992. Comparing evolvability and variability of quantitative traits. *Genetics*, 130: 195–204.

Howe, G.T., Aitken, S.N., Neale, D.B., Jermstad, K.D., Wheeler, N. C. & Chen, T.H.H. 2003. From genotype to phenotype: unraveling the complexities of cold adaptation in forest trees. *Canadian Journal of Botany*, 81: 1247–1266.

Hurme, P., Repo, T., Pääkkönen, T. & Savolainen, O. 1997. Climatic adaptation of bud set and frost hardiness in Scots pine (*Pinus sylvestris* L.). *Canadian Journal of Forest Research*, 27: 716–523.

Junttila, O. 1982. The cessation of apical growth in latitudinal ecotypes and ecotype crosses of *Salix pentandra* L. *Journal of Experimental Botany*, 33: 1021–1029.

Karhu, A., Hurme, P., Karjalainen, M., Karvonen, P., Kärkkäinen, K., Neale, D.B. & Savolainen, O. 1996. Do molecular markers reflect patterns of differentiation in adaptive traits of conifers? *Theoretical and Applied Genetics*, 93: 215–221.

Kawecki, T. & Ebert, D. 2004. Conceptual issues in local adaptation. *Ecology Letters*, 7: 1225–1241.

Kellomäki, S., Rouvinen, I., Peltola, H., Strandman, H. & Steinbrecher, R. 2001. Impact of global warming on the tree species composition of boreal forests in Finland and effects on emission of isoprenoids. *Global Change Biology*, 7: 531–544.

Kilpeläinen, A., Peltola, H., Ryyppö, A. & Kellomäki, S. 2005. Scots pine response to elevated temperature and carbon dioxide concentration: growth and wood properties. *Tree Physiology*, 25: 75–83.

Kleinschmidt, J. & Bastien, J.C. 1992. IUFRO's role in Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) tree improvement. *Silvae Genetica*, 41: 161–173.

Kremer, A., Zanetto, A. & Ducoussu, A. 1997. Multilocus and multitrait measures of differentiation for gene markers and phenotypic traits. *Genetics*, 145: 1229–1241.

Kremer, A., Kleinschmitt, J., Cottrell, J., Cundall, E.P., Deans, J. D., Ducousso, A. et al. 2002. Is there a correlation between chloroplastic and nuclear divergence, or what are the roles of history and selection on genetic diversity in European oaks? *Forest Ecology and Management*, 156: 75–87.

Lagercrantz, U. & Ryman, N. 1990. Genetic structure of Norway spruce (*Picea abies*): concordance of morphological and allozyme variation. *Evolution*, 44: 38–53.

Lynch, M. 1996. A quantitative-genetic perspective on conservation issues. pp. 479–501. in: J.C. Avise and J.L. Hamrick (editors). *Conservation genetics. Case histories from nature*. Chapman and Hall, UK.

Malcolm, J.R., Markham, A., Neilson, R.P. & Garaci, M. 2002. Estimated migration rates under scenarios of global climate change. *Journal of Biogeography*, 29: 835–849.

McKay, J.K. & Latta, R.G. 2002. Adaptive population divergence: markers, QTL and traits. *Trends in Ecology & Evolution*, 17: 285–291.

Merilä, J. & Crnokrak, P. 2001. Comparison of genetic differentiation at marker loci and quantitative traits. *Journal of Evolutionary Biology*, 14: 892–903.

Mikola, J. 1982. Bud-set phenology as an indicator of climatic adaptation of Scots pine in Finland. *Silva Fennica*, 16: 178–184.

Oldfield, S., Lusty, C. & McKinven, A. (editors). 1998. *The World List of Threatened Trees*. World Conservation Press, Cambridge, UK.

Palmroth, S., Berninger, F., Nikinmaa, E., Lloyd, J., Pulkkinen, P. & Hari, P. 1999. Structural adaptation rather than water conservation was observed in Scots pine over a range of wet to dry climates. *Oecologia*, 121: 302–309.

Prout, T. & Barker, J.S.F. 1989. Ecological aspects of the heritability of body size in *Drosophila buzzatii*. *Genetics*, 123: 803–813.

Prout, T. & Barker, J.S.F. 1993. F statistics in *Drosophila buzzattii*: selection, population size and inbreeding. *Genetics*, 134: 369–375.

Rehfeldt, G.R., Tchebakova, N.M., Parfenova, Y.I., Wykoff, W.R., Kuzmina, N.A. & Milyutin, L.I. 2002. Intraspecific responses to climate change in *Pinus sylvestris*. *Global Change Biology*, 8: 912–929.

Sabaté, S., Gracía, C.A. & Sánchez, A. 2002. Likely effects of climate change on growth of *Quercus ilex Pinus halepensis, Pinus pinaster, Pinus sylvestris* and *Fagus sylvatica* forests in the Mediterranean region. *Forest Ecology and Management*, 162: 23–37.

Savolainen, O., Bokma, F., García-Gil, M.R., Komulainen, P. & Repo, T. 2004. Genetic variation in cessation of growth and frost hardiness and consequences for adaptations of *Pinus sylvestris* to climatic changes. *Forest Ecology and Management*, 197: 79–89.

Shutyaev, A.M. & Giertych, M. 1997. Height growth variation in a comprehensive Eurasian provenance experiment of *Pinus sylvestris* L. *Silvae Genetica*, 46: 332–349.

Sirén, G. 1998. Results and conclusions of pine advance in subarctic Finland in the 20th century. *Finnish Forest Research Institute Research Papers*, 677: 7–16.

Viherä-Aarnio, A., Häkkinen, R., Partanen, J., Luomajoki, A. & Koski, V. 2005. Effects of seed origin and sowing time on timing of height growth cessation of *Betula pendula* seedlings. *Tree Physiology*, 25(1): 101–108.

Wu, H.X. & Ying, C.C. 2004. Geographic pattern of local optimality in natural populations of Lodgepole pine. *Forest Ecology and Management*, 194: 177–198.

Yang, R.-C., Yeh, F.C. & Yanchuk, A.D. 1996. A comparison of isozyme and quantitative genetic variation in *Pinus contorta* ssp. *latifolia* by *Fst*. *Genetics*, 142: 1045–1052.

HOW TO ADAPT FOREST MANAGEMENT IN RESPONSE TO THE CHALLENGES OF CLIMATE CHANGE?

Marcus Lindner

European Forest Institute, Joensuu, Finland

Introduction

Research on the possible impacts of climate change on forests in Europe and the development of adaptation and mitigation strategies started in the early 1990s, shortly after first concerns were raised about the consequences for Earth's climate of anthropogenic greenhouse gas emissions (e.g. Kanninen and Anttila 1992; Burschel et al. 1993; Kräuchi 1993; Bugmann 1994). Since then, assessments of climate change, its impacts and subsequent consequences to natural resource management have been the focus of continuous research efforts (Brown et al. 1996; Kellomäki et al. 1997; Kellomäki et al. 2000; Lindner 2000; Lasch et al. 2002; Lindner et al. 2002; Kellomäki and Sanna 2005).

The forest sector is very sensitive to changes in climate because trees have a long life span and it takes considerable time for forest ecosystems to adapt to changing environmental conditions. Unlike in agriculture, adaptation measures for forestry need to be planned well in advance of expected changes in growing conditions because the forests regenerated today will have to cope with the climate conditions of the next 60 to 100 years.

Despite the intensive research efforts, planning of adaptation measures for forest management, taking into account the anticipated climatic conditions for the rest of the 21st century, is a difficult task. This is because: (1) there is still considerable uncertainty about the future climate development and current climate projections are not yet trustworthy with regard to the projection of future climate variability and extreme events; and (2) the existing impact assessments vary a lot, depending on the simulation models applied and climate scenarios investigated. Consequently, decision-making needs to analyse ecosystem vulnerability and risks induced by climate change, and consider the associated uncertainties, while developing adaptation strategies.

This paper first summarizes the challenges that climate change creates for forest management in Europe, to build a

---

Lindner, M. 2007. How to adapt forest management in response to the challenges of climate change? In: Koskela, J., Buck, A. and Teissier du Cros, E., editors. Climate change and forest genetic diversity: Implications for sustainable forest management in Europe. Bioversity International, Rome, Italy. pp. 31–42.

basis for the following analysis of possible adaptation strategies. Opportunities and risks of adaptive forest management will be discussed, and based on this discussion, conclusions and recommendations will be drawn.

The challenge of climate change for forest management

The scientific community largely agrees that our climate is warming due to anthropogenic greenhouse gas emissions (Houghton et al. 2001). Climate change is already a reality. Temperature has increased by 0.8°C since 1900 (Hansen et al. 2006) and the 12 hottest years observed globally since 1880 all occurred between 1990 and 2005. Changes in precipitation have been more variable. Dore (2005) analyzed evidence of changing patterns of precipitation in observed weather data and found that variance of precipitation has increased everywhere. There was also a tendency for humid areas to become more humid, and dry and arid areas to become even drier.

Projected future changes of climate for Europe are varying, depending on the different emission scenarios and global circulation models applied (Mitchell et al. 2004; Schröter et al. 2005). There is still considerable regional and seasonal variance in different model projections, especially with respect to projected changes in precipitation. But all scenarios are consistently showing annual temperature increases of more than 2°C by 2080 compared with average temperatures of 1960–1990. Moreover, all scenarios project decreasing precipitation in the Mediterranean region.

Climate change may not only result in warmer average climatic conditions. Changes in the variability of climatic conditions from year to year could be even more important. Only recently have studies begun to investigate possible changes in climate variability and extreme events (Beniston and Stephenson 2004; Schär et al. 2004; Salinger 2005). Scherrer et al. (2005) analyzed changes in observed climate variability in Europe from 1961 to 2004 and in a set of climate change scenarios. They found a tendency for increasing variability in future summers, which could have more drastic impacts on ecosystems than the changes in average climatic conditions. The exceptional drought in the summer of 2003 has already demonstrated how severely such extreme weather conditions can affect ecosystems (Ciais et al. 2005).

Different studies on the potential impacts of climate change to European forests indicate a broad range of results, including both positive and negative growth responses (e.g. (Kellomäki et al. 2000; Lasch et al. 2002; Nabuurs et al. 2002; Sabaté et al. 2002; Schröter et al. 2005). While some of the differences in the results can be attributed to the application of contrasting climate change scenarios or to different responses in the simulation models to similar changes in climate (see e.g. Loehle and LeBlanc 1996), there are also large regional differences in the sensitivity of forests to climate change. This sensitivity depends strongly on the present environmental conditions of the forests. Figure 1 presents simulated growth response patterns for Scots pine (*Pinus sylvestris*) at three different sites under boreal, temperate-continental and Mediterranean climates. Growth responses to increases in temperature and changes in precipitation compared with the current climate vary drastically between the three sites. In Northern Finland, temperature is currently the main limiting growth factor and consequently the production at this site will increase quite strongly with higher temperatures. According to the simulation model applied, water availability at this site is not influencing the growth within the investigated range of precipitation changes. In a temperate-continental climate, temperature is less important because the main limiting growth factor is water availability. Reduced precipitation leads to drastic decreases in productivity, higher precipitation in contrast increases growth. Small temperature increases may still increase growth at a given level of precipitation, but the positive effect of increasing temperature diminishes when increases are larger than 3°C. In Spain, at the southern end of the distribution range of Scots pine, the growth response patterns are again different. Water availability strongly influences growth, and under the Mediterranean environmental conditions further temperature increases also reduce water availability and consequently forest productivity.

The frequency and intensity of disturbances may also be affected by climate change. Whereas the forest fire risk is directly influenced by changes in temperature and precipitation, less scientific evidence exists about possible increase in storm damage. Insects are likely to gain (e.g. Volney and Fleming 2000) but their impacts are very difficult to predict because of complex interactions with climate, other environmental factors, hosts and antagonistic species.

Our understanding of climate change will remain sketchy for quite some time. Many uncertainties in climate projections and the associated impacts on forests cannot be easily resolved. How to deal with uncertainties in climate change projections constitutes a big challenge for designing adaptation strategies in forest management.

Different concepts of adaptation to climate change

The previous section presented many faces of climate change: improving productivity in the north, increasing drought in the south, increasing variability in weather conditions, and possibly more severe extreme weather

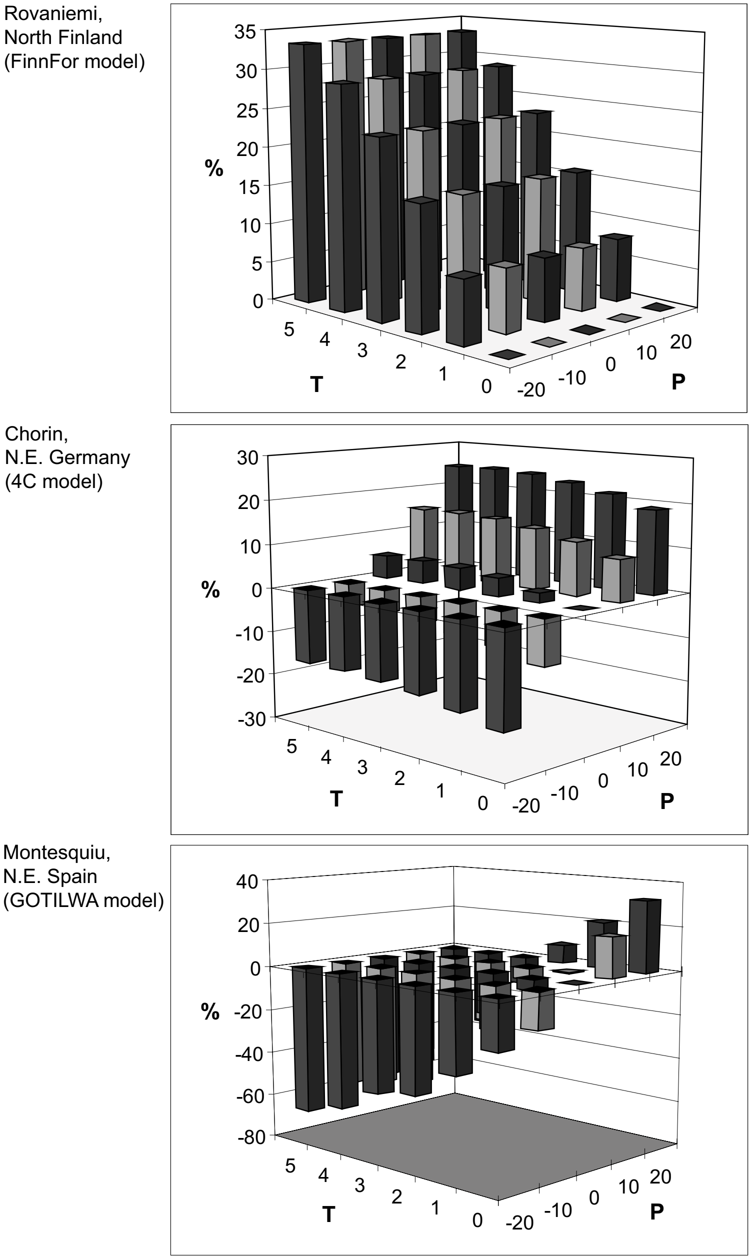

Figure 1. Relative changes in stem volume growth of Scots pine (*Pinus sylvestris*) in response to temperature increases of up to 5°C and variable precipitation from minus 20% to plus 20% compared with present average climatic conditions. Simulation results for three different sites across the distribution range of Scots pine: northern Finland; north-eastern Germany; and north-eastern Spain (Kellomäki and Sanna 2005).

events and disturbances all over Europe. This listing alone already suggests that there cannot be only one way to adapt forest management. So how can forest management be adapted to cope with these challenges? Different adaptation strategies are needed in different situations.

> "Adaptation refers to the actions that people take in response to, or in anticipation of, projected or actual changes in climate, to reduce adverse impacts or take advantage of the opportunities posed by climate change." (Tompkins and Adger 2004).

There is a growing literature on the subject of adaptation of forest management to climate change (Lindner 1999, 2000; Spittlehouse and Stewart 2003; Hulme 2005; Maciver and Wheaton 2005; Spittlehouse 2005). The EU-funded SILVISTRAT project (Kellomäki and Leinonen 2005) explored forest management response strategies to climate change at the stand and management unit level (Badeck et al. 2005; Gracia et al. 2005; Kellomäki et al. 2005). While these studies have been clearly advancing our understanding of the needs for adaptation and possible ways of exploring response options, there is still a huge gap between theory and application in practical forest management. There is increasing awareness that in addition to the general investigation of climate change impacts and adaptation options at the international level (e.g. as part of policy processes such as the United Nations Framework Convention on Climate Change) there should also be a bottom-up assessment component in the search for suitable adaptation strategies (Parry et al. 2005). This should be based on the analysis of past and current climate vulnerability, assessment of existing coping strategies, and suggestions on options for how these might be modified with climate change. Reducing vulnerability involves both a reduction in exposure to climate stress and an increase in adaptive capacity.

> "Adaptation strategies should aim to increase the flexibility in management of vulnerable ecosystems, enhance the inherent adaptability of the species and ecosystem processes within vulnerable natural systems, and reduce trends in environmental and social pressures that increase vulnerability to climate variability."
> (Hulme 2005)

The decision-making process in forest management will always be influenced by the risk attitude of a forest manager. Risk aversion and risk tolerance are two very contrasting approaches to living with risks, and both are applied in everyday life. The personal risk perception will determine to what extent risks are anticipated and how strongly management decisions will aim at reducing the anticipated risks. Burton et al. (1998) described different categories of adaptation strategies, including the acceptance of potential losses with the baseline response of ‘do nothing’, mitigation measures to reduce the threat, protection measures to prevent adverse effects, and adaptive changes in management practices.

Adaptive forest management can utilize species-specific characteristics to reduce risks of adverse effects of climate change and to mobilize potential benefits, such as increased production rates. Tree species differ in growth rate, drought sensitivity and susceptibility to disturbances. Forest management includes making choices about species selection and mixtures, using natural or artificial regeneration, the timing and intensity of thinning and harvesting, and the application of fertilizers (and possibly irrigation in intensive plantation systems).

Different forest management options create opportunities and trade-offs. In the following, pairs of contrasting management alternatives will be used to illustrate opposing orientations.

A reduced inputs strategy to respond to climate change relies on natural regeneration to maintain a wide genetic diversity, mixed species forests with varying ecological characteristics, and only restricted salvage logging after disturbances. This strategy aims at using natural processes as much as possible to maintain or develop a high adaptation potential. The reduction in the risk of adverse effects would be achieved with low costs.

An increased inputs strategy to cope with climate change, in contrast, would include planting of genetically improved seedlings, fertilization, optimized and possibly intensified thinning, and salvaging of deadwood after disturbances. This strategy aims to mobilize all possible potentials. The higher costs associated with this strategy would be at least compensated through increased yields.

In addition to stand-level management, there are also management options at higher hierarchical scales of management units, which are linked to other land use types creating landscape patterns. At this scale, the contrasting management strategies could be coined an integration approach versus a segregation approach. The integration approach favours multi-species mixtures and aims to achieve risk reduction in each individual stand. This requires compromises in species selection because the most productive tree species would be mixed with species having a wider climatic amplitude, but often also lower productivity. Thus, the applied cautionary principle would result in a reduced production capacity. The segregation approach, in contrast, mixes forest types and management regimes at the district level. Risk reduction would be achieved through diversifying forest types, but the opportunities for high growth potentials from productive species would be utilized on appropriate sites.

The integration approach has been traditionally supported in Central European management systems. For example, Müller (1997) suggested that nature-oriented mixed forests would be best adapted to a broad range of climatic conditions. Conversion of even-aged Norway spruce (*Picea abies*) monocultures to mixed forests has been supported in several countries because broadleaved species are less susceptible to disturbances (Spiecker et al. 2004). In other parts of the world, the segregation approach is more common. New Zealand is a well-known example of using intensive plantation forestry for wood production, while larger areas of natural forests are protected to enhance biodiversity.

Hypothetical examples of how German forests could look in 2100

Let us assume that all German forest managers would follow an integration approach with a reduced inputs strategy by implementing a conversion of all even-aged Norway spruce forests into mixed uneven-aged forests. On the one hand, this would reduce the risk of some adverse impacts of climate change, such as bark beetle infestations (Lexer and Hönninger 1998), but, on the other hand, such a change in management would also affect many other forest functions. One consequence would be that the forest area would become more uniform, with less variation between stands.

Another possible change in management for the abundant even-aged Norway spruce forests could be to replace them with Douglas fir (*Pseudotsuga menziesii*) stands. This species is also very productive, but it is much more drought tolerant and can grow under a broad range of site conditions. Private forest owners have already considerably expanded the use of Douglas fir, and under conditions of climate change it might offer the best economic prospects. The expansion of Douglas fir is, however, not well received by conservationists, because it is an introduced species from North America. Moreover, if managed in dense stands, the associated species diversity and amenity values are very low. Several federal states in Germany have specified restricted targets for the share of Douglas fir in species composition, but this mainly affects the species choice in state-owned forests. Anyway, if all private forest owners based their management decisions on economics alone, large areas of German forest land would be dominated by Douglas fir by 2100.

Whereas both of these contrasting management scenarios for Germany would have less favourable consequences for certain forest functions (e.g. biodiversity or amenity values), a combination of both management options at the landscape scale would have much better impacts. The positive aspects of both management strategies could still be utilized, while avoiding some of the negative side effects of the large-scale application of the same strategy.

Discussion

This paper reviewed some of the challenges posed by climate change to forest management in Europe. Possible response options in forest management were also outlined. The alternative adaptation strategies can be analysed in terms of opportunities and trade-offs. The contrast in management options is high, because there are still large uncertainties linked to the future climate projections and to ecosystem responses to climate change. These uncertainties span a broad range of possible future conditions and as we cannot yet assign probabilities to the different scenarios there is no way of identifying one management option as the best choice.

Although climate change scenarios are continuously improving, with better representation of climate variability and extreme events, there is reason to believe that forecasts of climate change impacts will remain rather uncertain in the near to intermediate term. We know surprisingly little about forest growth at the physiological limit because competition effects usually confound the fundamental niche of forest species (e.g. Austin and Smith 1989; Loehle and LeBlanc; 1996). Moreover, climate change consists not only of temperature and precipitation changes, and the impacts of CO_2 fertilization are still very controversial (e.g. Körner et al. 2005).

Over the past one-and-a-half decades, the methods applied in climate impact research have improved considerably. While the earlier assessments were based largely on empirically based bio-geographical models or forest gap models, research on mechanistic responses to climate change revealed that some of the early assessments overestimated the effects of the projected changes in climate (Loehle and LeBlanc 1996; Schenk 1996). Modelling developments have enabled investigation of the impacts of climate change with process-based forest growth models, incorporating growth responses to changes in average climate conditions and in atmospheric CO_2. But even the latest state-of-the-art models applied in climate impact research may differ a lot in their simulated responses to climate change (Kramer et al. 2002; Lindner et al. 2005). Consequently, management recommendations should not be based on the outputs of single model simulations.

It is important that uncertainties inherent in the projections are explicitly included in the decision-making process. There are well-established economic methods to incorporate risk perceptions in management decisions (Valsta 1992). One approach would be to estimate the opportunity costs of the alternative adaptation strategies. Different climate change scenarios can be analyzed with considerations of the associated uncertainties of the climate change scenarios and impact assessments. Under any given climate change scenario, there will be one optimum management in economic terms. All other adaptation strategies will incur opportunity costs. Unfortunately, we still do not know which climate change scenario has the highest probability of becoming reality. It would be possible, however, to analyze a large set of plausible scenarios and select the adaptation strategy which on average returns the best results.

What complicates the problem even further is that in addition to economics, there are many other criteria influencing management decisions today. Biodiversity consideration and amenity values, just to name two examples, will often not be favoured by the economically best adaptation strategy. Personal preferences of the forest manager and the societal context will therefore have a strong influence on management choice. Nevertheless, an analysis of opportunity costs and trade-offs with other important functions will be very helpful in selecting good strategies. If we accept the fact that multifunctional forest management does not need to be achieved in each individual forest stand, it is possible to reduce the trade-offs considerably by incorporating to some extent a segregation of functions at the management unit or landscape level. One guiding principle could be, for example, to use a reduced inputs strategy on low-productivity sites while intensifying production opportunities on more productive sites.

The long lifespan of forest trees creates another challenge for decision-making: when is the best time for a change in species composition? Is it wiser to favour the species best adapted for current environmental conditions? Or should the species best adapted for future climatic conditions be introduced? And when would be the best time for this? The currently productive species may eventually decline, but a less productive species could perhaps prevent a possible die-back. Both options would probably result in opportunity costs, either now or later. It is very likely that all adaptation strategies will result in certain compromises.

We can conclude from this analysis that it is not very helpful to search for one single adaptation strategy. Diversifying adaptation strategies leaves more options under uncertain future conditions. Parameters might involve the choice of species, forest types and forest management strategies in individual stands of a management unit. But diversification goes beyond that by assigning preferences to different forest products and services according to bio-physical site conditions and location of stands with respect to societal demands on the forests. This also means that diversification may include both intensification and extensification, as both are appropriate options in different places.

The current degree of uncertainty in future climate development makes it necessary to frequently adjust management planning so as to adapt to unforeseeable developments. Responding to unexpected events, such as disturbances, can in fact also create opportunities for adaptation. For example, a change in species composition can be implemented faster by reconsidering the species selection after larger disturbance events. Past management principles resulted in a preference for rather uniform stand types and the dominance of few species on large forest areas. Today, the demand has changed towards more varied products and services from forests. Modern silvicultural strategies are more flexible and can take advantage of smaller-scale variability. This is an important prerequisite for the successful implementation of adaptation strategies in a climate change situation.

References

Austin, M.P. & Smith, T.M. 1989. A new model for the continuum concept. *Vegetatio*, 83: 35–47.

Badeck, F., C. Fürstenau, P. Lasch, F. Suckow, H. Peltola, J. Garcia-Gonzalo et al. 2005. Adaptive forest management at the scale of management units. pp. 315–382, in: S. Kellomäki and S. Leinonen (editors). *Management of European forests under changing climatic conditions*. Final Report of the Project Silvicultural Response Strategies to Climatic Change in Management of European Forests funded by the European Union under Contract EVK2-2000-00723 (SilviStrat). University of Joensuu, Faculty of Forestry, Joensuu, Finland.

Beniston, M. & Stephenson, D.B. 2004. Extreme climatic events and their evolution under changing climatic conditions. *Global and Planetary Change*, 44: 1–9.

Brown, S., Sathaye, J. & Cannell, M. 1996. Management of forests for mitigation of greenhouse gas emissions. pp. 773–797, in: R.T. Watson, M.C. Zinyowera and R.H. Moss (editors). *Climate Change 1995. Impacts, Adaptation and Mitigation of Climate Change: Scientific-technical Analyses*. Contribution of WG II to the Second Assessment Report of the IPCC. Cambridge University Press, Cambridge, UK.

Bugmann, H. 1994. *On the ecology of mountainous forests in a changing climate: A simulation study*. PhD thesis. ETH Zürich, Zürich, Switzerland.

Burschel, P., Kürsten, E., Larson, B.C. & Weber, M. 1993. Present role of German forests and forestry in the national carbon budget and options to its increase. *Water Air and Soil Pollution*, 70: 325–340.

Burton, I., Smith, J.B. & Lenhard, S. 1998. Adapation to climate change: theory and assessment. in: J.F. Feenstra, I. Burton, J.B. Smith and R.S.J. Tol (editors). *Handbook on methods for climate change impact assessment and adaptation strategies*. United Nations Environment Programme, and Vrije Universiteit, Amsterdam, The Netherlands.

Ciais, P., Reichstein, M., Viovy, N., Granier, A., Ogee, J., Allard, V. et al. 2005. Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature*, 437(7058): 529–533.

Dore, M.H.I. 2005. Climate change and changes in global precipitation patterns: What do we know? *Environment International*, 31: 1103–1212.

Gracia, C., Sánchez, A., Pla, E., Sabaté, S., Lexer, M. & Jäger, D. 2005. Adaptive forest management strategies. pp. 159–252, in: S. Kellomäki and S. Leinonen (editors). *Management of European forests under changing climatic conditions*. Final Report of the Project Silvicultural Response Strategies to Climatic Change in Management of European Forests funded by the European Union under Contract EVK2-2000-00723 (SilviStrat). University of Joensuu, Faculty of Forestry, Joensuu, Finland.

Hansen, J., Ruedy, R., Sato, M. & Lo, K. 2006. GISS Surface Temperature Analysis. *Global Temperature Trends: 2005. Summation*. Taken from the Web site of NASA Goddard Institute for Space Studies and Columbia University Earth Institute, New York, NY, USA. Web page last updated 16 January 2006. Page viewed on 16 August 2006. See: http:\\data.giss.nasa.gov/gistemp/2005/

Houghton, J.T., Ding, Y., Griggs, D.J., Noguer, M., Linden, P.J.v.d. & Xiaosu, D. (editors).

2001. *Climate Change 2001. The Scientific basis.* Contribution of Working Group I to the third assessment report of the Intergovernmental Panel on Climatic Change (IPCC). Cambridge University Press, Cambridge, UK.

Hulme, P.E. 2005. Adapting to climate change: is there scope for ecological management in the face of a global threat? *Journal of Applied Ecology*, 42: 784–794.

Kanninen, M., & Anttila, P. 1992. *The Finnish Research Programme on Climate Change. Progress Report*. VAPK Publ., Helsinki, Finland.

Kellomäki, S. & Leinonen, S. 2005. *Management of European forests under changing climatic conditions.* Joensuun yliopisto, Metsätieteellinen tiedekunta, Joensuu, Finland.

Kellomäki, S. & Sanna, L. 2005. *Management of European forests under changing climatic conditions*. Final Report of the Project Silvicultural Response Strategies to Climatic Change in Management of European Forests funded by the European Union under Contract EVK2-2000-00723 (SilviStrat). University of Joensuu, Faculty of Forestry, Joensuu, Finland.

Kellomäki, S., Karjalainen, T., Mohren, F. & Lapveteläinen, T. (editors). 2000. *Expert assessment on the likely impacts of climate change on forests and forestry in Europe*. European Forest Institute, Joensuu, Finland.

Kellomäki, S., Karjalainen, T. & Väisänen, H. 1997. More timber from boreal forests under changing climate? *Forest Ecology and Management*, 94: 195–208.

Kellomäki, S., Peltola, H., Bauwens, B., Dekker, M., Mohren, F., Badeck, F.-W. et al. 2005. European mitigation and adaptation potentials: Conclusions and recommendations. pp. 401–427, in: S. Kellomäki and S. Leinonen (editors). *Management of European forests under changing climatic conditions*. Final Report of the Project Silvicultural Response Strategies to Climatic Change in Management of European Forests funded by the European Union under Contract EVK2-2000-00723 (SilviStrat). University of Joensuu, Faculty of Forestry, Joensuu, Finland.

Körner, C., Asshoff, R., Bignucolo, O., Hattenschwiler, S., Keel, S.G., Pelaez-Riedl, S. et al. 2005. Carbon flux and growth in mature deciduous forest trees exposed to elevated CO_2. *Science*, 309: 1360–1362.

Kramer, K., Leinonen, I., Bartelink, H.H., Berbigier, P., Borghetti, M., Bernhofer, C. et al. 2002. Evaluation of six process-based forest growth models using eddy-covariance measurements of CO_2 and H_2O fluxes at six forest sites in Europe. *Global Change Biology*, 8: 213–230.

Kräuchi, N. 1993. Climate change and forest ecosystems - an overview. pp. 53–76, in: R. Schlaepfer (editor). *Long-term implications of climate change and air pollution on forest ecosystems*. Progress report of the IUFRO Task Force on Forest, Climate Change and Air Pollution. Published as IUFRO World Series Vol. 4. IUFRO, Vienna Austria, and WSL, Birmensdorf, Switzerland. 132 p.

Lasch, P., Lindner, M., Erhard, M., Suckow, F. & Wenzel, A. 2002. Regional impact assessment on forest structure and functions under climate change – the Brandenburg case study. *Forest Ecology and Management*, 162: 73–86.

Lexer, M.J. & Hönninger, K. 1998. Simulated effects of bark beetle infestations on stand dynamics in Picea abies stands: Coupling a patch model and a stand risk model. pp. 289–308, in: M. Beniston and J.L. Innes (editors). *The impacts of climate variability on forests*. Springer Verlag, Berlin, Germany.

Lindner, M. 1999. Waldbaustrategien im Kontext möglicher Klimaänderungen. *Forstwissensch. Centralblatt*, 118: 1–13.

Lindner, M. 2000. Developing adaptive forest management strategies to cope with climate change. *Tree Physiology*, 20: 299–307.

Lindner, M., Badeck, F., Bartelheimer, P., Bonk, S., Cramer, W., Dieter, M. et al. 2002. Integrating forest growth dynamics, forest economics and decision making to assess the sensitivity of the German forest sector to climate change. *Forstwiss. Centralblatt* 121 (Suppl. 1): 191–208.

Lindner, M., Lasch, P., Badeck, F., Beguiristain, P.B., Junge, S., Kellomäki, S. et al. 2005. SilviStrat model evaluation exercises. pp. 117–157, in: S. Kellomäki and S. Leinonen (editors). *Management of European forests under changing climatic conditions*. Final Report of the Project Silvicultural Response Strategies to Climatic Change in Management of European Forests funded by the European Union under Contract EVK2-2000-00723 (SilviStrat). University of Joensuu, Faculty of Forestry, Joensuu, Finland.

Loehle, C. & LeBlanc, D. 1996. Model-based assessments of climate change effects on forests: a critical review. *Ecological Modelling*, 90: 1–31.

Maciver, D.C. & Wheaton, E. 2005. Tomorrow's forests: adapting to a changing climate. *Climatic Change*, 70: 273–282.

Mitchell, T.D., Carter, T.R., Jones, P.D., Hulme, M. & New, M. 2004. *A comprehensive set of high-resolution grids of monthly climate for Europe and the globe: the observed record (1901–2000) and 16 scenarios (2001–2100)*. Tyndall Centre for Climate Change Research, University of East Anglia, UK.

Müller, F. 1997. Waldbauliche Anpassungsstrategien - Orientierungshilfe und Forschungsbedarf für waldbauliche Entscheidungen. pp. 62–74, in: Ö. Forstverein (editor). *Klimaänderung - Mögliche Einflüsse auf den Wald und waldbauliche Anpassungsstrategien*. Österreichischer Forstverein, Vienna, Austria.

Nabuurs, G., Pussinen, A., Karjalainen, T., Erhard, M. & Kramer, K.2002. Stemwood volume increment changes in European forests due to climate change - a simulation study with the EFISCEN model. *Global Change Biology*, 8: 304–316.

Parry, J.-E., Hammill, A. & Drexhage, J. 2005. *Climate Change and Adaptation*. International Institute for Sustainable Development, Winnipeg, Canada.

Sabaté, S., Gracia, C.A. & Sánchez, A. 2002. Likely effects of climate change on growth of *Quercus ilex, Pinus halepensis, Pinus pinaster, Pinus sylvestris* and *Fagus sylvatica* forests in the Mediterranean region. *Forest Ecology and Management*, 162: 23–37.

Salinger, M.J. 2005. Climate Variability and Change: Past, Present and Future – An Overview. *Climatic Change*, 70: 9–29.

Schär, C., Vidale, P.L., Luthi, D., Frei, C., Haberli, C., Liniger, M.A. & Appenzeller, C. 2004. The role of increasing temperature variability in European summer heatwaves. *Nature*, 427: 332–336.

Schenk, H.J. 1996. Modelling the effects of temperature on growth and persistence of tree species: a critical review of tree population models. *Ecological Modelling*, 92: 1–32.

Scherrer, S.C., Appenzeller, C., Liniger, M.A. & Schär, C. 2005. European temperature distribution changes in observations and climate change scenarios. *Geophysical Research Letters*, 32(19) Article no. L19705.

Schröter, D., Cramer, W., Leemans, R., Prentice, I.C., Araujo, M.B., Arnell, N.W. et al. 2005. Ecosystem service supply and vulnerability to global change in Europe. *Science*, 310: 1333–1337.

Spiecker, H., Hansen, J., Klimo, E., Skovsgaard, J.P., Sterba, H. & Teuffel, K.v. (editors). 2004. *Norway Spruce Conversion – Options and Consequences*. Brill, Leiden and Cologne, Germany, and Boston MA, USA.

Spittlehouse, D.L. 2005. Integrating climate change adaptation into forest management. *The Forestry Chronicle*, 81: 691–695.

Spittlehouse, D.L. & Stewart, R.B. 2003. Adaptation to climate change in forest management. *BC Journal of Ecosystems and Management*, 4: 1–11.

Tompkins, E.L. & Adger, W.N. 2004. Does adaptive management of natural resources enhance resilience to climate change? *Ecology and Society*, 9: 10–23.

Valsta, L.T. 1992. A scenario approach to stochastic anticipatory optimization in stand management. *Forest Science*, 38: 430–447.

Volney, W.J.A. & Fleming, R.A. 2000. Climate change and impacts of boreal forest insects. *Agriculture Ecosystems & Environment*, 82: 283–294.

RESILIENCE OF EUROPEAN FORESTS: TOWARDS A NON-EQUILIBRIUM VIEW FOR THE MANAGEMENT OF DIVERSITY

Koen Kramer

Forest Ecosystems Team, Alterra, Wageningen, The Netherlands

Introduction

Changes in the environment and in society expose forest managers to new challenges. In the environment, not only the climate is changing but also inputs of nitrogen and air pollution to a forest, for example. In society, not only timber is demanded from a forest but also a wide array of wood and non-wood goods and services. These include carbon sequestration and water holding capacity, biodiversity conservation, and recreation. Changes in the environment mean that the forest is no longer in equilibrium with the prevailing abiotic conditions. Consequently, the genetic composition for functional traits of trees needs adjustment, and it may even mean that the species composition of forests needs adjustment.

Classically, in genetic and ecological theories, the assumption is that the system is in a dynamic equilibrium. For example, in seed collection protocols it is generally assumed that all parent trees contribute alleles to a seed sample in proportion to the allele distribution in the parent population. However, a spatial genetic structure may exist in the forest due to limited dispersal of pollen and seed rather than due to selection caused by local abiotic differences. The distribution of adaptive traits is therefore not yet in equilibrium with the distribution of abiotic gradients, such as moisture and nutrient availability, which influences an optimal sampling protocol. An ecological example of an implicit equilibrium assumption is succession of tree species. This is often considered a predictable sequence of events based on niche differentiation between species. Niche differentiation supposes that species either co-exist, because after a long evolutionary process they are sufficiently dissimilar, so that competitive exclusion is eliminated; or that the better competitor replaces the poor competitor under the prevailing conditions. The implicit equilibrium assumption is that the plant-to-plant interactions operate for a sufficiently long period for competitive exclusion to reach its conclusion. This assumption is disputed by the non-equilibrium explanation of species co-existence, discussed below.

Kramer, K. 2007. Resilience of European forests: towards a non-equilibrium view for the management of diversity. In: Koskela, J., Buck, A. and Teissier du Cros, E., editors. Climate change and forest genetic diversity: Implications for sustainable forest management in Europe. Bioversity International, Rome, Italy. pp. 43–52.

The validity of assuming equilibrium or non-equilibrium has been largely a rather abstract, academic discussion, especially in ecology. However, climate change requires an urgent response to the question of how to manage forests that are not in equilibrium with the local climate, in terms of both genetic and species composition. This challenging situation demands the rapid integration of genetic, ecological and silvicultural research to arrive at common standards for the evaluation of management options that aim to maintain genetic and ecological diversity in the forest and to provide the goods and services required by society.

A non-equilibrium concept of resilience is proposed in this paper as a tool for such an evaluation of the effects of climate change on forests by different scientific disciplines. With this concept of resilience, existing guidelines on forest management and general forest policies should be re-evaluated for their validity in the context of climate change.

The overall aim of this paper is to provide an introduction to the concepts of equilibrium, non-equilibrium and resilience in genetics and ecology, and to suggest guidelines for the management of forests in the face of climate change and varying societal demands.

Equilibrium and non-equilibrium concepts in ecology and genetics

Equilibrium or non-equilibrium is assumed in many theories in genetics and ecology, either implicitly or explicitly. The purpose of this section is, firstly, to present a general introduction on equilibrium versus non-equilibrium in ecology considering the co-existence of species and species distribution, and to discuss some of the underlying genetic and evolutionary assumptions. Secondly, this section aims to present a concise introduction to the concept of resilience from both equilibrium and non-equilibrium points of view.

Species co-existence

Many alternative hypotheses on co-existence of plant species exist in the literature. Without going into the details of each of these, only the broad categories are considered here. One hypothesis assuming equilibrium between the species and the abiotic environment is based on the principle of the balance of nature, and another assumes non-equilibrium between the species and the abiotic environment due to variation in space and time in the species' environment. The equilibrium and the non-equilibrium approaches are often considered to be so fundamentally different that they are referred to as different paradigms (Hengeveld and Walter 1999).

The 'balance of nature' paradigm assumes that tree species living together in an area have a long history of joint evolution, which has resulted in each species becoming adapted to a specific set of biotic and abiotic conditions, which together represent its niche. It is thus assumed that the climate is stationary relative to the rate of adaptation, although it is recognized that the climate and the abiotic environment are variable during that time-span. Abiotic conditions form boundary conditions to which a species must adapt so that it survives and reproduces in the first place. Nevertheless, differentiation between species is ultimately explained by biotic causes. This species differentiation results in prevention of competitive exclusion leading to sustainable coexistence and thereby species communities. Increasing specialization leads to increasing species diversity and increasing community complexity. Population dynamics are thus assumed to be mainly controlled by density-dependent factors leading to numerical equilibria between species. Research should focus on demographic behaviour of species, which is why the equilibrium paradigm is also termed the demographic paradigm in ecology (Hengeveld and Walter 1999).

The non-equilibrium paradigm, in contrast, recognizes that nature is variable in space and in time at all scales, and that stochastically occurring disturbances drive that variability. Hence, the adaptive response of species ever lags behind trends in both the climate and abiotic factors. Co-existence between tree species that share limiting resources is then explained by the fact that competitive exclusion is slow relative to ongoing disturbances that make these resources available again, such as nutrients, water and space. A tree species must therefore ‘track’ the availability of suitable sites to regenerate, establish, grow and reproduce for its sustainable existence. This tracking of suitable sites can be either through dispersal of seeds and vegetative propagules to find those suitable sites at other locations, or by using a ‘wait-and-see’ strategy by establishing dormant seeds in a seed bank at the location where the adult plant is eventually replaced. In the non-equilibrium paradigm, evolution shapes a plant species with life history traits so that it uniquely responds to competitors, climatic factors and the availability of regeneration sites created by disturbances. The non-equilibrium paradigm thus focuses on the individualistic behaviour of tree species, which is why this paradigm is also called the autecological paradigm (Hengeveld and Walter 1999).

Geographic range of tree species

Much of the assessments of the impact of climate change on species distribution are based on modelling studies that ignore genetic processes. Species distribution models can be grouped into two general classes: climatic envelope models, and dynamic models.

Climatic envelope models assume, firstly, that climate exerts a dominant control over the natural distribution of species (Pearson and Dawson 2003), and, secondly, that the current species range is in equilibrium with its climatic potential area. If valid, statistical correlations between climate variables at the limits of the species' geographical distribution can be used to describe current ranges. Critical macroclimatic factors include minimum frost temperature, duration of the growing season, and indicators of water stress during the growing season. Implicitly it is thus assumed in these models that physiological mechanisms have evolved, such as (1) frost hardiness of vulnerable tissues to tolerate frosts; (2) perception of cues from the environment, such as photoperiod or chilling, and forcing requirements to break dormancy for the synchronization of the climatic seasonality of the site with the active growing phase of the tree; and (3) stomatal mechanisms or a hydrological architecture to avoid or tolerate water stress.

Dynamic models for the range of tree species can again be broadly divided into two classes. One class of models dynamically considers physiological limiting mechanisms for winter cold tolerance, drought tolerance, and either photoperiod or forcing and chilling requirements to break dormancy and start the growing season (Sykes et al. 1996). These limiting mechanisms are often also represented by bioclimatic variables, hence with essentially the same genetic assumptions on tolerance as the envelope models. The second class considers forest succession models that include not only descriptions of the physiological limiting factors, but also biotic interaction, including competition for limiting shared resources such as light, water and nutrients (Prentice et al. 1991), and dispersal of propagules and the occurrence of stochastic disturbance events (Kramer et al. 2003). In addition to implicit genetic assumptions on adaptation to abiotic factors, forest succession models assume adaptation to biotic interactions too. These models are therefore explanatory tools for transient dynamics following environmental changes, as well as for eventual equilibrium states.

Both the climatic envelope models and the dynamic models based on bioclimatic variables thus follow the equilibrium paradigm, whereas the forest succession models based on gap-phase replacement assume the non-equilibrium hypothesis. In the face of climate change, land use change, nutrient deposition and pollution, equilibrium models cannot produce a reliable future projection of even the potential distribution of plant species or biomes, and we therefore need to apply non-equilibrium approaches.

Resilience

The concept of resilience differs fundamentally between the equilibrium and non-equilibrium paradigms. In equilibrium theory, resilience is the time required to return to a stable state (Pimm 1991). The quicker the return time, the larger the resilience, and therefore the system is more predictable. In genetics and ecology, much of the theory is developed to determine equilibrium conditions, and therefore the return rate to a stable state. In ecology, examples of equilibrium approaches include the widely-used Lotka-Volterra equations and refinements thereof, and the resource-ratio equations of Tilman (1985) to assess the possible co-existence of plant species. In genetics, stable states are described by the Hardy-Weinberg equilibrium of allele frequencies, and assessments of the effects of selection pressure thereon. The time to return to pre-disturbed equilibria can be calculated based on first-order derivatives. A technical but crucial point of this theory is that it applies only to *small* deviations from the stable state.

This notion of resilience is equivalent to stability, or, more precisely, to neighbourhood stability (Lewontin 1969). Neighbourhood stability needs to be distinguished from temporal stability, which refers to constancy or lack of variability.

In non-equilibrium theory, resilience refers to the conditions that allow a system to absorb changes in the environment and still persist (Holling 1973). This notion of resilience recognizes that random events, spatial heterogeneity and changes in external drivers can bring a system to a state far from equilibrium. Changes in climate, land use, nutrient deposition and pollution may very well push the system so far from equilibrium that stability analysis is no longer applicable. Therefore, an alternative approach is needed to the classical theory on return time to a pre-disturbed stable state.

In ecology, much research is done on the importance of spatial processes, including disturbances (Tilman and Kareiva 1997) and dispersal limitation in fragmented landscapes, as exemplified by many studies on metapopulation dynamics (Hanski and Gilpin 1997). A general condition for a resilient metapopulation is that there should be sufficient connectivity between habitat islands to allow a metapopulation to persist despite recurring local extinction.

In forest genetics, an example of this notion of resilience is the often-stressed importance of having sufficient genetic variation in a forest as a general condition to allow adaptation. However, relatively new is the insight that populations are not in Hardy-Weinberg equilibrium for adaptive traits, nor for genetic markers. Indeed, spatial genetic structure in both adaptive traits and genetic markers (see case study below) is often found, violating the elementary assumption of the Hardy-Weinberg equilibrium. This urges us to study gene flow through pollen and seeds, which is now possible as a result of techniques using the highly polymorphic genetic markers that are available for many tree species.

Hence, in both genetics and ecology, the scientific approaches move from the demographic, population-genetic, equilibrium point of view towards the individualistic, autecological and non-equilibrium point of view. However, scientific insight has not yet resulted in refined forest management strategies to maximize adaptive potential of tree species. An example of a study that aimed to provide the first steps in that direction is outlined below.

Case study on the management of European beech

The DynaBeech project was aimed to bridge genetics and ecology to provide management recommendations for sustainable management of European beech (*Fagus sylvatica*) (Kramer 2004). The interactions between selection for adaptive traits, gene flow and management practice were studied to evaluate the impacts of forest management on the dynamics of genetic and ecological diversity of European beech. The overall aim was to assess the adaptive potential of beech, as a model tree species, to environmental changes based on its genetic and ecophysiological characteristics. Three sub-aims were formulated: (1) the development of a coupled genetic–ecological individual-tree model and its parameterization for beech, either based on field studies performed within the DynaBeech project or obtained from literature sources; (2) the evaluation of the adaptive response of a beech stand to environmental changes (through sensitivity analyses of (*a*) initial genetic diversity, (*b*) pollen dispersal distance, (*c*) heritability of selected phenotypic traits, and (*d*) forest management, ranging from the least intensive system without management to the most intensive system represented by so-called sheltercut management); and (3) the evaluation, by model simulation, of the responses of selected phenotypic traits and their genetic diversity to a range of management systems applied at the study plots.

In summary, the main results of the DynaBeech project were:

Gene flow: a substantial proportion of pollen was coming in from outside the stands (44.6% and 71.8% for the Sainte-Baume and Ventoux sites, respectively (G.G. Vendramin, personal communication). The results of the sensitivity analyses showed that, with a short pollen dispersal distance, the genetic diversity decreases over time, and more so in the sheltercut system compared with a no-management system. Thus, long-distance gene flow can be an important mechanism to counteract the loss in genetic diversity caused by selection and drift (Hamrick 2004).

Heritability of phenotypic traits: selective responses are low if the heritability is low, and vice versa. The results of the sensitivity analysis show that genetic diversity indeed declines with increasing heritability of a functional trait under the sheltercut system. In that system, selection on emerging recruitment is allowed to operate about every 120 years, thereby removing poorly adapted saplings and thus reducing genetic diversity. Such a trend is much less apparent in the no-management system because effective selection moments are determined by the longevity of beech, i.e. about 250 years.

Selection pressure on a trait: a given environmental change will not affect all traits similarly. In DynaBeech, we evaluated four types of trait: (1) a neutral trait, which is selected neither for nor against, and changes due to genetic drift only; (2) bud burst day, which changes due to natural selection only; (3) spiral grain, which changes due to artificial selection only; and (4) height growth rate, changing due to both natural and artificial selection. Based on the simulated responses, the selection pressure imposed on the selected traits increases in this order and genetic diversity decreases proportionally to the selection pressure. Of the adaptive traits, bud burst day shows a small response, and height growth rate shows a strong one, even though the heritabilities were set to the same value in the model.

Recruitment interval: the rate of adaptation of trees to environmental changes depends not so much on the longevity of individual trees, but on successful recruitment events during the lifetime of a tree. Recruitment interval is in most forests determined by the management practice rather than through natural forest dynamics. Our modelling analysis on the effects of forest management at 10 study sites showed that the loss of genetic diversity is directly related to management activity, which increases from the no–management system to the sheltercut system (with several management regimes of intermediate intensity). The results indicated that selection mainly operates during recruitment events. Hence, the duration of the interval between the recruitment events is an important factor determining the adaptive response of the forest.

Overall, the modelling results indicated that the highest level of genetic variation is maintained in a forest by applying no forest management. However, the no-management regime also led to a spatial genetic structure for some traits, hence inbreeding circles. If environmental conditions change, this system is the least suitable, as there are few moments in time where adaptation most effectively operates, i.e. the recruitment stage. These adaptive moments occur more frequently with increasing management intensity, thereby increasing the selective response of adaptive traits. This takes place with a minor loss of both genetic diversity and potentially adaptive alleles.

Hence, by spatial-explicit modelling of competitive interactions between individual trees, dispersal of seeds and pollen, and including a simple genetic model to allow adaptive responses of functional traits, the non-equilibrium approach to the dynamics of a beech forest is applied, while allowing equilibria in frequencies of alleles for adaptive traits. The modelling tool, named FORGEM, can be used to assess transient responses of tree populations and tree species composition to climate change and to determine optimal forest management to meet multiple goals.

An interesting observational result was that in the virgin forest site of Dobra, indications existed of a spatial structure for bud burst phenology. This suggests that so-called 'inbreeding circles' of closely related adults occur in a group rather than throughout the forest. In the half-sib experiments of DynaBeech, phenology was found to have a relatively high narrow-sense heritability (Teissier du Cros et al. 2004), and in the full-sib trial, indications of quantitative trait loci were found for bud burst (Scalfi et al. 2004). This makes bud burst phenology a good candidate to assess phenotypically whether a spatial genetic structure exists in a forest, without extensive laboratory tests. It is still under debate whether bud burst phenology of beech is also a good candidate for the evaluation of climate change effects because the experimental findings on a control by either photoperiod or temperature or both are conflicting (Falusi and Calamassi 1990, 1996; Heide 1993a, b).

Conclusions and recommendations

Society demands today from forest managers not only a reliable supply of timber in sufficient quality and amount, but also a wide array of goods and services, ranging from carbon sequestration, biodiversity conservation, water retention and purification to aesthetic values. Guidelines for forest management to optimize the genetic diversity in a stand for a sustainable yield must therefore be embedded in guidelines for the management of other forest functions.

Changes in climate, land use, nitrogen deposition and air pollution occur simultaneously, resulting in a situation where stands, forests and species distributions are no longer in equilibrium with the prevailing abiotic conditions. This situation demands that forests be managed in a way that enables adaptation (in a genetic sense) and adjustment (in an ecological sense) to such changes. Genetic diversity, structural diversity and species diversity are, in general terms, conditions that allow the forest to adapt and adjust.

From a research point of view, more integration between genetic, ecological and silvicultural disciplines for the management of diversity is required. This should include studies on stand productivity, tree species composition of forests, biogeochemical cycling at the landscape scale, and changes in geographic distributions of tree species. It is essential that both field studies, e.g. provenance trials, and modelling studies, should be used simultaneously to complement each other. Additionally, common quantifiable concepts should be developed. Here the concept of resilience, defined as the conditions that allow a system to absorb disturbances and environmental stress, should be made operational and quantified for both genetic and ecological aspects of diversity at the stand, landscape and regional scales. From a genetic point of view, the resilience concept is already quite well developed at the stand scale with the importance of maintaining genetic diversity, whilst taking a spatial genetic structure and limitations of gene flow into account. Matching ecological concepts may, however, need further attention.

From a forest policy point of view, the current situation is that international policies on biodiversity, such as the Convention on Biological Diversity (CBD), recognize that humans have caused a dramatic loss in biodiversity. This has led to the development of policies and management guidelines aiming to prevent ongoing loss and to restore biodiversity. Such guidelines, protocols and (inter-)national policies on forest genetics should reflect the realization that classical equilibrium concepts may no longer be valid for systems that are now essentially in non-equilibrium due to climate change. Implementation of policies aiming at returning to a pre-disturbed reference situation may therefore not be feasible and the resilience of forests to ongoing environmental change becomes of central importance.

References

Falusi, M. & Calamassi, R. 1990. Bud dormancy in beech (*Fagus sylvatica* L.). Effect of chilling and photoperiod on dormancy release of beech seedlings. *Tree Physiology*, 6: 429–438.

Falusi, M. & Calamassi, R. 1996. Geographic variation and bud dormancy in beech seedlings (*Fagus sylvatica* L.). *Annales des Sciences Forestieres Paris*, 53: 967–979.

Hamrick, J.L. 2004. Response of forest trees to global environmental changes. *Forest Ecology and Management*, 197: 323–335.

Hanski, I. & Gilpin, M.E. 1997. *Metapopulation biology: ecology, genetics and evolution*. Academic Press, San Diego, USA. 512 p.

Heide, O.M. 1993a. Daylength and thermal time responses of budburst during dormancy release in some northern deciduous trees. *Physiologia Plantarum*, 88: 531–540.

Heide, O.M. 1993b. Dormancy release in beech buds (*Fagus sylvatica*) requires both chilling and long days. *Physiologia Plantarum*, 89: 187–191.

Hengeveld, R. & Walter, G.H. 1999. The two coexisting ecological paradigms. *Acta Biotheoretica*, 47: 141–170.

Holling, C.S. 1973. Resilience and Stability of Ecological Systems. *Annual Review of Ecology and Systematics*, 4: 1–23.

Kramer, K. (editor). 2004. *Effects of silvicultural regimes on dynamics of genetic and ecological diversity of European beech forests. Impact assessment and recommendations for sustainable forestry*. Final Report of 5th Framework Project DynaBeech, QLK5-CT-1999-1210. Alterra, Wageningen, The Netherlands. 269 p.

Kramer, K., Groen, T.A. & van Wieren, S.E. 2003. The interacting effects of ungulates and fire on forest dynamics: an analysis using the model FORSPACE. *Forest Ecology and Management*, 181: 205–222.

Lewontin, R.C. 1969. *The meaning of stability*. Diversity and Stability – Ecological Systems. Brookhaven Symposium of Biology. 12 p.

Pearson, R.G. & Dawson, T.P. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography*, 12: 361–371.

Pimm, S.L. 1991. *The balance of Nature? Ecological issues and the conservation of species and communities*, The University of Chicago Press, Chicago, USA, and London, UK.

Prentice, I.C., Sykes, M.T. & Cramer, W. 1991. The possible dynamic response of northern forests to global warming. *Global Ecology and Biogeography Letters*, 1: 129–135.

Scalfi, M., Troggio, M., Piovani, P., Leonardi, S., Magnaschi, G., Vendramin, G.G. & Menozzi, P. 2004. A RAPD, AFLP and SSR linkage map, and QTL analysis in European beech (*Fagus sylvatica* L.). *Theoretical and Applied Genetics*, 108: 433–441.

Sykes, M.T., Prentice, I.C. & Cramer, W. 1996. A bioclimatic model for the potential distributions of north European tree species under present and future climates. *Journal of Biogeography*, 23: 203–233.

Teissier du Cros, E., Forstreuter, M. & Ducrey, M. 2004. *Genetic control of adaptive traits*. pp. 134–141, *in*: Kramer 2004, *q.v.*

Tilman, D. 1985. The resource-ratio hypothesis of plant succession. *American Naturalist*, 125: 827–852.

Tilman, D. & Kareiva, P. 1997. *Spatial ecology. The role of space in population dynamics and interspecific interactions*. Princeton University Press, Princeton NJ, USA. 368 p.

WHAT DO FIELD TRIALS TELL ABOUT THE FUTURE USE OF FOREST REPRODUCTIVE MATERIAL?

Csaba Mátyás

Institute of Environmental Sciences, University of West Hungary, Sopron, Hungary

Introduction: the forestry perspective of climate and vegetation shift

In view of the current concern over climate change, the fundamental question is how forest cover and tree populations will react, and what the chances are to maintain and enhance their adaptability. Modelling of vegetation shifts according to various climate change scenarios has been widely applied in the temperate zone. For Europe, it has been forecast that the Mediterranean scrub will invade the British Isles, broadleaved forests might grow in the High Alps instead of conifers, and that treeless grasslands could conquer not only the Carpathian Basin, but also the central part of eastern Germany and Poland.

Apart from the great uncertainty in forecast scenarios (especially regarding the amount of rainfall), the preparation for expected changes of this magnitude presents tasks not encountered before in forestry. The large-scale preparation and conversion of forests to future climatic conditions will present grave economic and technological challenges. However, it would be a very biased approach to treat this problem solely as an economic and ecological question, since forests bear also important cultural, aesthetic and emotional values. The existence of forests is an important element of life quality in the European tradition.

Predicted climate change demands that a high priority be assigned to the study of the climatic requirements of forest tree species and zonal forest types (i.e. vegetation types determined primarily by macroclimate), especially of their xeric or lower limits, which are determined by tolerance to water stress and high temperatures. The climatic (zonal) limit of greatest concern is the lower limit of closed temperate forests and its dominant species towards continental grasslands or Mediterranean scrub, because the shift of this limit has dramatic consequences for forestry and ecology, as well as for life quality in general.

Mátyás, C. 2007. What do field trials tell about the future use of forest reproductive material? In: Koskela, J., Buck, A. and Teissier du Cros, E., editors. Climate change and forest genetic diversity: Implications for sustainable forest management in Europe. Bioversity International, Rome, Italy. pp. 53–69

The neglected synthesis of ecology and genetics in climate change studies

Any prediction about the effects of future climate change scenarios on stability and yield of forests requires information on the tolerance and adaptability of tree species. The maintenance of adaptive and evolutionary capacity has to be considered as a precondition for stability of forest ecosystems (Ledig and Kitzmiller 1992; Eriksson et al. 1993; Mátyás 1997). It is strange to observe that, although the mentioned requirement is hard to interpret without genetic background, there are practically no ecological or conservation biology studies dealing with climate change effects that incorporate the aspect of genetic regulation of the response. Applied ecology papers dealing with the responses of species to climate change (reviewed by Hulme 2005) cover limited geographical areas and short periods, and usually concentrate on responses in abundance with time or spatial distribution. Practically none of the papers reviewed by Hulme (2005) deals with the genetics of adaptation.

Nor have quantitative response to change and limits of tolerance—seemingly trivial questions—been among the priority themes of current genetic research. One of the reasons for this neglect lies in the limited scientific reputation of research in quantitative trait variation. In addition, such studies are time-consuming and expensive. It also has to be conceded that until recent decades, behaviour of populations under changed or extreme conditions had little practical relevance.

Current forest genetics research concentrates on molecular genetic analysis because this approach promises a faster elucidation of genetic regulation of stability and tolerance, although ecological interpretation of molecular markers with adaptive value has remained dubious in most cases. Out of genetic forces shaping variability, the random effects of migration, mutation and drift have been studied most, while adaptive response to selection has received significantly less attention.

Options of genetic adaptation on population and individual level

The genetic system and adaptability of trees have been shaped by eons of evolution. On an evolutionary scale, most species are ephemeral creatures on Earth. Forest trees, especially the evolutionarily more ancient conifers, certainly belong to the more persisting class of species. Tree species have not only successfully survived changing geological periods, but also endure during an individual's lifetime considerable fluctuations of environment without the chance of escaping to more favourable habitats. Environmental instability, evolutionary history and genetic forces have shaped the natural adaptive strategy of trees; a life form with extremely long generation times, incomparably high within-population genetic diversity and heterozygosity, and immense population sizes, both areally and numerically.

There are various genetic and non-genetic mechanisms operating on the individual, population, species and ecosystem levels, balancing changes in environmental conditions. On species and ecosystem or landscape levels, a possibility of responding to large-scale changes in the environment is migration through seed (and pollen) dispersal. Palaeoecological evidence of migration during the epochs of glacials and interglacials is abundant—and this is the response mechanism expected and described by most ecologically-oriented future scenarios as well. On the level of populations, natural selection adjusts the average fitness of a population to changing conditions. The directed genetic change of the population's gene pool towards an optimum state is genetic adaptation in the strict sense. It is a well-accepted concept that the basic precondition for fast and effective genetic adaptation lies in sufficiently large variation, i.e. in genetic diversity. Long-term genetic adaptability is therefore directly depending on the conservation or even reconstruction of adaptive genetic variance.

On the individual genotype level, environmentally influenced phenotypic plasticity provides the ability to survive in a wide range of environments, without genetic change in the classic sense. Plasticity means that the phenotypic expression of genes is influenced by the environment, thus the organism may modify its responses within genetically set limits. Phenotypic plasticity will set the limits of environmental heterogeneity in which a genotype or population can endure within its lifetime.

Environmental signals might also trigger genetic carryover effects. Genetic carryover effects (imprinting, 'after-effects') are lasting changes in genetic regulation, which can be inherited (Jablonka et al. 1995; for a review, see Martienssen and Colot 2001). First proofs of existence of such effects in certain forest trees were detected in boreal populations of Norway spruce (*Picea abies*) (Skrøppa and Johnsen 2000) and some other conifers. The significance of genetic carryover in adaptation is so far unclear and should be treated with caution.

When preparing to meet the challenges of changing climate, it is important to realize which of the described mechanisms will gain importance in adaptation, what their action time frame is, and which mechanisms might be even negligible.

Processes of adjustment in the extant (currently growing) generation

Natural selection is eliminating the genotypes of low fitness and tolerance in the lifetime of a population, and this leads to better adaptation. Although some studies on adaptation deal with selection processes and with changes in the genetic composition, few studies have in practice been implemented under conditions of severe change where populations are reaching their tolerance limits. In such margin situations, the effectiveness of adjustment through selection ceases and mass mortality may follow.

A much less observed mechanism, phenotypic plasticity, provides the ability of individual adjustment without any change in the inherited genetic resources of the population. Mainly for reasons of difficulty of experimental analysis, reaction norms and limits of adaptability set by phenotypic plasticity are rarely considered in connection with adaptation. Compared with plasticity, spontaneous natural selection will play a smaller role than presumed, due to the speed of expected changes, as explained below. Plasticity should gain therefore an increasing role as a preferred trait for forest reproductive material in artificial regeneration, nature conservation and restoration ecology.

Processes of adjustment in the following generations

Studies on long-distance gene flow through pollen have shed light on this very effective mechanism of constant replenishment of genetic resources, which probably contributes to the unexpectedly high diversity of boreal tree populations. A possibility for responding to large-scale changes in the environment is also migration through seed dispersal. Preconditions for effective adjustment in both cases are landscape connectivity (availability of pollen or seed) and suitable speed, matching the pace of change. The constraints for both are discussed below.

Constraints to spontaneous adaptation and why human interference is needed

A basic question of mitigation strategy is how much natural genetic processes, such as migration, gene flow and natural selection, will spontaneously compensate for the effects of climate change. Migration and genetic adaptation are investigated here as they are usually taken for granted in climate change modelling.

Is forest community change by spontaneous migration automatic?

It could be argued that, as in the past, species and communities will keep pace with changes and counterbalance these changing scenarios by colonizing new habitats. Authoritative studies on the effects of climate change on vegetation cover take the automatic adjustment of distribution areas of species (i.e. adaptation through migration) for granted, irrespective of the migration possibilities and potentials. Analogies could be taken from observation of spontaneous changes in the insect fauna. However, there are fundamental differences between the migration potential of insects and of forest trees. It should be emphasized that changes in distribution areas and vegetation cover are predicted to be of such a magnitude that they could never happen through natural succession and migration of forest trees. There are two obvious reasons for this.

Firstly, the natural migration ability of forest trees is slower than the forecast scenario change. Effective species migration has to match, *inter alia*, the pace of expected change. For Central European conditions it can be shown that, based on a scenario of an average temperature increase of 2°C in 35 years, isotherms would move north at an average speed of 3 km per year, and vertically 12 m per year in altitude (see Box 1). This has to be compared with the natural migration speed of tree species. It is known from palaeobotanical studies that tree populations migrate—depending on migration abilities—at rates of 0.1 to 0.4 km per year (Davis and Shaw 2001). The difference between the expected and the potential value is roughly one magnitude for horizontal migration (vertical migration seems to be possible if geomorphologic and distribution patterns are favourable).

Secondly, insurmountable obstacles to migration are the intensely managed and fragmented landscapes of temperate Europe. Even if tree migration could catch up with the speed of climate shift, and if migration routes were available, spontaneous changes would be impeded due to the nearly total human domination of forest ecosystems through forest management, which has regulated regeneration and species composition for centuries. As much as it is an obstacle, this situation also offers a serious opportunity for human support to natural processes.

Another constraint to migration into new habitats is the limited availability of such new habitats, due to unfavourable geomorphological and distributional conditions. Typical examples are populations restricted to mountain tops, such as Spanish fir (*Abies pinsapo*) in northern Africa (Eriksson and Ekberg 2001)

Box 1. Comparison of migration and isotherm shift velocities

Natural migration velocities through seed dispersal (from palaeobotanical data):

- Quercus, Fagus: 100 to 250 m/year
- *Betula, Pinus*: 200 to 400 m/year

Velocity of isotherm shift (scenario: 2.0°C in 35 years)

Direction	Gradient	Velocity
S ⇒ N horizontal	50 km/°C	3000 m/year
Vertical (altitudinal)	200 m/°C	11.5 m altitude/year

or Scots pine (*Pinus sylvestris*) in Spain, which simply have nowhere to migrate. In general, any tree species settled in a habitat that does not provide a spatially contiguous escape route will be affected. In addition to high-altitude tree species, coastal Mediterranean species may also be exposed to this threat.

Are genetic adaptation mechanisms sufficient?

Regarding the genetic component of climatic adaptation, there is no general agreement, even among geneticists, on the urgency and modes of mitigation measures. Some scientists (e.g. Hamrick 2004) argue that in the temperate zone, no silvicultural measures will be needed to mitigate the effects of changing conditions because:

- there is enough genetic variability in the populations, which might be further replenished by migration;
- regeneration is secured through the persistence, phenotypic plasticity and long life cycle of forest tree populations;
- palaeoecological data indicate that enough variation accumulates and is saved in refugia, and the selection pressure of recent climatic fluctuations was without effect; and
- genetic adaptation may happen in relatively short periods, within two or three generations.

These arguments may be valid, but primarily in boreal regions with predominantly nature-close conditions, where human land use has yet had no serious impact. In certain nature conservation areas or national parks, cyclical changes of vegetation do not pose serious problems as long as the dynamism of vegetation and fauna is accepted (Westphal and Millar 2004). However, in landscapes and regions transformed by humans, there is no room left for such fluctuations, especially when approaching the lower distribution limits of a vegetation type or a species. This approach does not consider genetically set tolerance limits, and assumes practically limitless adaptation. And last but not least, ecological and economic consequences for forestry and human life quality are omitted completely from these arguments.

A support for accelerated adaptation of populations is the flux of pollen from distant sources. Depending on random wind trajectories, this long-distance migration probably plays a certain role in adaptation (Lindgren et al. 1995). The speed of adaptation of a gene pool through pollen flow can be assumed to be higher than that deriving from migration by dispersed seed. It is the central and northern part of distribution ranges in the northern hemisphere where influx of pollen might contribute to adjustment to change. Relatively continuous distribution of a species, populations close to the natural state and general application of natural regeneration techniques are, however, general preconditions for effective gene flow. Neither of these can be taken for granted. In addition, the adaptability-improving role of gene flow comes into effect only in subsequent generations.

Common gardens: sources of valuable information on limits of tolerance and plasticity

From the point of view of selection effects of climatic extremes, studies on tolerance and plasticity traits are essential. Tolerance can be defined as the ability of a genotype to maintain its fitness despite damage. Tolerance is presumably genetically correlated with phenotypic plasticity, i.e. with growth vigour across environments (Weis et al. 2000; Mátyás and Nagy 2005). Limits of tolerance are genetically set and will determine the presence or absence of species (Figure 1). Even under zonal conditions, the limit cannot be described properly in terms of average climate, as limiting conditions are bound to irregularly appearing extremes, usually triggering damage by diseases and pests. The effects of climate parameter shifts are frequently modelled but seldom studied; observations on tolerance limits are scarce, as forest management strives to operate well above the tolerance limits to secure economic returns.

The study of the effect of natural selection and the phenotypic response of forest trees presents serious methodical challenges in the field (Berki and Rasztovics 2004). Such effects are much easier to follow in common-garden tests, i.e. in provenance trials. Provenance tests established since the second half of the 19th century are probably among the most important contributions of foresters to the science of biology. They are unique because they have been established with natural-state populations, adapted to specific conditions. They are unique also because these tests have been established across continents, at many sites and maintained over decades. Nonetheless, these tests have remained unnoticed by evolutionary ecologists.

When testing a set of populations at a given site, a characteristic response pattern can be observed, where growth and vigour of populations originating from the area of the test site tend to be the best and the performance of less adapted populations decreases with the ecological distance from the location of origin (Mátyás and Yeatman 1992). Equations describing these phenomena have been developed by a large number of authors, and response functions have been broadly utilized to define seed transfer rules and to delimit seed zones. Most of these models rely on describing genetic variation patterns on a geographical basis using latitude, longitude and elevation as independent variables to describe variation patterns for a given area. The ecological relevance of these variables is ambiguous.

The idea of transfer analysis, i.e. modelling of responses and forecasting responses to scenarios based on provenance data, was proposed originally by Mátyás and

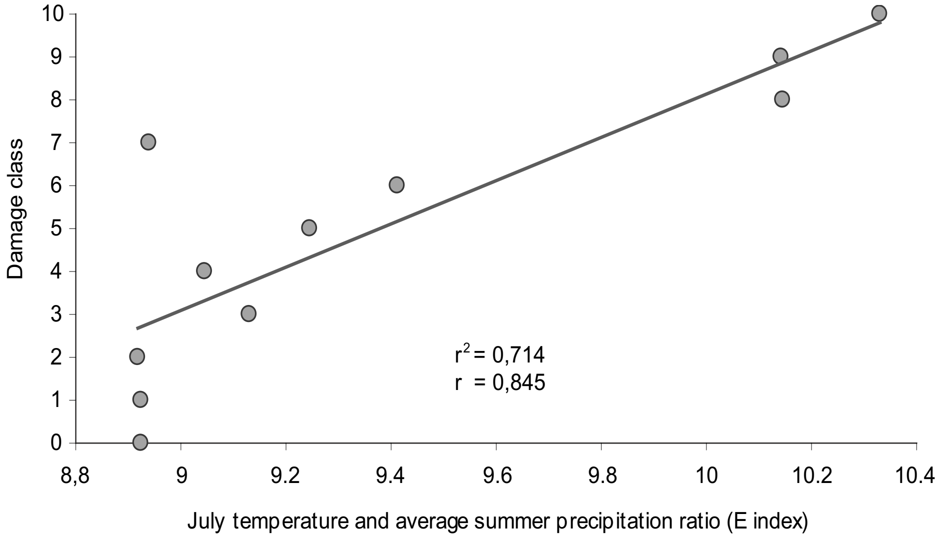

Figure 1. Approaching the genetically set limits of tolerance: average moisture stress climate (E index) of leaf damage classes of beech in permanent monitoring plots in Hungary. The graph shows the change in health status from healthy (class 0) to dead (class 10) along a climate gradient of sites with increasing summer moisture stress (screened data averaged for 1991 to 2001; analysis by G. Veperdi).

Yeatman (1987) and Mátyás (1994). The principle of this approach is the use of ecological variables to express the change of environment through transfer to the test site. Adaptive responses to changes can be interpreted, generalized and compared more easily if expressed as ecological distances. To observe tolerance and plasticity, populations (provenances) are assessed in different environmental conditions. Regression analysis can be applied to describe the change in fitness. The slope of the function represents the sensitivity to change and the possible limits of tolerance. Taking growth and health condition as proxy for fitness, the function is interpreted as the species' reaction norm of fitness to the variable investigated (precipitation, drought). Thus, growth and survival of natural populations adapted to a given site, transferred and tested in other environments as part of common-garden tests, can be interpreted as a simulation of ambient changes at the original location. The transfer analysis facilitates the forecasting of adaptive response and of effects of environmental change (Mátyás and Nagy 2005; Rehfeldt et al. 2003).

Quantitative response to change

The quantitative assessments of common-garden tests have yielded some generally valid results, which are summarized below.

Width of adaptability: phenotypic plasticity

Analysis of field tests shows remarkable width of adaptability and persistence (and, in consequence, the extended width of 'local' adaptation) in the face of even dramatic changes in thermal conditions and, to a lesser extent, in moisture supply. This phenomenon indicates the substantial conservatism in the climatic adaptation of numerous tested tree species, which has an inherent genetic basis and may have been enhanced by evolution (Mátyás and Nagy 2005).

Value of autochthonous, local source

The superiority of locally adapted, autochthonous populations is an unchallenged axiom in silviculture. The evaluation of provenance tests shows a more differentiated picture. It seems that the fitness of local sources expressed in (height) growth is clearest at locations with extreme conditions. Under more favourable conditions, locally adapted provenances show less superiority (Mátyás 2002).

Asymmetry of response

An important outcome of analysis results is the asymmetry of response. The effect of environmental change on populations in different parts of the distribution range is divergent as different climatic factors exert their selection pressure. It should be noted that a species is not responding as a monolithic unit, due to within-species genetic structure. The boreal limit of tree distribution is temperature dependent. In provenance tests, populations originating from the upper limit of a species distribution show their maximum performance in much milder conditions. The effect diminishes with increasing temperature sum of the location of origin.

At the southern limit of distribution, drought stress is the main controlling factor. Transfer of populations towards a cooler climate (and better moisture supply) results in accelerated growth. Transfer distance to optimum diminishes with decreasing temperature sum of the location of origin. Accordingly, the reaction of indigenous tree populations to changing conditions will differ according to climatic zones (Figure 2). In the thermally-limited northern-boreal zone, the expected rise in temperature will lead to strong growth acceleration with no significant genetic change. At lower altitudes, in the temperate-maritime zone, growth will accelerate too, along with higher temperatures and increasing or at least unchanged rainfall. In the semi-arid temperate-continental and semi-arid Mediterranean zones, however, even relatively minor temperature increases, coupled with growing drought stress, will trigger loss of compatibility, higher susceptibility to diseases, and increased mortality. As a result, temperature increase leads to relatively fast growth and productivity loss, and selective mortality (Berki and Rasztovics 2004; Mátyás 2005). It should be noted that the described phenomena are generalizations. Substantial deviations may be caused by the genetic

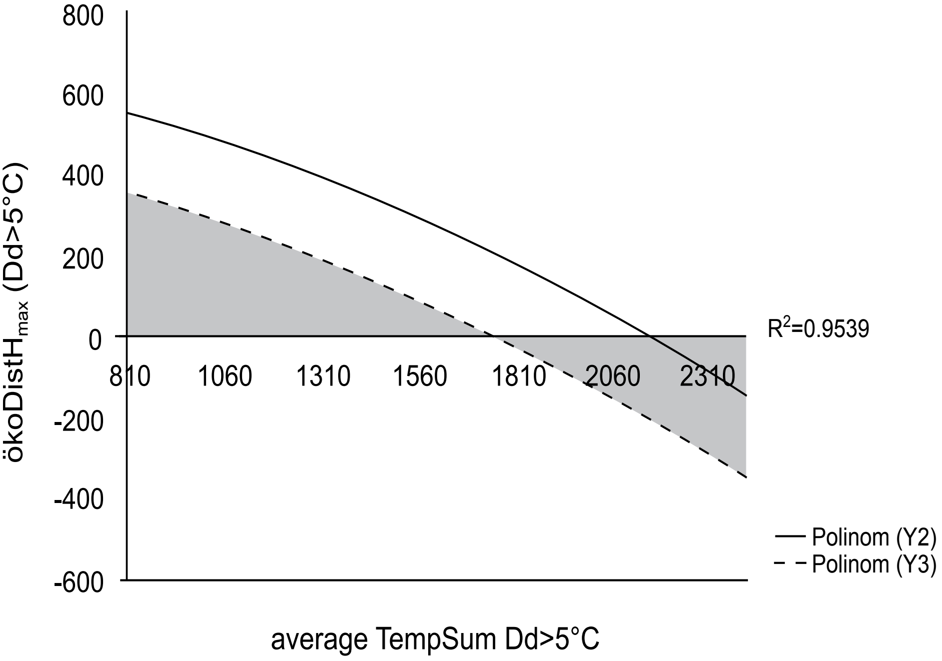

Figure 2. Schematic characterization of response to an ‘annual temperature rise of +200 degree-days’ climate scenario along a N–S transect of differently adapted populations of Scots pine (*Pinus sylvestris*) in eastern Europe. The horizontal axis is the local sum of degree-days. The shaded area indicates direction of growth response: positive in the North and negative in the South (source: Mátyás and Nagy 2005).

system of the species, the evolutionary-migratory past, and regional or local site effects. For example, there are indications that in certain regions of the boreal zone, where moisture stress is already present due to low precipitation, higher temperatures and increased drought stress may also lead to incremental decline (Lapenis et al. 2005).

Changes in genetic diversity following climatic stress

Expectable genetic changes will be minor in the northern part of the distribution range despite the speed of predicted change. Improved growing conditions can be utilized through the plasticity potential of tree populations, without much selection. As inherited plasticity will determine the response to change, there is little room left for genetic adaptation. In the temperate-Atlantic Europe zone, where moisture stress is predicted to stay low, populations will also be well buffered by their adaptability.

The situation is completely different along the xeric limit of main tree species, and at the limit of closed temperate forests. Here, natural selection becomes effective in the form of irregularly appearing health decline and mortality waves following weather extremes. The symptoms of pests (gradations) and diseases might be mistaken for primary causes (this was the case in many countries in recent decades). High mortality rates will certainly exert a strong effect on the genetic resources of exposed populations, and if stress situations aggravate, it may lead to local population extinction, even for once well-distributed, dominant species. This underlines the importance of management and conservation of forest genetic resources.

Response of communities

Studies on quantitative genetic variation patterns and adaptive response indicate significant differences between species' reactions—a result of differences in their genetic systems and evolutionary history. Therefore, potential distribution areas of different species will not shift uniformly. A corollary is that changing climatic conditions will generate communities not identical with the present ones. The coupled grave effect of changes in fauna and flora of forest ecosystems are not discussed here as this question is well covered by literature on species biodiversity change and conservation.

Effect on ecosystem carbon balance

Expected warming also affects the functioning of the forest ecosystem as a carbon sink. Increased drought frequency leads to growth decline and the quantity of sequestered carbon decreases. Simultaneously, the decomposition rate of dead organic matter accelerates, causing additional carbon release into the atmosphere. In areas favourably affected by temperature increase, growth acceleration leads to higher yields, as observed already across Western Europe (Kramer and Mohren 2001). Closer to the boreal limit, however, the carbon balance might turn strongly negative because of accelerated decomposition rates.

Consequences for forest management

In drought stress climates, incremental loss and higher incidence of diseases and pests will challenge the economics of forest operations, and will move emphasis more towards maintenance of ecological functions and conservation of stability and of genetic resources.

Thus, considering the long regeneration cycle of trees, the pace of the predicted climate change will be too swift to permit sufficient time for proper genetic adaptation of tree populations. A temperature shift will in any case negatively affect a large part of the area of a species' distribution. At low elevations and in the southern outliers of distribution areas, close to the lower (xeric) limit of the species, temperature increase will certainly lead to the thinning out and local extinction of the species.

At the northern limits, temperature increase will bring an improvement in site conditions. This offers the theoretical possibility of a migration advance for the species, as often modelled in climate scenarios. However, even in the long term, the utilization of climatically improved zones outside the present forest limits will be constrained by soil conditions. The development of soil profiles takes millennia, and the usually shallow, less developed soils of high altitudes and high latitudes will not change fast enough. Consequently, contrary to general belief, high altitude and high latitude site potential will not immediately follow the improvement in climate.

It can be concluded that mitigation policy cannot rely on natural self-regulation and acclimation of ecosystems. Tasks are imminent both in forest management and in conservation of genetic resources. The two areas are closely linked by our knowledge of the genetics of forest trees, which provides the basis for action. As a consequence, human interference will be essential for the maintenance of adaptability under changing conditions, not only in the present distribution range of the species, but also to extend the ranges of species at the northern peripheries of their distribution. This will be especially the case in the boreal zone, where possible temperature increases might be considerably higher than at medium latitudes (See Box 2).

Conclusions: tasks for mitigation

In general, in the core distribution area of widely dispersed tree species with effective gene flow, there is still no emergency for preparatory measures if the stands have been properly managed and regenerated. Active preparatory measures should have priority in the case of rare, fragmented tree species with limited or impeded dispersal ability. Species occupying extreme habitats should also receive special attention (see Box 2.).

Box 2. Urgency of preventive action: species characteristics to be considered

Low urgency	High urgency
Continuous distribution	Fragmented, isolated distribution
High density	Small populations
Naturally regenerated	Artificially regenerated
Effective gene flow	Limited replenishment of gene pool
Spontaneously spreading	Low dispersal capacity
Extensive, zonal habitats	Extreme sites as habitats
Reproduction unaffected	Disturbances in flowering and seeding

However, even major, widely distributed tree species need special consideration in the following situations:

- where there are isolated populations on the southern or continental fringes of the distribution area;
- where there are isolated mountain populations with no 'reserve altitude';
- in locations where conditions in the potential colonization area are unsuitable (high alpine or boreal conditions);
- where the areas were regenerated with reproductive material of obviously low adaptability; and
- where there are populations with high phenotypic plasticity.

Populations at the southern or continental distribution limits are threatened in particular due to strong productivity loss, i.e. weakened competitive ability and hindered sexual reproduction (Mátyás 2000). Investigations have shown that changes in climatic conditions may affect reproduction processes, which may influence regeneration and dispersal ability of the species. In addition to decline in fructification and higher mortality of mature trees, low regeneration success and high interspecific competition (especially with shrubs and weeds) demand additional efforts to maintain genetic diversity and adaptive potential. In the case of seriously threatened minor tree species and valuable populations, active gene conservation measures will be necessary through evacuation or transfer to gene banks. At the same time, the maintenance or reconstruction of non-adaptive, random allelic frequency patterns is less pressing. A typical example of this would be the maintenance of random, non-adaptive geographic variation patterns due to colonization, such as detected for European white oaks (Petit et al. 2002).

Mitigation priorities

When deciding on priorities in conserving and utilizing climatically threatened genetic resources of tree populations, genetic information on adaptability should be used, if available. There is a generally accepted approach to judging adaptability, based on genetic diversity at biochemical or molecular level. Much of recent evidence indicates, however, that inference based on quantitative genetic characteristics, such as phenotypic plasticity and adaptedness on the basis of molecular genetic parameters, is at present unreliable. Therefore, adaptively important, quantitative traits should receive at least as much attention as molecular genetic diversity. For the quantitative assessment of these traits, field experiments are indispensable and will remain so for the coming decades.

Forest management

Climate change mitigation is a newly emerging aspect of regulating the use of forest reproductive material. The present guidelines usually leave this aspect unconsidered in most countries. Rules and guidelines should be reconsidered in the light of recent research findings. The general need to reconsider regulations should be utilized as an opportunity to reach flexible, effective, genetically sound, continent-wide guidelines that derive from generally accepted principles. To reach consensus on these questions should be an eminent task for the coming years.

Artificial support for migration, i.e. guided transfer of identified provenances and preferring populations exhibiting plasticity, offer probably the most efficient possibilities for mitigation through proper use of forest reproductive material. Among the possible silvicultural management options, the most efficient interference is the proper selection of tending measures in threatened regions by regulating species mixture, canopy closure and stem density in order to improve stability. Genetically, supporting effective gene flow by selecting proper natural regeneration techniques might be sufficient in the mildest cases of climatic threat. When planning silvicultural mitigating strategies, tasks in natural and anthropogenic forests have to be considered separately.

Conservation of forest genetic resources

There is a strong need to put into practice the principles and guidelines of gene conservation that have been formulated as a Europe-wide common effort under the auspices of EUFORGEN. This calls for cooperative action irrespective of national boundaries.

Research

The challenge of environmental instability introduces new dimensions for forest genetic research and demands a review of current research priorities. It points towards more efforts to elucidate natural selection processes and regulation of phenotypic responses. Both continent-wide international collaboration and trade opportunities for forest reproductive material have developed enormously following the political and economic changes in Europe in recent years. For the use of forest reproductive material, this means new challenges, both positive and negative. Scientific collaboration through international research networks must deal with these changing challenges and find proper answers. In parallel, there is a need to review results of common-garden tests established during the last century and to identify gaps in our knowledge, with the aim of agreeing on new, complementary test networks to provide a solid foundation for future use of reproductive material.

Need for a common plan of action

The fundamental basis of adaptability is the genetic variability inherent in natural tree populations. Climate change research results indicate that, because of the conservative nature of the genetic adaptation process, and the relative speed of expected change, even agricultural crops will demand a strategy to facilitate adaptation. Long-lived, immobile organisms, such as trees, will especially need human interference, in spite of an impressive adaptation capacity. To counteract genetic erosion and extinction, populations and outliers along the southern (or low-elevation) limits of species' distribution areas will need special attention.

Through international cooperation, guidelines for adaptive silviculture and for the use and transfer of forest reproductive material have to be adjusted in the face of climate change. The tasks and principles described have to be incorporated into the agenda of national forest programmes. To elaborate genetically sound guidelines, strengthening of field experimentation should be promoted. In a period of scarce financial support for this, efforts should be joint and based on international cooperation and sharing of responsibilities.

References

Berki, I. & Rasztovics, E. 2004. [Research in drought tolerance of zonal tree species, with special regard to sessile oak.] (Hungarian with English summary) pp. 209–220, *in:* Cs. Mátyás and P. Vig, (editors). *Erdö és klima – Forest and Climate IV*. Sopron, Hungary.

Davis, M.B. & Shaw R.G. 2001. Range shifts and adaptive responses to quaternary climate change. *Science*, 292: 673–679.

Eriksson, G. & Ekberg, I. 2001. *Introduction to Forest Genetics*. SLU Press, Uppsala, Sweden.

Eriksson, G., Namkoong, G. & Roberds, J.H. 1993. Dynamic gene conservation for uncertain futures. *Forest Ecology and Management*, 62: 15–37.

Hamrick, J.L. 2004. Response of forest trees to global environmental changes. *Forest Ecology and Management*, 197: 1–3, 323–336.

Hulme, P.E. 2005. Adapting to climate change: is there scope for ecological management in the face of a global threat? *Journal of Applied Ecology*, 42: 784–794.

Jablonka, E., Oborny, B., Molnár, I., Kisdi, É., Hofbauer, J. & Czárán, T. 1995. The adaptive advantage of phenotypic memory in changing environments. *Philosophical Transactions of the Royal Society London, Series B*, 350: 133–141.

Kramer, K. & Mohren, G. 2001. Long-term effects of climate change on carbon budgets of forests in Europe. *Alterra Report*, No. 194.

Lapenis, A., Shvidenko, A., Shepaschenko, D., Nilsson, S. & Aiyyer, A. 2005. Acclimation of Russian forests to recent changes. *Global Change Biology*, 11: 2090–2102.

Ledig, F.T. & Kitzmiller, J.H. 1992. Genetic strategies for reforestation in the face of global climate change. *Forest Ecology and Management*, 50: 153–169.

Lindgren, D., Paule, L., Xihuan, S., Yazdani, R., Segerström, U., Wallin, J.E. & Lejdebro, M.L. 1995. Can viable pollen carry Scots pine genes over long distances? *Grana*, 34: 64–69.

Martienssen, R.A. & Colot, V. 2001. DNA methylation and epigenetic inheritance in plants and filamentous fungi. *Science*, 293: 1070–1074.

Mátyás, Cs. 1994. Modelling climate change effects with provenance test data. *Tree Physiology*, 14: 797–804.

Mátyás, Cs. (editor). 1997. Perspectives of forest genetics and tree breeding in a changing world. *IUFRO World Series* Vol. 6. IUFRO, Vienna, Austria. 160 p.

Mátyás Cs. 2000. Riding on a wave of anxious concern: genetic implications of expected climate instability at the southern forest limits. pp. 44–47, *in:* J. Turok and Th. Geburek (editors). *International collaboration on forest genetic resources: the role of Europe.* Proceedings of the 2nd EUFORGEN Steering Committee Meeting, 26–29 November 1998, Vienna, Austria. IPGRI, Rome, Italy.

Mátyás, Cs. 2002. Can advantages of natural regeneration be challenged by genetics? pp. 51–63, in: A. Meier-Dinkel and W. Steiner (editors). Forest tree breeding in an ecologically oriented forest management system. Sauerlaenders Verl., Frankfurt, Germany. (Schriften aus der Forstlichen Fakultät der Universitaet Göttingen und der Niedersächsischen Forstlichen Versuchsanstalt). 134 p.

Mátyás, Cs. 2005. Expected climate instability and its consequences for conservation of forest genetic resources. pp. 465–476, *in:* T. Geburek and J. Turok (editors). *Conservation and Management of Forest Genetic Resources in Europe*, Arbora Publ., Zvolen, Slovakia.

Mátyás, Cs. & Nagy, L. 2005. Genetic potential of plastic response to climate change. pp. 55–69, *in:* M. Konnert (editor). Results of genetic field trials and laboratory studies and their applications in practical forestry. Tagungsbericht 11, Forum Genetik und Wald, Teisendorf, Germany, 20–22 September 2004. Bavarian Office for Forest Seed and Nurseries, Teisendorf, Germany. 354 p.

Mátyás, Cs. &Yeatman, C.W. 1987. [Adaptive variation of height growth of *Pinus banksiana* populations] (in Hungarian with English summary). EFE Tudományos Közleményei (Proceedings of Sopron University) 1–2: 191–197.

Mátyás, Cs. & Yeatman, C.W. 1992. Effect of geographical transfer on growth and survival of jack pine (*Pinus banksiana* Lamb.) populations. *Silvae Genetica*, 43: 6, 370–376.

Petit, R.J., Brewer, S., Bordacs, S., Burg, K., Cheddadi, R., Coart, E. & 22 co-authors. 2002. Identification of refugia and postglacial colonisation routes of European white oaks based on chloroplast DNA and fossil pollen evidence. *Forest Ecology and Management* 156(1–3)(Special issue): 49–74.

Rehfeldt, G.E., Tchebakova, N.M., Milyutin, L.I., Parfenova, E.I., Wykoff, W.R. & Kouzmina, N.A. 2003. Assessing population responses to climate in *Pinus silvestris* and *Larix* spp. of Eurasia with climate transfer models. *Eurasian Journal of Forestry Research*, 6(2): 83–98.

Skrøppa, T. & Johnsen, G. 2000. Pattern of adaptive variation in forest tree species: the reproductive element as an evolutionary force in *Picea abies*. pp. 49–58, *in:* Cs. Mátyás (editor). *Forest genetics and sustainability.* Kluwer Academic, Dordecht, The Netherlands.

Weis, A.E., Simms, E.L. & Hochberg, M.E. 2000. Will plant vigor and tolerance be genetically correlated? *Evolution Ecology*, 14: 331–352.

Westphal, R.D. & Millar, C.I. 2004. Genetic consequences of forest population dynamics influenced by historic climate variability in the western USA. *Forest Ecology and Management*, 197 (Special issue): 159–170.

FOREST GENETIC DIVERSITY AND CLIMATE CHANGE: ECONOMIC CONSIDERATIONS

Bo Jellesmark Thorsen[1] *and Erik Dahl Kjær*[2]

1. Forest and Landscape, Royal Veterinary and Agricultural University, Frederiksberg C, Denmark
2. Forest and Landscape, Royal Veterinary and Agricultural University, Hørsholm, Denmark

Introduction

In the face of climate change and the inherent uncertainty it implies, there is a need for reconsidering the way we evaluate and undertake different decision alternatives. While this could be said to be true for so many things in everyday life liable to be affected by climate change, it is likely to be particularly true and important for decisions with a long time horizon. Such decisions abound in many aspects of forest management and, among them, perhaps the most long-ranging decisions are those concerned with forest genetic resources and their diversity at various spatial scales. In this paper, we will briefly point out how decisions concerning forest genetic diversity may affect the state and flow of values of our future forests. We provide some practical considerations and recommendations on ways such decisions could better incorporate the aspects of uncertainty related to climate change.

Throughout this paper, forest genetic diversity is taken to concern the genetic variation within the tree component of forests, e.g. tree species, provenances or individual trees or clones. In line with Namkoong *et al* (1996), we also include the concern for genetic processes that can ensure continued adaptability. We realize that forest genetic diversity in this narrow definition ('tree genetic resources') constitutes only part of forest biodiversity in general, but it should be noted that it constitutes a very important component. Trees are keystone species in the forest ecosystem and forest genetic diversity may prove crucial for maintaining various forest habitats at all scales, which support forest biodiversity at large and hence also the values derived from biodiversity in a broader perspective.

The point of departure here is that large values may be at stake. Many of the commercially planted trees have natural distribution areas covering several ecogeographical regions. A century of provenance research in many countries

---

Thorsen, B.J. and Kjær, E.D. 2007. Forest genetic diversity and climate change: economic considerations. In: Koskela, J., Buck, A. and Teissier du Cros, E., editors. Climate change and forest genetic diversity: Implications for sustainable forest management in Europe. Bioversity International, Rome, Italy. pp. 69–84.

worldwide has shown that for many species provenances are strongly differentiated, and it is therefore important to choose seed sources that are adapted to the growing conditions at a given site. In Denmark, for example, we have accumulated knowledge from a large number of provenance studies, and for many tree species (e.g. Douglas fir (*Pseudotsuga menziesii*)), selecting the wrong provenance can lead to total failure of the plantings. As a consequence, detailed recommendations for selecting seed sources exist in Denmark, as well as in many other countries, including seed transfer guidelines limiting the transfer of seed across strong environmental gradients (see e.g. Lillesø et al. 2001; Ledig 1996; Sorensen 1992; O'Neil and Yanchuk 2005a). Many large-scale tree improvement programmes cope with this genotype × environment interaction (i.e. the fact that the relative superiority of genetic material depends on the site (Matheson and Cotterill 1990)) by breeding in multiple zones (cf. Namkoong et al. 1980) with the objective to develop separate gene pools for different zones. In Sweden, this concept has been refined to cover a range of environments, including some that may develop as a result of climate change. All this work reflects the important finding that one must expect regional adaptation to be common. The implication is that climate change will be a challenge to the local genetic resources everywhere, and that the effects in terms of reduced health, growth and stability, could be substantial.

Our paper is structured in the following manner. We begin with a brief overview of the economic benefits that could be dependent on or affected, directly or indirectly, by our decisions on forest genetic resources, with climate change or not. Following that, we focus on the uncertainty concerning the implications of climate change for the health and vitality of forests, notably tree species, and point out key economic aspects of this uncertainty. We highlight the possible role of forest genetic diversity in trying to control the economic implications. Because decisions of the type considered here have such a long time horizon and tend to be irreversible, there is a lot to be said for flexible management strategies when facing the uncertainty of climate change. We devote a section to discussing and illustrating the economic value of flexibility in forest management, i.e. the embedded value of real options, and we provide simple examples of how forest genetic diversity might play an important role in preserving flexible management options in the face of climate change. We conclude with a brief section pointing out some recommendations, or perhaps more precisely some considerations, for policy-makers, decision-makers and forest managers to bear in mind when making decisions on the future status of forest genetic resources and diversity.

The economic values in question – concepts and examples

It is almost trivial to point out that we derive a large variety of goods and economic value from forests as such. Most prominent is, of course, the wood produced for a number of possible uses; improvement in the production of wood, either volume or quality, has been and remains a primary aim of forest genetic research. A number of other goods, however, also show considerable value in the market place. In Denmark, hunting leases is one such prominent good; in other places, berry and mushroom picking produce significant marketable values.

These values are all easily identified because they are traded in the marketplace. However, as pointed out by so many others before us (Elsasser 2005; Caparrós et al. 2003; Hultkrantz 1992), large parts of the value societies derive from forests are not in the form of marketed products. They are instead non-market goods or services, and their value is more difficult to assess, but in many cases easily observed and identified. This is because the non-marketed goods also comprise a number of so-called use-values, i.e. values we derive from continuously using forests or forest products, or both. An important such non-market use is the recreational use of forest areas for hiking, picnicking, etc. Other uses are more indirect, but sometimes equally important in terms of economic value. These include soil preservation and erosion control, flood and avalanche control, and filtration and protection of water resources. The value of the indirect uses represented by many environmental services can be very significant, and are part of the reason for the large value estimates found in studies trying to assess the total value of ecosystems, or even the global ecosystem (Costanza et al. 1997).

Apart from the distinction between marketed and non-marketed goods, we have already started to use the widespread distinction between use (including indirect use) and non-use values. The non-use values are usually divided into two groups: option values, and existence (or intrinsic) values. We will spend more time below on the option values, and only note here that option values arise when uncertainty exists about the future value of a resource, coupled with decisions which imply irreversible shifts in the state of the resource.

An example close to the topic of this paper is the much discussed potential of discovering new important pharmaceuticals in the biodiversity hotspots of tropical forests (Mendelsohn and Balick 1995; Simpson et al. 1996). The potential application of a given genetic resource for planting in different countries or new environments is another option value that should be considered in the face of climate change. As an example, Kjær et al. (1998) mention gum acacia (*Acacia senegal*), a very important species in the Sahel region producing many goods, including gum arabic. Trees adapted to areas with low precipitation are important, because such trees are potential seed sources for future plantings on similar dry sites in the Sahel region.

However, such gene pools are already being lost due to ongoing desertification in the region (SYGGA III 1989 *passim*). The lost potential of using such adapted seed sources will represent lost options for all people who would like to grow this species in the future. With ongoing climate change in the region, this loss of options is serious, because many areas are likely to become increasingly dry in the future.

The genetic resources of many rare, high value tropical species is another example of a resource that potentially has an important option value (Kjær 2004). The value of the species in terms of timber trade will typically be small (because they are rare and therefore seldom harvested), but the potential economic benefit of growing such high value timber species in plantations may be enormous, given that appropriate silvicultural or horticultural regimes and marketing are implemented. Many such tree species are at present endangered, and their genetic resources quickly erode even if the option value may be very large (Leakey and Newton 1994). Kjær et al. (2004) mention Thailand rosewood (*Dalbergia cochinchinensis*) as an example. It is a very valuable rosewood species that apparently can grow well in plantations. Annual increment is estimated to be 10 m^3 ha^{-1}, worth of thousands of US dollars, but the species is not planted at present, and the gene pool of the species is endangered. There are many such ‘valuable under-utilized species’ where the option value must be considered to be much larger than the value of the present timber occasionally harvested from natural forests. Loss of such species will be a loss of options.

The existence value, or intrinsic value, i.e. beyond the potential future use of trees, is also a widely acknowledged component of the value of many natural resources. This part is the hardest to grasp and measure (Dasgupta 2000; see Haab and McConnel 2002 for an excellent introduction to technical and applied aspects of environmental valuation techniques). We may think of it, for example, as the value people apply to the simple existence of forest species or entire forest habitats—even if they know they are never going to derive any direct use from them. An example from Denmark is a recent study of the willingness-to-pay for increased efforts to preserve the remaining Danish heath lands (J.B. Jacobsen, personal communication). It revealed a significant willingness-to-pay for the preservation of 25 threatened species, approximately € 1.5 per year per household for each species. The point being that most of the species in question are small and insignificant insects, lichens and mosses, which most people would never experience themselves. Yet, the respondents identified them as having a value in their own right.

Forest genetic diversity – sustaining the values of breeding and continued adaptation

Forest genetic research has primarily had as its aim to improve the use value of forests related to wood production. Examples include breeding and provenance trials for improved productivity in terms of wood volume, wood quality, frost hardiness and the like (see e.g. Burley et al. 2004; Hansen and Kjær 1999). The theoretical value of such gains has been explored to some degree (Löfgren 1988, 1990, 1992), and estimates of 'likely gain' based on different scenarios have been calculated (see e.g. Foster et al. 1995). Applied, empirical economic evaluations of genetic gains are not abundant, although examples exist (see e.g. Ahtikoski and Pulkkinen 2003; Li et al. 1999; SkogForsk 1995). More holistic analysis of the economics of 'tree gene management programmes' are rare, even if these are underpinned by legislation in EU and many OECD countries and considered to be an important public obligation in many countries worldwide (see, e.g. Graudal and Kjær 2001).

Economic analysis of tree improvement programmes as such is fairly straightforward as it needs primarily to deal with marketed goods, and the techniques for partial analysis using cost-benefit analysis are well developed. However, the actual quantification of the actual realized gain is less easy to achieve, because of the time span from the initiation of a breeding programme to harvest of the improved trees at the end of rotation. The amount of empirical data on realized gains is therefore limited, even from the improvement programmes initiated in the 1960s and 1970s. Nevertheless, one could expect more *ex ante* or simulation studies to exist in the literature. Economic analyses of genetic gains in agriculture are easier to perform and so more common, but still not as common as one would expect—given the many activities and costs associated with genetic improvement strategies (Drucker et al. 2005).

The value of forest genetic *diversity* as such is broader and difficult to handle. Examples of option values from genetic resources were given above, but they are difficult to assess in economic terms. Conservation of forest genetic resources for keeping 'options open' seems to be an important strategy, but as there are thousands of tree species with potentially endangered genetic resources and conservation is costly, choices must be—or inevitably are—made as to which ones to conserve, but it is difficult to assess if those conserved are the more valuable. This is not new, and some guidelines are provided by Graudal et al. (1997).

It is important to realize that the presence of genetic diversity is a prerequisite for future adaptation of any species because natural selection only works when genetic diversity is present. This is well known, through the Darwin-Wallace 'Survival of the fittest' theory (cf. Darwin 1902) and is even more clearly pictured in Van Valen's (1973) 'Red Queen Theory' that sees all species as being exposed to constant competition from other species. Species compete and interact continuously, and co-adaptation and development is therefore necessary for any species in order to avoid extinction over time. In the face of rapid climate change, the need for genetic diversity becomes evident because of the likely speed of the changes. The response to natural selection is proportional to the level of genetic diversity (Fisher 1958), so less diversity will cause slower response. Maintaining genetic diversity within and between populations of trees in that sense becomes a parameter for the future stability of tree populations and hence forest ecosystems. Therefore, forest genetic diversity may prove crucial for the maintenance of various forest habitats at all scales, and consequently also the values, goods and services derived from forest ecosystems. Thus, because decisions concerning forest genetic diversity may influence the long-term ecosystem stability and health, these decisions may influence the future flow of indirect use values derived from the environmental goods and services. In general, we would worry if lack of genetic diversity would put this flow under risk.

The existence or intrinsic value of biodiversity is a much analyzed and discussed issue. The question here is 'Does forest genetic diversity in itself possess such a value?' Elsasser (2005) points out that the concept makes little sense at the genetic level, but this will depend on how 'genetic level' is defined. At the species level, it is quite obvious that intrinsic values also exist for forests and trees. For example, the national tree of Brazil, Brazilwood (*Caesalpinia echinata*) is known to many Brazilians because it gave name to the country. Harvesting and reduction of the Atlantic Coastal Forest have reduced the distribution of this species dramatically, and exploitation probably still continues because of the highly valued timber. The potential loss of Brazilwood implies much more than loss of (present and future) timber production value, because the species is also the symbol for the country. The UNEP-Flora and Faunas 'Global Tree Campaign' highlights Brazilwood as one of thousands of endangered tree species (See http://www.globaltrees.org/reso_tree.asp), and that kind of focus is probably due to the extra intrinsic value affiliated to this particular species.

One can argue that intrinsic values make sense only when discussing the protection values of rare species or significant habitats—not for specific genetic variations in DNA base-pair sequences. At the same time, intrinsic values are also affiliated to genetic diversity lower than the species level. This is the case when preserving the 'native Danish sessile oak' (*Quercus petraea*) or even 'local sessile oak', although these species are by no means endemic to Denmark. The long life time of forests means that they often 'tell history', and the crooked stem form of sessile oak in western Denmark, believed partly to be due to dysgenic human selection and deforestation over centuries (and disqualifying them from production of high value timber) can therefore be of intrinsic value. The Danish Forest and Nature Agency thus recommends plantings 'of conservation value' in Danish shrub oak forests to be limited to seedlings of local origin, to support the shrub forests in maintaining their bended and twisted phenotypes. Surely, some people also attach intrinsic value to preserving 'local populations of species' even if the species as such is not endangered. The same can probably be the case for unique trees and their progenies. Planting of a small grafting from Denmark's oldest tree ('Kongegen'—expected to be 1500 years old and with declining health) was for example an event that was broadcast by the national television service (DR) in 2005.

Actually, all genetic variation—both between species and within species—is due to DNA base-pair differences. Forest gene conservation programmes target species and populations as well as the genetic processes ensuring future evolution (Guldager 1975; Erikson et al. 1993). Because forest genetic diversity may play a big role in sustaining the existence, health and stability of many forest habitats, it also sustains the existence of a much wider array of species in the ecosystems—and their existence value.

Returning from the more abstract values to ones more mundane, we should note that for a decision-maker such as a forest manager, diversity is not always an obvious good. From a traditional production point of view, a critical trade-off may exist between diversity and wood production potential. In a deterministic world, optimized production of wood in plantation forestry may imply the use of the best tree species, provenances or clones on all suitable sites, as evident from the fact that monocultures with only very few clones (genotypes) have been considered to be an optimal way to run plantation forestry when dealing with well tested planting material (Lindgren 1992). Deviating from the single species, provenance or clone perceived to be best is generally seen as a costly alternative, especially when highly improved material is available, due to values 'forgone' from not harvesting the added gain from genetic improvement. This, however, requires planting material that is carefully tested, and can be deployed by the forester according to the specific results, at least in cases where genotype × environment variation is substantial. Such detailed, fine tuned knowledge is rarely available—neither in terms of specific site × genotype matching nor in terms of knowledge on which type of product will obtain best prices in future markets. The strategy can therefore change if we bring uncertainty into the picture, and in the face of climate change, uncertainty is perhaps the dominant feature.

The uncertainty aspect

For decades, the threat of human-induced climate change has been climbing ever higher on the agenda of scientists and interest groups initially, followed by the general public, politicians, and now even decision-makers in private industry. Consequently, scientists have debated the likely effects of climate change on trees and, more broadly, on forest ecosystems (Mohren et al. 1998). Much has been accomplished and revealed about various climate-tree interactions, and yet much remains to be discovered and elucidated. In particular, the exact directions climate change will take in various regions around the world simply remain to be seen. The predicted climate change may occur quite swiftly compared to the length of a tree generation, not to mention the adaptive mechanisms of long-lived ecosystems like forests, and the overall changes within a single tree generation can be substantial (O'Neill and Yanchuk 2005; see also http://genetics.forestry.ubc.ca/cfgc/projects.html#climatechange). Nevertheless, it will appear too slow for decision-makers to have any clear idea of its direction and the consequences for forests they manage. Hence, decisions must inevitably be made in the face of great uncertainty. In economics, the issue of decision-making under risk and uncertainty has been of great interest. We will draw forward two aspects from the economics research, which can be used to illuminate important economic aspects of the management of forest genetic diversity.

The first aspect is that of risk and the disutility associated with risk for most individuals. Since the seminal work by von Morgenstern and Morgenstern (1953), it has been recognized that because people tend to be risk averse, risky returns are less desirable than certain returns, *ceteris paribus*. Climate change implies a greater uncertainty concerning the future returns to any forest investments, because it is unknown how climate change will affect the growth, health and stability of forest stands.

Forest owners have the option to diversify against risk in their forest management, and a forest's genetic diversity could be one vehicle to secure such diversification—also with respect to climate change. If we expect different species, provenances or clones to react differently, at least to some extent, to climate changes, then we can reduce the risk by increasing our use of species, provenances or clones, as appropriate and relevant. An example from Denmark is Norway spruce (*Picea abies*) which is an exotic species in the Danish forestry sector and which is expected to suffer impaired health if winters become milder. Current thinking is that such impairment in health can be expected and would probably be quite serious for the long-term health of the species under Danish conditions, and therefore undermine any economic justification for the species. In contrast, Douglas fir is an exotic species that at present often suffers from climatic damage. One can therefore expect this species to gain from milder climates, whereas colder climates could be quite problematic. The future development of the climate in Denmark is unknown, although we currently expect the climate to warm. By having more tree species with varying climatic preferences in the forests, we reduce risk. The same situation applies in choosing provenances. Field trials in Denmark have shown that it is not the same provenances of pedunculate oak (*Quercus robur*) that are expected to be the best performers on protected sites compared with more exposed sites. The forest owner must therefore choose a provenance depending on the growing conditions as they anticipate them to be for the next 100 years. For improved clones of Sitka spruce (*Picea sitchensis)* or other highly selected clones, the same will be the case. At the time of establishment, the forest owner can choose clones that perform well on milder sites, or clones that perform best at more exposed sites. Without knowing what climate change will bring, picking different clones with different preferences will reduce the risk.

In most economic decisions, diversifying to reduce risk in returns comes at a cost in terms of lower expected returns. This may also be the case for the forest owner, but since the risk in this case may not be well defined or known for the various choices available, it is perhaps impossible to say which choice of species is likely to reduce the expected returns. Apparently, diversification against climate-change-related risk may not differ much, in principle, from diversifying against roundwood price variations through mixed-species forestry, except that the risk is better described and known in the case of roundwood prices. The forest owner may be able to achieve the risk reduction by having, say, *n* species (or provenances or genotypes) growing in *n* different homogenous stands in his forest. Some stands will cope and provide the forest owner with economic returns, whereas other stands may be less fortunate, develop poorly and perhaps even collapse. On average, the forest owner will in principle be just as well off with *n* pure stands as they would have been had they used *n* species in, say, 3*n* stands—i.e. smaller stands, but still monocultures. In fact, if there are returns to scale in establishing the stands, they might favour larger stands and hence the *n*-stand version.

For society, however, this choice of how to implement risk diversification may not be trivial, even if society as such is less concerned with the risk in returns of the single forest owner than they themself might be. The problem for society is that if climate change implies the risk of severe stability and health problems, and potential collapse of larger forest areas, then these areas may also stop producing a number of the non-marketed environmental services of great value to society. An example from Denmark is the problem of serious nutrient leaching following large scale windthrows of Norway spruce. The larger the area in question, the more likely negative impacts will be. Hence, society may prefer the forest owner to implement diversification in a much more elaborate way than might be considered optimal by the forest owner. The reason is that the social value function of forests includes a number of elements likely to be of much less importance to the forest owner than to society.

An elaborated kind of risk diversification in plantation forestry could be random planting of several species in each reforestation site—resulting in a high degree of inter-specific forest genetic diversity in the stand. This kind of mixed-species forestry, however, is often impossible for silvicultural reasons. Very different species tend to develop very differently in their early stages, and often such initially diverse stands quickly grow into more or less monocultural ones through inter-species competition in the young stand—in which case little or nothing has been achieved by the high cost in terms of management and production lost. A different approach would be to plant stands of one species per stand while ensuring large levels of genetic diversity in each stand. Kjær et al. (1995) suggested deploying seed sources for long rotation species that maintain an effective population number of 20 or above. Assuming that different genotypes fit in different climates (genotype × environmental interaction), such an approach will reduce risk in returns, compared with selecting a more narrow genetic basis for the planting material, and would ensure that sufficient genetic variation is present for selection to have an effect. A low-risk strategy could further be supported by selecting genotypes that perform well over a suite of different sites (little genotype × environment interaction). Use of genetically diverse, unimproved provenances might be an easier alternative, but if improved planting material is available, such a strategy will imply a cost penalty, i.e. 'values forgone' in terms of productivity by not using sources based on selected trees. Different species can be planted at different sites matching soil conditions and diversifying the species grown.

In continuous-cover forestry, where natural regeneration is the norm, the handling of climate change risk through decisions concerning forest genetic diversity could imply the introduction of exogenous genetic material to the forest. In that case, the considerations will be much as described above.

What we have discussed so far is the potential for forest genetic diversity to reduce risk in a traditional portfolio selection way (Markowitz 1952). This way of coping with climate change risk is likely to be important at the individual or firm level. In this specific case, we argue that the way diversification is undertaken in forest management is likely to also have great influence on the expected societal value of forests.

It is implicitly assumed above that once we have decided upon some specific forest genetic diversity in or between our new forest stands, we will wait for climate change to unfold itself and see which stands fail and which stands succeed. The planning mode is best described as anticipatory. The forest owner would make a loss with the stands that fail (as would society), relative to those that succeed. With this approach, the next decision point for the forest owner would be to salvage the poorly performing stands (to reduce the loss of alternative production forgone) once they can recognize them, and replace them with new trees of different and perhaps better genotypes. The initial decision on forest genetic diversity is an irreversible decision in an economic sense because the initial costs of establishing the forest and the production lost because of poorly performing types cannot be recovered.

When decisions are irreversible and there is uncertainty about the future value of some decision alternatives, delaying the irreversible decision includes an option value. This is the second important economic aspect we wish to discuss in relation to forest genetic diversity. Having the option to delay important irreversible decisions requires that we are able to design and implement flexible forest management strategies. Flexible strategies ‘buy time’. We will discuss these possibilities in the next section.

The value of flexible strategies

As we briefly pointed out in the second section, one component of the value of any natural resource is the option value. This value arises when there is uncertainty about the future (use-)value of a natural resource and decisions concerning its use are irreversible. The option value was first identified by Arrow and Fisher (1974) and Henry (1974) in the cases of irreversible development of a nature reserve, whose future value is known to be uncertain. They showed that conserving the nature reserve for some time period implies an option value in addition to the current (use-)value of the reserve. This option value arises because conservation over a period embeds the option to see if the value of the nature reserve increases or decreases, and then make a new decision based on this information. If it increases further, conservation may still be optimal, but if it decreases too much, it may be optimal to develop the nature reserve. This does not imply that conservation is always optimal but it does imply that for development to be optimal the value should exceed not only the use value of conservation but also the option value of developing the reserve later, should it prove optimal at that stage. This kind of adaptive decision-making was later also described in managerial economics as the ‘value of waiting’ (McDonald and Siegel 1986) and it has been developed into the field of real options analysis (Dixit and Pindyck 1994).

We will briefly discuss how flexible forest management strategies with respect to forest genetic diversity may incorporate such option values related to the uncertainty caused by climate change. For example, if we can defer the decision of which species, provenance or clone we want to use as a dominating and primary wood producer on a piece of land, we may learn more about the evolution of climate change and the effects on the various kinds of tree. The simplest and crudest way of doing that is, of course, to simply plant a new stand. This, however, may be impossible in the case of reforestation of forest land, and is certainly likely to be too costly if the land cannot be used for other purposes while waiting. In the case of afforestation of agricultural land, it may be a reasonable option (Thorsen 1999).

Another approach to introduce flexibility into the forest management plan is to establish a stand with two or more species, provenances, clones or whatever is relevant, and then observe their evolution as they grow and climate change evolves and affects their growth. Next, the forest manager may enter the young or medium-aged stand and through selective thinning remove the trees, provenances or species that turn out to be ill-fitted to the climate change and allow the better fitted to make use of the space liberated. Of course, such an approach requires rotations of some extended time span or climate changes of some speed and magnitude to result in significant option values. See Jacobsen and Thorsen (2003) for a deeper analysis of such a case. It would probably be right to argue that such species or genotype mixes will sometimes be impossible for silvicultural reasons, or because they are costly in terms of higher establishment and management costs. The gains in option values should exceed these additional costs—otherwise the approach is not advisable. Note, however, that what has been described here is in fact similar behaviour to that exhibited in many forest management plans in which forest stands are established with a stem number much larger than that aimed for in the final mature stand. The superfluous trees are subsequently removed through selective thinning, at a time when the forest manager is able to take advantage of new knowledge (i.e. which trees turned out to have the better genetic material or to be planted at the better microsite).

Climate change effects will occur only after some time. Societies must therefore support strategies that allow for an adaptive strategy over such long time horizons. For plantation forestry, it is important that forest genetic diversity is not reduced through widespread deployment of genetically narrow seed sources. Because we have imperfect knowledge of which species, provenances or genotypes will do well in the future, we need to have a variety of these growing under a variety of conditions to gain new knowledge on which to base future decisions. In continuous-cover forestry, where natural regeneration is dominating, other challenges may appear: what if the genetic material in these forests is already quite narrow? Will they be able to adapt swiftly enough to survive under the future pressure of climate change? Or should forest management also seek to introduce increased variation through genetic enrichment plantings? Close-to-nature forestry increases the role of the forest owner in terms of genetic management because trees are in general based on natural seed fall and less often planted from seed sources outside the forest. In Denmark, large-scale planting of ash trees (*Fraxinus excelsior*) from a 2-clonal seed orchard has taken place during the last four decades. Genetic studies of the consequences of this are in progress, but it may be that, at least in some close-to-nature-driven forests, there is a need to consider introducing planting material from more diverse seed sources in order to mitigate any effect of inbreeding and to speed up adaptation. Naturally regenerated forest also presents challenges from a genetic perspective (see e.g. Namkoong 1999) and these must also be considered when planning for sound genetic management of forests. In any case, forest genetic research on species with long rotation cycles should probably not focus only on bringing about increasingly specialized clones to be deployed at very specific planting sites. Rather, tree improvement and deployment strategies for long-rotation species should ensure that genetic variation is mobilized and maintained in forests not only to facilitate response and adaptation, but also to buy time and flexibility for the forest owner. This is not about abandoning forest genetic research and doing nothing in the field—to the contrary, it requires development and implementation of genetically sound forest management.

Recommendations

With little interdisciplinary research in the field of forest genetics and economics, and inadequate knowledge on the future effects of climate change, we have relied on general economic principles to address some of the issues in this paper. Several recommendations follow from the above discussion:

We know too little about the socio-economic value of forest genetic improvement and genetic management programmes in a wider perspective than simple increase in wood production. It is recommendable that policy-makers close this knowledge gap by requiring more applied societal cost-benefit analyses to be undertaken.

As a consequence of little knowledge on the global socio-economic value of forest genetic improvement, we also know too little about the value of forest genetic diversity. It is therefore recommended to develop economic theory and tools to assess this. This research would need to address the aspects of uncertainty, as well as potential gains and losses, from increasing genetic diversity. Such analysis can draw on available knowledge on genotype × environment interaction as can be observed in international species, provenance, progeny and clonal trials. International cooperation in this field should therefore be encouraged.

It is advisable to take risk considerations into account before pursuing forest genetic management strategies that are vulnerable to failures of specific genotypes. Diversification through increased forest genetic diversity could be a recommendable risk-reduction strategy for the forest owner.

The social value of forests might be better protected by risk-diversification strategies, including strategies based on the proactive use of genetic diversity in forest plantings. It is therefore recommended—on a case-by-case basis—to examine to what extent private and social values of forests are optimized at the same or different levels of genetic diversity.

It is recommended to develop different policy instruments designed to provide incentives for private forest owners to choose optimal diversification strategies from the point of view of society in situations where this differs from the private optimum.

Option values are potentially very big for forest genetic resources, especially in the face of climate change. Forest management strategies and decisions on forest genetic diversity that provide flexibility with respect to adaptation strategies for climate change should be encouraged as they may increase expected both societal and private value of the forest.

Acknowledgement

We would like to thank Lars Graudal for valuable comments to the earlier version of this paper.

References

Ahtikoski, A. & Pulkkinen, P. 2003. Cost-benefit analysis of using orchard or stand seed in Scots pine sowing, the case of northern Finland. *New Forests*, 26: 247–262.

Arrow, K.J. & Fisher, A.C. 1974. Environmental preservation, uncertainty and irreversibility. *Quarterly Journal of Economics*, 88: 312–319.

Burley, J., Evans, J. & Youngquist, J.A. (editors). 2004. *Encylopedia of Forest Science*. Elsevier Academic Press, Amsterdam, The Netherlands.

Caparrós, A., Campos, P. & Montero, G. 2003. An operative framework for total Hicksian income measurement: application to a multiple-use forest. *Environmental and Resource Economics*, 26: 173–198.

Costanza, R.R., d'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B. et al. 1997. The value of the world's ecosystem services and natural capital. *Nature*, 387: 253–269.

Darwin, C. 1902. Origin of species by means of natural selection or the preservation of favoured races in the struggle for life. 4th edition. John Murray, Albemarle Street, London, UK.

Dasgupta, P. 2000. Economic value of biodiversity: overview. pp. 291–305, *in:* S. Levin (editor). *Encyclopedia of Biodiversity.* Academic Press, New York NY, USA.

Dixit, A. & Pindyck, R.S. 1994. *Investment under uncertainty*. Princeton University Press, Princeton NJ, USA.

Drucker, A.G., Smale, M. & Zambrano, P. 2005. Valuation and sustainable management of crop and livestock biodiversity: a review of applied economics literature. A review paper prepared for the System-wide Genetic Resources Programme of CGIAR. 70 p.

Eriksson, G., Namkoong, G. & Roberds, J.H. 1993. Dynamic gene conservation for uncertain futures. *Forest Ecology and Management*, 62: 15–37.

Elsasser, P. 2005. Economic methodologies for valuing forest genetic resources. pp. 89–109, *in:* Th. Geburek and J. Turok (editors). *Conservation and Management of Forest Genetic Resources in Europe.* Arbora Publishers, Zvolen, Slovakia.

Fisher, R.A. 1958. The Genetical Theory of Natural Selection. Dover Publications. 291 p.

Foster, G.S., Jones, N. & Kjær, E.D. 1995. Economics of tree improvement in development projects in the tropics. pp. 95–128, *in:* S. Shen and A. Contreras-Hermosilla (editors). *Environmental & economic issues in forestry: Selected case studies in Asia.* World Bank Technical Paper No. 281. The World Bank, Washington DC, USA.

Graudal. L., Kjær, E.D., Thomsen, A. & Larsen, A.B. 1997. Planning national programmes for conservation of forest genetic resources. Danida Forest Seed Centre Series of Technical Notes, No. 48. Danida Forest Seed Centre, Humlebæk, Denmark.

Graudal, L. & Kjær, E.D. 2001. Can national tree seed programmes generate economical, social and/or environmental benefits that cover their costs? pp. 15–28, *in:* O. Eyog-Matg, B. Kigomo and J.-M. Boffa (editors). *Recent research and development in Forest Genetic Resources.* Proceedings of the Training Workshop on the Conservation and Sustainable Use of Forest Genetic Resources in Eastern and Southern Africa, Nairobi, Kenya, 6–11 December 1999. IPGRI, Nairobi, Kenya.

Guldager, P. 1975. *Ex situ* conservation stands in the tropics. pp. 85–92, *in: The methodology of conservation of forest genetic resources*. Report on a pilot study. FAO, Rome, Italy.

Haab, T.C. & McConnell, K.E. 2002. Valuing Environmental and Natural Resources. The econometrics of non-market valuation. Edward Elgar, Cheltenham, UK. 326 p.

Hansen, C.P. & Kjaer, E.D. 1999. Appropriate planting material in tree plantings: Opportunities and critical factors. pp. 51–73, *in:* S. Barros and M.I. Campodónico (editors). Proceedings of the *International Expert Meeting on the Role of Planted Forests for Sustainable Forest Development.* Santiago, Chile, 6–10 April 1999. Corporación Nacional Forestal, Chile.

Henry, C. 1974. Option values in the economics of irreplaceable assets. *Review of Economic Studies*, 41: 89–104.

Hultkrantz, L. 1992: National account of timber and forest environmental services in Sweden. *Environmental and Resource Economics*, 2: 283–305.

Jacobsen, J.B. & Thorsen, B.J. 2003. A Danish example of optimal thinning strategies in mixed-species forest under changing growth conditions caused by climate change. *Forest Ecology and Management*, 180: 375–388.

Kjær, E.D. 2004. Tropical hardwoods breeding and genetic resources. pp. 1527–1532, *in:* J. Burley, J.J. Evans and J.A. Youngquist (editors). *Encylopedia of Forest Science*. Elsevier, Academic Press, Amsterdam, The Netherlands.

Kjær, E., Amaral, W., Yanchuk, A. & Graudal, L. 2004. Strategies for conservation of forest genetic resources. pp. 4–24, *in: Forest Genetic Resources: Conservation and management*. *Vol. 1: Overview, concepts and some systematic approaches*. IPGRI, Rome, Italy.

Kjær, E.D., Graudal L. & Hansen, C.P. 1998. Conservation of forest genetic resources for improved tree plantings in the tropics. pp. 56–72, *in:* D.J. Macintosh and T. Nielsen (editors). *Biodiversity and Development*. Proceedings from a conference held at Eigveds Pakhus, Copenhagen. CenTER, University of Aarhus. Reprint available at http://www.sl.kvl.dk/upload/1.pdf

Kjær, E.D., Graudal, L. & Myrthue, Å.K. 1995. Vurdering af genetisk variation i klonfrøplantager – belyst med et eksempel fra sitkagran [The required number of clones in seed orchards]. *Dansk Skovbrugs Tidsskrift*, 80: 57–77.

Leakey, R.R.B. & Newton, A.C. (editors). 1994. *Tropical trees: the potential for domestication and the rebuilding of forest resources.* Proceedings of a Conference held at Heriot-Watt University, Edinburgh, 23–28 August 1992. HMSO, London. UK.

Ledig, F.T. 1996. Management of genetic resources by controlling seed movement. *In* D.L. Rodgers and F.T. Ledig (editors). *The Status of Temperate North American Forest Genetic Resources*. Report No. 16. Genetic Resources Program, Division of Agriculture and Natural Resources, University of California, Davis, California, USA.

Li, B., McKeand, S. Weir, R. 1999. Tree improvement and sustainable forestry – impact of two cycles of loblolly pine breeding in the USA. *Forest Genetics*, 6(4): 229–240.

Lillesø, J-P.B., Dhakal, L.P., Shrestha, T.B., Tamrakar, P.R., Shrestha, R., Nayaju, R.P. & Kjær E.D. 2001. Planting zones in Nepal. TISC Tech. Paper 103. DFSC Case Study no.

1. HMG/Danida NARMSAP, Katmandu, Nepal, & Danida Forest Seed Centre, DK-3050 Humlebæk, Denmark.

Lindgren, D. 1992. The population biology of clonal deployment. *In:* M.R. Ahuja and W.J. Libby (editors). *Clonal forestry I: Genetics and biotechnology.* Springer Verlag, Berlin, Germany.

Löfgren, K.-G. 1988. On the economic value of genetic progress in forestry. *Forest Science*, 34: 708–723.

Löfgren, K.-G. 1990. The measurement of welfare gains from genetic progress in forestry: General equilibrium and disequilibrium results. *Natural Resource Modelling*, 4: 447–494.

Löfgren, K.-G. 1992. A note on the welfare gains from genetic progress in forestry: What can the market tell us? *Forest Science*, 38: 479–483.

Markowitz, H. 1952. Portfolio selection. *Journal of Finance*, 7: 77–91.

Matheson, A.C. & Cotterill, P.P. 1990. Utility of genotype × environment interactions. *Forest Ecology and Management*, 30: 159–174.

McDonald, R. & Siegel, D. 1986. The value of waiting to invest. *Quarterly Journal of Economics*, 101: 707–728.

Mendelsohn, R. & Balick, M.J. 1995. The value of undiscovered pharmaceuticals in tropical forests. *Economic Botany*, 49: 223–228.

Mohren, G.M.J., Kramer, K. & Sabaté, S. (editors). 1998. *Impacts of global change on tree physiology and forest ecosystems.* Proceedings of the International Conference on Impacts of Global Change on Tree Physiology and Forest Ecosystems, Wageningen, The Netherlands, 26–29 November 1996. Kluwer Academic Publishers, Dordecht, The Netherlands. Published as *Forestry Sciences*, Vol. 52. 388 p.

von Morgenstern, J. & O. Morgenstern 1953. *Theory of Games and Economic Behaviour.* 2nd edition, Princeton University Press, Princeton, New Jersey.

Namkoong, G. 1999. Plantations versus naturally regenerated forests: risks and stability in using bred, cloned, or biotech products. pp. 147–154, *in:* C. Mátyás (editor). *Forest Genetics and Sustainability.* Forestry Sciences, Vol. 63. Kluwer Academic Publishers, Dordecht, The Netherlands.

Namkoong, G., Barnes, R.D. & Burley, J. 1980. A philosophy of breeding strategy for tropical trees. Tropical Forestry Papers No. 16. Commonwealth Forestry Institute, UK.

Namkoong, G., Boyle, T., Gregorius, H.-R., Joly, H., Savolainen, O., Ratnam, W. & Young, A. 1996. Testing criteria and indicators for assessing the sustainability of forest management: Genetic criteria and indicators. *CIFOR Working Paper,* No. 10.

O'Neill, G. & Yanchuk, A. 2005a. A Primer on Seed Transfer for Compliance and Enforcement in B.C. Research Branch, BC MoF. See: http://www.for.gov.bc.ca/hre/forgen/seedtransfer/SeedTransferPrimer20.pdf Last accessed 12 Nov. 2006.

Simpson, R.D., Sedjo, R.A. & Reid, J.W. 1996. Valuing biodiversity for use in pharmaceutical research. *Journal of Political Economy*, 104: 163–185.

SkogForsk. 1995. Strategi för fremtida skogsträförädling och fremställing af förödlat skogsodlingsmaterial i Sverige. SkogForsk, Uppsala, Sweden. 258 p.

Sorensen, F.C. 1992. Genetic variation and seed transfer guidelines for Lodgepole pine in central Oregon. Research Paper PNW-RP-453. Forest Service, Pacific Northwest Research Station, USDA Portland OR, USA. 30 p.

SYGGA III. 1989. SYGGA III: Troisième symposium sous regional sur le gommier et la gomme arabique. Saint-Louis, Sénégal, 25–28 October 1988. Institut Senegalais de Researches Agricoles, Dakar, Senegal.

Thorsen, B.J. 1999. Afforestation as a real option: Some policy implications. *Forest Science*, 45: 171–178.

Van Valen, L. 1973. A new evolutionary law. *Evolutionary Theory*, 1: 1–30.

FINLAND'S NATIONAL STRATEGY FOR ADAPTATION TO CLIMATE CHANGE

Mari Rusanen[1] *and Heikki Granholm*[2]

1. Finnish Forest Research Institute, Vantaa, Finland
2. Ministry of Agriculture and Forestry, Helsinki, Finland

Introduction

Finland's National Strategy for Adaptation to Climate Change was prepared by an inter-ministerial task force coordinated by the Ministry of Agriculture and Forestry, in response to a request by the Parliament. The strategy gives a detailed account of the impacts of climate change in different sectors and presents measures to be taken until 2080. The objective of the Adaptation Strategy is to reinforce and increase the capacity of society to adapt to climate change.

Management of natural resources, and forestry in particular, is one of the key sectors to be influenced by climate change. Genetic diversity ensures the success of species in environments that are subject to change. Ultimately, the genetic diversity of trees forms the basis of forestry and related forest industries. Therefore, genetic aspects should be integrated in the forest policy through the National Forest Programme.

In this article we summarize the contents and the preparation process of the National Strategy for Adaptation to Climate Change, with emphasis on the links to forest genetic diversity. In addition, the National Programme for Forest Genetic Resource Management is briefly described.

Preparation of the National Adaptation Strategy

The first National Climate Strategy, in 2001, emphasized mitigation of the negative effects of climate change. However, it soon became obvious that in addition to mitigation there was also a clear need to identify possible ways to adapt to the change. The current climate scenarios show no significant downturn in the global warming trend for decades into the future, regardless of the mitigation measures taken in different scenarios. The need to identify adaptation measures to climate change was identified in the Parliament and the preparation of the National Strategy for Adaptation to Climate Change began at the end of 2003, through a broad-based working group (Anonymous 2005).

Rusanen, M. and Granholm, H. 2007. Finland's National Strategy for Adaptation to Climate Change. In: Koskela, J., Buck, A. and Teissier du Cros, E., editors. Climate change and forest genetic diversity: Implications for sustainable forest management in Europe. Bioversity International, Rome, Italy. pp. 85–93.

The objective of the Adaptation Strategy is to reinforce and increase the capacity of society to adapt to climate change. Adaptation to climate change refers to the capacity of nature and humans to adjust to the environmental changes, either through minimizing the adverse impacts or by taking advantage of the benefits.

The Ministry of Agriculture and Forestry coordinated the actual work, while representatives from the Ministry of Transport and Communications, Ministry of Trade and Industry, Ministry of Social Affairs and Health, Ministry of the Environment, Ministry for Foreign Affairs, Finnish Meteorological Institute and Finnish Environment Institute took part in the preparation process. The work used as its reference a set of existing scenarios for future climate in Finland, and the Government Institute for Economic Research prepared long-term economic scenarios. Several top Finnish scientists in the field of climate change and its impacts, other experts and representatives of various sectors were also involved in the work. The draft strategy was circulated widely for comments, and Finnish stakeholders and citizens had the opportunity to offer their comments on the Internet. The comments were duly taken into account in finalizing the strategy.

The strategy includes all the key sectors of society, namely natural resources (agriculture and food production, forestry, fisheries, reindeer husbandry, game management and water resources), biological diversity, industry, energy, transportation and communication, land use and construction, health, tourism and insurance.

Predicted climate change in Finland and its impacts

The third assessment report of the Intergovernmental Panel on Climate Change (IPCC) states that Earth's average temperature is expected to rise by 1.4 to 5.8°C between 1990 and 2100, and the increase in Finland will be at least the same rate. Globally, sea level is estimated to rise by 0.09-0.88 m, but in Finland the expected rise is less because land uplift relative to mean sea level still continues. Globally, precipitation is expected to increase, but there will be considerable variation in the magnitude of the change between different regions. Over Finland, precipitation is expected to increase, especially during winter. Climate change is expected to increase the occurrence of extreme weather events. Estimates concerning increased storminess in Finland involve a great deal of uncertainty, but winter storms and thunderstorms may occur more frequently. All in all, the increases in the frequency or magnitude of extreme weather events can be expected to have more significant negative impacts on different sectors of the Finnish economy and the functioning of society in comparison with gradual and sometimes beneficial average changes.

The Adaptation Strategy gives a detailed account of the impacts of climate change in different sectors and presents measures to be taken until 2080. The main elements of the strategy are also included in the National Energy and Climate Strategy, which focuses on measures to be launched during the next 5 to 10 years. Priorities identified for increasing adaptation capacities include:

- mainstreaming climate change impacts and adaptation into sectoral policies;
- addressing long-term investments;
- coping with extreme weather events;
- improving observation systems;
- strengthening the research and development base; and
- enhancing international cooperation.

The main negative impacts on the forest sector will probably be connected with reduction in ground frost and an increase in various pathogens, whereas the most important advantages will be the increased growth and better seed yields of forest trees. Climate change will also change the relative proportions of species, as broadleaves—mainly birch (*Betula* spp.)—will benefit from the change. However, the development of stand composition will also be steered by forest management, and Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) will continue to thrive in southern Finland. A summary of the possible impacts is presented in Table 1.

Cross-sectoral adaptation measures in 2005–2015

A major target of the Adaptation Strategy is that a detailed assessment of the impacts of climate change be incorporated into the regular planning, implementation and monitoring processes of the different sectors. All sectors should enhance their use of research results and increase cooperation and coordination with different administrative sectors, institutes and other actors. In its first stage, the mainstreaming of climate change impacts and adaptation calls for the development of research and assessment methods. At the same time, relevant aspects of climate change may be incorporated into environmental planning, environmental impact assessment and risk management. There is an obvious need to strengthen policy-relevant research and development. In addition to general research on future climate, processes of climate change adaptation and the costs of impacts and adaptation, sector-specific studies are also needed. A five-year research programme on adaptation was launched in Finland in 2006. It aims to reinforce adaptive capacity and help build a sufficient knowledge base to support practical adaptation measures. The programme was prepared jointly by different ministries during 2005, and its main objective is to produce information and methods that can be applied in practice. The information obtained by the new research programme will be used to further specify necessary adaptation measures in different sectors. The

Table 1. Main impacts of climate change on the forest sector in Finland.

Disadvantages	**Direction unclear or both**	**Advantageous**
Nutrient leaching	The proportions of tree species will change	Increases in carbon dioxide concentration, temperature and precipitation will add to the productivity of the boreal belt
Wind damage and weakened anchoring of trees to the soil as ground frost declines	The tree line will move farther north	
The combined impacts of air pollutants (ozone) and UV radiation on ecosystems will be intensified		Felling opportunities will increase
Pests and forest pathogens		Plants will have access to more nutrients
Potentially reduced ground frost will make forest harvesting more difficult		The seed yield of trees will improve and natural regeneration in poor site types in Northern Finland will become easier
Longer thaw period in spring will impose additional demands on machine capacity and wood storage		
The wood quality of conifers may suffer		

information will also be used for the revision of the Adaptation Strategy.

Specific adaptation measures in forestry in 2005–2015

The National Adaptation Strategy identified the following sector-specific adaptation measures as important priorities for the forest sector:

- Incorporation of climate change into the planning of national forest policy.
- Development of forest management, wood harvesting and prevention of forest damages adapted to the climate change.
- Incorporation of the assessment and monitoring of the impacts of climate change into projects and programmes concerning the protection and management of biological diversity.
- Evaluation of the coverage of nature conservation in changing climate conditions.
- Development of the management of economic risks and mitigating the economic risk to insurance institutions through bonds and derivatives.

- Development of insurance systems against damage caused by extreme weather events.
- Clarification of the division of tasks and responsibilities between public and private insurance.

Among other measures, the use of forest genetic resources for adaptation to climate change has been mentioned in the strategy, stating that genetic diversity in the common tree species is extensive enough to make adaptation possible. Forest management methods can be used to shorten the time needed for nature's own adaptation measures. In forest regeneration, it is important to use suitable tree species of appropriate origin that can adapt to the changing climatic conditions. Preference in artificial regeneration should be given to provenances originating somewhat south of the place of cultivation. However, forest reproductive material should be moved carefully, with proper attention to tree survival through the seedling stage, during which the climate might not yet have warmed as much as in the subsequent stages of growth. Scots pine of Central European origin cannot be successfully moved to Finland because the provenances have adapted to different photoperiods. Trees of southern origin will also be vulnerable to Scleroderris canker caused by the fungus *Gremmeniella abietina* because they are in a susceptible phenological state when they become exposed.

The testing of tree species' origins must be carried out across the boundaries of the current breeding zones, and different targets for improvement can be established within the breeding zones. Properties to be improved in the future include, among others, adaptation to increased mean temperature and an extended growing season, as well as resistance to pests and diseases. The most significant method of utilizing the results of tree improvement in practical forestry is to establish seed orchards and promote them as preferred sources of seed. In order to prepare for climate change, it is important to know as precisely as possible the genetic origin of the artificial regeneration material. This will make it possible to determine the potential use area for a certain batch of seed, taking into consideration climate change. In this respect, seed from seed orchards is much better and safer than seed collected from forests.

Implementation, monitoring and revision

The National Strategy for Adaptation to Climate Change is being implemented between 2005 and 2015, primarily through sector-specific programmes and actions. Citizens are also likely to respond to the changes through their own voluntary actions. The implementation of the Adaptation Strategy will be evaluated within 6 to 8 years, by which time research and dissemination activities in different sectors should have produced new and more detailed information and views on climate change, its impacts, and the need and means for adaptation. It is also likely that there will be more information available on mitigation of greenhouse gas emissions at a global scale, as well as a clearer idea of the pace at which climate change is progressing.

Management of genetic resources of forest trees

The management of genetic diversity has been given high priority in Finland. A National Plant Genetic Resources Programme, covering plant genetic resources in agriculture, horticulture and forestry, was launched by the Ministry of Agriculture and Forestry to promote the conservation and sustainable use of genetic resources (Anonymous 2001). The implementation of the programme for agriculture and forestry is monitored by an advisory board, which acts as a link between various ministries, participates in the preparation of legislation concerning plant genetic resources and deals with the Nordic and international issues related to plant genetic resources. The Finnish Forest Research Institute, which is responsible for all forest tree breeding in Finland, is also responsible for the conservation of forest genetic resources.

The purpose of conserving forest genetic resources is to maintain hereditary variation in species and local populations far into the future so that their viability and adaptability would be sufficient to cope with changing environmental conditions. The appropriate methods for genetic conservation depend on ecological and biological variables, the most important ones being reproductive biology, colonization habits and competitive ability of a given species. In the strategy for forest genetic resource management, indigenous tree species have been classified roughly into two groups. The first group includes wind-pollinated species bearing light seed and having more-or-less continuous distribution, and the second group contains rare species that have limited gene flow because of fragmented distribution, requirement for insect pollination or short-distance seed dispersal. The main conservation method for the first group is *in situ* gene reserve forests, whereas for the second group, *ex situ* collections are the predominant gene conservation method. The strategy is described in detail in Rusanen et al. (2004).

In situ conservation normally requires that a representative area of undisturbed natural forest or a naturally regenerated commercial forest is set aside as a gene reserve forest. Currently (late 2006) there are altogether 42 gene reserve forests in Finland, and their combined area is about 7000 ha. As these forest stands are spread over different climatic zones, they include a large range of adaptive traits. Gene reserves are mostly selected for conservation of Scots pine, Norway spruce, silver birch (*Betula pendula*) and pubescent birch (*Betula pubescens*).

The basic requirements for a gene reserve forest are that it is of local origin and preferably has been naturally regenerated. Normally, a stand is selected as a reserve for a certain tree species, but a mix of other species is allowed. The area should also comprise several age classes of the target tree species. Gene reserve forests of wind-pollinated tree species should be large enough for sufficient pollination to be secured within the forest. The general objective is that a gene reserve forest should cover an area of at least 100 ha, but initially the area can be smaller if it can be expanded later using a seed source from the same stand. Since pure birch or Norway spruce forests are seldom large enough in southern Finland, suitable mixed stands consisting of two or three tree species have also been selected as joint gene reserves. For noble hardwoods, which are rare and only grow in small patches, strips or mixed stands in Finland, smaller areas covering only a few hectares are accepted as gene reserve forests.

Protected areas and habitats that are mentioned in the Nature Conservation Act may support genetic conservation in certain areas for some species. However, the principal objective of national parks and nature reserves is to preserve forest ecosystems and they have limitations for genetic conservation purposes. In many cases, the protection prevents forest management that would be needed to promote regeneration, and often the regulations of the protected areas also restrict the utilization of genetic resources. The objectives of ecosystem and gene conservation are more consistent in the natural forests rich in noble hardwoods or black alder (*Alnus glutinosa*) and juniper (*Juniperus communis*) meadows. For these protected habitats, the Nature Conservation Act allows treatment that does not endanger the special features (e.g. noble hardwoods) of the areas.

Ex situ conservation is appropriate when the tree species is rare and grows only in small patches, when the site is threatened or when regeneration is uncertain. The principal method for the *ex situ* conservation of forest tree species is the establishment of tree collections. The individual trees are either propagated by grafting and the grafts moved to clone collections, or seed is collected from the original trees and so-called family collections are established with seedlings. In the family collections, several seedlings of one family are planted near each other, and thinning is carried out so that only one tree, representing the family is finally left growing. The families representing the same forest are distributed within the collection so that they can also be used for seed production after thinning. One of the benefits of the tree collections is that some selection takes place within them. They produce well-adapted and genetically variable seed that can be used in forest regeneration or in landscaping.

The *ex situ* collections have been established mainly for noble hardwoods, namely Norway maple (*Acer platanoides*), common ash (*Fraxinus excelsior*), pedunculate oak (*Quercus robur*), small-leaved lime (*Tilia cordata*), mountain elm (*Ulmus glabra*) and European white elm (*Ulmus laevis*). Material for the collections has been gathered from several (20 to 90) forest stands, usually from 5 to 10 trees in each stand, so that the whole distribution area of the tree species is covered. The number of stands and trees per stand varies among species because the availability of seeds has directed the practical work. The trees selected for genetic resource collections are not necessarily the best trees from the point of view of forestry and the economy as the aim has been to collect a random sample of the existing genetic variation.

Conclusions

The National Strategy for Adaptation to Climate Change is quite comprehensive and covers all the key sectors of society. This was possible because the Parliament gave a clear political mandate and requested an adaptation strategy to complement the earlier mitigation strategy. Scientific information together with expert assessments and judgements formed the basis for identifying key actors and priority measures. Broad participation and transparency were ensured not only through various working groups and political meetings but also by making it possible for the public to provide feedback through the Internet.

Although the strategy has been drafted with a long-term perspective, it identifies several key activities, the implementation of which can start immediately. However, further research is needed, and when more information becomes available, the actions and priorities will be reviewed accordingly. The sectoral strategies will be monitored through a follow-up process and the complete Adaptation Strategy will be reviewed within 6 to 8 years.

The linkage between the Forest Genetic Resource Management Programme and the objectives of the Adaptation Strategy is obvious, but since the latter covers broad societal needs, there is very little emphasis on genetic aspects. A natural instrument to connect management of forest genetic resources with adaptation to climate change would be the National Forest Programme. The National Forest Programme 2010 defines the objectives of forest policy for the next few years. The aim of the Programme is to guarantee work and livelihood based on forests, the biodiversity and vitality of forests, as well as the recreational and cultural values provided by forests for the entire population. The Programme was evaluated in 2005 and is currently under revision. This provides an opportunity to address the role of genetic resources in the adaptation of the Finnish forest sector to climate change.

References

Anonymous. 2001. [Suomen maa- ja metsätalouden kansallinen kasvigeenivaraohjelma.] MMM:n julkaisuja 12/2001. Maa- ja metsätalousministeriö, Helsinki, Finland. 98 p. Summary in English.

Anonymous. 2005. [Ilmastonmuutoksen kansallinen sopeutumisstrategia.] MMM:n julkaisuja 1/2005. Maa- ja metsätalousministeriö, Vammala, Finland. 272 p. Summary in English. Full English version available from: http://www.mmm.fi/sopeutumisstrategia/

Rusanen, M., Napola, J., Nikkanen, T., Haapanen, M., Herrala, T., Vakkari, P. & Yrjänä, L. 2004. *Forest genetic resource management in Finland*. Finnish Forest Research Institute and Ministry of Agriculture and Forestry. Helsinki, Finland. 20 p. (Available at http://www.metla.fi/julkaisut/muut/genetic-resource-management-2004.pdf)

CONSERVATION OF FOREST GENETIC RESOURCES UNDER CLIMATE CHANGE: THE CASE OF FRANCE

François Lefèvre

INRA, Unité de Recherches Forestières Méditerranéennes, Avignon, France

Introduction

Forest gene conservation programmes aim at preserving genetic diversity in the long term to maintain the capacity of forests to respond to societal demands in the context of environmental change. National conservation strategies for forest genetic resources contribute to the collective effort towards sustainable management of European forests. Since 1994, international coordination of these efforts has been strengthened by the European Forest Genetic Resources Programme (EUFORGEN) as part of the Ministerial Conference on the Protection of Forests in Europe (MCPFE) process. These conservation strategies are generally developed at species level and combine *ex situ* and *in situ* approaches in a complementary way. The *ex situ* approach (germplasm collections) can be used for any species that is vegetatively or generatively propagated, but it becomes time consuming and costly when the objective is to achieve dynamic gene conservation. The *in situ* approach is a dynamic gene conservation strategy based on natural regeneration, but it is classically limited to those species that form large populations in a reasonably manageable area, and suitable methodologies for scattered or pioneer species have not yet been developed. Beside specific conservation networks, other activities such as silvicultural practices and natural reserves also have a significant impact on long-term evolution of genetic resources.

In this perspective, climate change is a challenge because of the magnitude and time scale of the environmental shift, which was not expected when conservation programmes were initiated in the 1980s. Will the current forests withstand the change that is occurring within one or two generations of trees? Will the forests have time to evolve and adapt genetically to new conditions? Will the tree species have the capacity to migrate in latitude or elevation and follow the shift of their potential distribution range?

In this paper, the French forest genetic resources conservation programme is used as a case study. Its aims, principles

---

Lefèvre, F. 2007. Conservation of forest genetic resources under climate change: the case of France. In: Koskela, J., Buck, A. and Teissier du Cros, E., editors. Climate change and forest genetic diversity: Implications for sustainable forest management in Europe. Bioversity International, Rome, Italy. pp. 95–101

and achievements are reviewed with a focus on each decision step. Then, basic principles for gene conservation are re-considered in the context of rapid climate change. Finally, recommendations are made in terms of the definition of the objectives for genetic resources conservation, as well as for conservation methodologies.

Aims, principles and achievements of the current forest genetic resources conservation programme in France

The French forest genetic resources conservation programme is 20 years old (Teissier du Cros et al. 2001). A first working group on forest genetic resources (FGR) was initiated by scientists (M. Arbez and G. Steinmetz) in 1985. Four years later, in 1989, the National Commission of Forest Genetic Resources was created by the Ministry in charge of agriculture, with the objective of maintaining a large resource of genetic diversity for priority species in the long term, by implementing specific conservation networks at national level, to preserve the adaptive capacity of the resources. Five pilot species were selected to develop a conservation strategy based on conservation networks (beech (*Fagus sylvatica*), silver fir (*Abies alba*), wild cherry (*Prunus avium*), elm (*Ulmus laevis*) and black poplar (*Populus nigra*)). In 1991, the first *in situ* conservation networks for beech and silver fir were officially established by the Ministry. In 1997, a charter for the conservation of FGR was prepared by the Commission, and signed by all partners of the 'FGR chain': the public forest service, representatives of the private sector, research and development organizations, and forestry schools. Today (in 2006), 11 specific conservation networks are operational (the five initial pilot species plus sessile oak (*Quercus petraea*), maritime pine (*Pinus pinaster*), Norway spruce (*Picea abies*), service tree (*Sorbus domestica*), wild service tree (*S. torminalis*) and walnut (*Juglans regia*)) (Balsemin and Collin 2004). Priority is given to *in situ* conservation as a dynamic strategy that allows the evolution of genetic diversity in response to environmental changes. *Ex situ* conservation is reserved for the most threatened species or when an *in situ* approach is not applicable.

Besides the conservation networks, the Commission has two plenary meetings each year, and four working groups have been established: (1) definition of criteria and indicators for *in situ* conservation networks (chairs: B. Fady and A. Valadon); (2) dissemination and use of FGR maintained in the national *ex situ* collection (chairs: E. Collin and M. Villar); (3) development of new approaches for the dynamic conservation of scattered tree species (chairs: N. Frascaria-Lacoste and B. Musch); and (4) coordination among network managers (chairs: A. Ducousso and A. Valadon).

The national strategy developed by the Commission includes the following decision-making steps:

- selection of a range of pilot tree species for which conservation strategies are specifically adapted (*in situ* or *ex situ* or both) and strategies that can be extended further to any other species having the same biological or ecological characteristics;
- establishment and management of *in situ* conservation networks:
  - › selection of the conservation units that will contribute to the network,
  - › definition of the management plan for each conservation unit, and
  - › definition of criteria and indicators for monitoring the conservation units and the network;
- establishment and management of *ex situ* collections:
  - › definition of a sampling strategy to establish and regularly update the collection, and
  - › definition of the conservation methodology (*in vivo* or *in vitro*) and procedures;
- definition of a strategy for the valuation of conserved genetic resources; and
- public awareness.

As an illustration, I will briefly review the decision steps for *in situ* conservation.

It is considered that a network of 30 gene conservation units offers a good compromise with sufficient diversity in a still manageable organization. The objective assigned by the French Commission to the network of *in situ* conservation units is to represent the adaptive diversity existing in the main distribution range of the species, including some marginal populations, all material being autochthonous. Of course, the information available for the establishment of the network varies among species. The first conservation networks for beech and silver fir have been extended several years after their initial establishment, to account for the most recent results on the structure of genetic diversity, whereas, by contrast, much more detailed information was initially available when establishing the conservation network for sessile oak. Legal status and ownership of the land is also important information for the selection of conservation units. In the case of silver fir, we are facing a situation where a potentially original resource in the western part of the country only occurs on private land, and the question is how to ensure long-term conservation of such conservation units.

Each conservation unit has a common structure with a core area, where the target species must be autochthonous and be represented by more than 500 seed trees, with a minimum density of 60 trees/ha, and a peripheral zone where no alien origin of the target species is allowed. Management plans of the conservation units allow any silvicultural treatment, but the following three objectives should be met: (1) natural regeneration is sufficient in quantity (it can be assisted by using local seed from the core); (2) good genetic quality of the regenerated seedlings is ensured (enough diversity and reduced consanguinity); and (3) local phenotypic identity is maintained (mainly adaptation to local conditions). In particular, in even-aged silviculture, regeneration of the core must be conducted prior to the peripheral area, applying given critical values for the number and density of seed trees. Natural regeneration is preferred, but assisted regeneration from local seed sources is an alternative when the three previous requirements can not be met.

As previously mentioned, this species-based approach cannot be applied to all forest tree species. Moreover, classical *in situ* methodology is not readily applicable to highly scattered species that do not form obvious populations or stands, nor to strictly pioneer species in which regeneration dynamics is governed by extinction versus colonization processes not related to silvicultural management (e.g. in riparian forests). *Ex situ* strategies are preferable in such cases. This also emphasizes the need to develop criteria and indicators for monitoring the evolution of genetic resources under 'normal silviculture' outside specific conservation networks, and the need for enhanced coordination between genetic resources conservation and habitat conservation programmes.

How does climate change influence forest genetic resources conservation programmes?

Various climate change scenarios have been predicted on a regional basis (see http://www.ipcc.ch). Although the predictions still vary from one scenario to another, it is likely that once changes start occurring, they will be rapid (within a time scale of one tree generation) and differ among geographical zones. For example, in Europe, the Mediterranean area will experience a decrease in annual rainfall, whereas northern areas might rather experience seasonal fluctuations within each year, not necessarily accompanied with total annual deficit. Climate change might also result in higher frequency of exceptional weather events, beyond biological thresholds, leading to catastrophic damage to the present forests. In practice, climatic events have already affected our forest genetic resources: the big storm of 1999 destroyed large parts of *in situ* conservation units of beech in north-east France and the severe drought of 2003 led to die-back of silver fir in south-eastern parts of the country, and the mortality of silver fir in 2006 was still increasing as an after effect. Experimentally, these situations also provide an excellent opportunity to evaluate the robustness of our genetic resources conservation networks, but this evaluation has not yet been done.

Theoretically, climate change can influence each of the decision steps listed above. Firstly, it should be incorporated within risk assessment more explicitly than before: what are the areas of higher risk due to climate change (drought, temperature, catastrophes)? What are the species or habitats most susceptible to climate change? These considerations will affect the choice of priority species and priority areas for gene conservation. One problem is that the real impact of climate change on forest genetic resources results from complex processes and is not yet predictable. Therefore, we must reconsider our objectives and make them evolve from the preservation of existing genetic diversity to the conservation of the capacity of forest genetic resources to 'keep on running'. It is clear that we have to manage adaptive capacity in the long term. Genetic resources must be considered from a dynamic perspective and exposed to constant evolution. The current values of diversity parameter estimates should not be simply considered as an objective for management, but rather as indicators of evolutionary processes. For sustainable management of forests in the context of rapid environmental change, three conditions are required: (1) existing resources do not completely disappear; (2) remaining trees are able to regenerate and produce a new generation better adapted to the new conditions (examples of transplantations have shown that genetic changes in adaptive potential can occur in just one generation (Skrøppa and Kohmann 1997; Rehfeldt et al. 2001)); and (3) the migration process allows trees to follow a geographical shift in their potential distributional range.

Rather than just genetic diversity, gene conservation strategies should focus more directly on adaptive capacity, which includes three components: (1) plasticity, i.e. the capacity of existing trees to respond differently to different environmental conditions; (2) adaptation, which includes adaptive genetic diversity and the occurrence of natural selection in a dynamic management system; and (3) migration potential through natural dissemination of seeds or artificial seed transfer, or both. In other words, forest genetic resources conservation programmes must evolve from a perspective with a focus on population management, to the management of evolutionary trajectories. This must be seen as an adjustment of our objectives, not a complete shift.

From a scientific point of view, information on climate change scenarios, as well as on the biological processes underlying adaptive capacity, is rapidly increasing. However, the knowledge of biological processes has increased for so-called model species, but little effort has been made to transfer this knowledge to non-model species, which represent the vast majority of the genetic resources of interest. Therefore, the challenge is to develop dynamic forest genetic resources conservation programmes and permanently integrate the most recent research results into these programmes to improve their effectiveness.

Conclusions and recommendations

We have to improve the conservation programmes of forest genetic resources in a context of rapid environmental change, i.e. conservation plans will probably need to be evaluated in a context that differs from when these were initially elaborated. More than ever, it is clear that we must develop process-based conservation strategies rather than just diversity-based strategies, i.e. move from the management of genetic diversity to the management of the evolutionary processes that shape the diversity. Research priorities should be to study plasticity, adaptation and migration processes. Applied conservation strategies should benefit from the most recent research developments in biology and modelling. This requires specific efforts by the scientific community towards vertical integration (from the molecular to the ecosystem scale) and horizontal transfer (from model species to broader biodiversity) of biological knowledge.

The development of genetic criteria and indicators for *in situ* management is an urgent need. Some lists have recently been proposed at the level of the population, but they are still rarely used (Namkoong et al. 1996; Brown et al. 1997; Koski et al. 1997; Lefèvre et al. 2001; Eriksson et al. 1993). However, the context of climate change has not really been taken into account yet. This work is favoured by the emergence of new process-oriented rather than species-oriented working groups as part of Phase III of EUFORGEN. Furthermore, effective coordination among all programmes and activities that directly or indirectly contribute to the conservation of genetic resources is urgently needed, including *in situ* and *ex situ* conservation networks, nature reserves and protected habitats. This could require the development of new criteria and indicators for the management of genetic resources at ecosystem level, although the proposed frameworks for genetic criteria and indicators are probably acceptable. The problem lies in their practical implementation. Furthermore, MCPFE has adopted a decision that the ecosystem approach and sustainable forest management are consistent one with the other.

Since climate change scenarios vary geographically, international coordination for monitoring the impact of climate change on forest health at regional scale is also needed for prioritizing areas, habitats and species for conservation.

Scientific knowledge should be continuously assimilated into FGR conservation strategies. However, a common trend in research is to increase scientific knowledge vertically, based on a limited range of biological models, with little horizontal transfer across species. It will become a challenge to apply research results from a large diversity of organisms in a diversity of local contexts. Therefore, two priorities emerge for research: (1) the integration of the various disciplines and approaches that address the questions of plasticity, adaptation and migration, such as integrative biology, demo-genetic modelling or the study of biotic interactions at ecosystem level; and (2) the transfer of scientific knowledge based on model species to a broader biodiversity. The Network of Excellence EVOLTREE (http://www.evoltree.org) should provide a major contribution to these efforts.

Finally, we can conclude that existing conservation networks in France were based on objectives and principles that remain valid in the context of climate change. However, they need to be extended, as follows:

- the objective should be extended from genetic diversity alone to plasticity, adaptation and migration potential;
- process-based rather than diversity-based criteria and indicators should be developed, which consider processes at all scales;
- there is a need for coordination between habitat and FGR conservation programmes;
- priority areas, priority ecosystems and priority species should be identified in relation to climate change scenarios;
- European forest genetic resources conservation programmes should pay attention to the situation outside Europe, in particular in the Mediterranean and boreal zones; and
- robustness of existing networks regarding climatic hazard should be monitored whenever singular climatic events occur.

References

Balsemin, E. & Collin, E. 2004. Conservation *in situ* des ressources génétiques des arbres forestiers en France métropolitaine. *Ingénieries*, 40: 51–60.

Brown, A., Young, A. Burdon, J. Christidis, L. Clarke, G. Coates D. & Sherwin, W. 1997. Genetic indicators for state of the environment reporting. State of the Environment Technical Paper Series (Environmental indicators). Department of the Environment, Sport and Territories, Canberra, Australia.

Eriksson, G., Namkoong, G. & Roberds, J.H. 1993. Dynamic gene conservation for uncertain futures. *Forest Ecology and Management*, 62: 15–37.

Koski, V., Skrøppa, T., Paule, L., Wolf, H. & Turok, J. 1997. Technical guidelines for genetic conservation of Norway spruce (*Picea abies* (L.) Karst.). IPGRI, Rome, Italy.

Lefèvre, F., Barsoum, N., Heinze, B., Kajba, D., Rotach, P., de Vries, S.M.G. & Turok, J. 2001. Technical bulletin: *in situ* conservation of *Populus nigra*. IPGRI, Rome, Italy.

Namkoong, G., Boyle, T., Gregorius, H.R., Joly, H., Savolainen, O., Ratman, W. & Young, A. 1996. Testing criteria and indicators for assessing the sustainability of forest management: genetic criteria and indicators. *CIFOR Working Paper,* No. 10.

Rehfeldt, G.E., Wykoff, W.R. & Ying, C.C. 2001. Physiological plasticity, evolution, and impacts of a changing climate on *Pinus contorta*. *Climatic Change*, 50: 355–376.

Skrøppa, T. & Kohmann, K. 1997. Adaptation to local conditions after one generation in Norway spruce. *Forest Genetics*, 4: 171–177.

Teissier du Cros, E., Bilger I. & Lefèvre, F. 2001. Réalisations et programmes en cours en matière de conservation des ressources génétiques forestières en France et en Europe. *Revue Forestière Française*, 53: 117–124.

LIST OF PARTICIPANTS

Workshop on climate change and forest genetic diversity: Implications for sustainable forest management in Europe

Paris, France, 15–16 March 2006

Thomas Geburek
Department of Genetics
Research and Training Centre for Forests,
Natural Hazards and Landscape (BFW)
Hauptstrasse 7
1140 Vienna
Austria
Tel: (43-1) 87838 2109
Fax: (43-1) 87838 2250
Email: thomas.geburek@bfw.gv.at

Bart De Cuyper
Research Institute for Nature and Forest
Gaverstraat 4
9500 Geraardsbergen
Belgium
Tel: (32) 477 444130
Fax: (32) 54 436160
Email: Bart.Decuyper@inbo.be

Alain Servais
Ministry of the Walloon Region
Division Nature and Forest - Forest tree seed Center
Z.I. D'Aye, Rue Feher 2
6900 Marche-en-Famenne
Belgium
Tel: (32-84) 316597
Fax: (32-84) 322245
Email: a.servais@mrw.wallonie.be

Alexander H. Alexandrov
Forest Research Institute
Kliment Ohridski Blvd. 132
1756 Sofia
Bulgaria
Tel: (359-2) 8622052
Fax: (359-2) 9620447
Email: forestin@bas.bg

Stefan Yurukov
Ministry of Agriculture and Forestry
55, Hristo Botev Blvd.
1040 Sofia
Bulgaria
Tel: (359-2) 98511205
Fax: (359-2) 9815840
Email: syurukov@nug.bg

Davorin Kajba
Dept. of Forest Genetics, Dendrology and Botany
Faculty of Forestry, University of Zagreb
Svetosimunska 25
10 000 Zagreb
Croatia
Tel: (385-1) 235 2427
Fax: (385-1) 235 2505
Email: davorin.kajba@zg.htnet.hr

Josef Frýdl
Forestry and Game Management Research Institute
Jíloviště - Strnady
15604 Praha 5 - Zbraslav
Czech Republic
Tel: (420) 257 892271
Fax: (420) 257 921444
Email: frydl@vulhm.cz

Karel Vancura
Department of External Relations
Forestry Management Institute
Nabrezni 1326
250 01 Brandys n.L.
Czech Republic
Tel: (420-322) 319867
Fax: (420-326) 902434
Email: vancura@uhul.cz

Bjerne Ditlevsen
State Tree Improvement Station
Statsskovenes Planteavlsstationen
Krogerupvej 21
3050 Humlebaek
Denmark
Tel: (45) 49190214
Fax: (45) 49160016
Email: bjd@sns.dk

Gunnar Friis Proschowsky
Danish Forest and Nature Agency
The State Forest Tree Improvement Station
Krogerupvej 21
3050 Humlebaek
Denmark
Tel: (45) 49 190214
Fax: (45) 49 160016
Email: gfr@sns.dk

Kirsten Thomsen
Danish Forest and Nature Agency
The State Forest Tree Improvement Station
Krogerupvej 21
3050 Humlebaek
Denmark
Tel: (45) 49 190214
Fax: (45) 49 160016
Email: kth@sns.dk

Bo Jellesmark Thorsen
Forest and Landscape
Royal Veterinary and Agricultural University
Rolighedsvej 23
1958 Frederiksberg C
Denmark
Tel: (45) 3528 1701
Fax: (45) 3528 1517
Email: bjt@kvl.dk

Leena Karjalainen-Balk
Ministry of the Environment
Kasarmikatu 25
00023 Helsinki
Finland
Tel: (358-9) 16039443
Fax: (358-9) 16039364
Email: leena.karjalainen-balk@ymparisto.fi

Mari Rusanen
Finnish Forest Research Institute
Vantaa Research Centre
P.O. Box 18
01301 Vantaa
Finland
Tel: (358-10) 211 2518
Fax: (358-10) 211 2205
Email: mari.rusanen@metla.fi

Outi Savolainen
Department of Biology
University of Oulu
90014 Oulu
Finland
Tel: (358-8) 5531782
Fax: (358-8) 5531061
Email: outi.savolainen@oulu.fi

Leena Yrjänä
Finnish Forest Research Institute
PO Box 18
01301 Vantaa
Finland
Tel: (358-10) 211 2317
Fax: (358-10) 211 2205
Email: Leena.yrjana@metla.fi

Sylvie Alexandre
Adjointe au Directeur général de la forêt et des affaires rurales
Ministère de l'agriculture et de la pêche
19, avenue du Maine
75 732 Paris
France
Tel: (33) 1 49555129
Fax: (33) 1 49554073
Email: sylvie.alexandre@agriculture.gouv.fr

Isabelle Bilger
CEMAGREF
U.R. Ecosystèmes Forestiers
Domaine des Barres
45290 Nogent-sur-Vernisson
France
Tel: (33) 238950353
Fax: (33) 238950349
Email: isabelle.bilger@cemagref.fr

Yves Birot
INRA
5 alle Canto Cigalo
30400 Villeneuve-les-Avignon
France
Tel: (33) 689151326
Email: yves.birot@free.fr

Patricia Bossard
Ministère de l'agriculture et de la pêche
DGFAR / Sous-direction de la forêt et du bois - Bureau de la forêt et des territoires
19, avenue du Maine
75 732 Paris Cédex 15
France
Tel: (33) 1 49555196
Fax: (33) 1 49558143
Email: patricia.bossard@agriculture.gouv.fr

Pierre Bouillon
Ministère de l'agriculture et de la pêche
DGFAR/Sous-direction de la forêt et du boi, Bureau de l'orientation de la sylviculture
19, avenue du Maine
75732 Paris Cédex 15
France
Tel: (33) 1 49555126
Fax: (33) 1 49554076
Email: pierre.bouillon@agriculture.gouv.fr

Alain Chaudron
Ministère de l'agriculture et de la pêche
DGFAR/Sous-direction de la forêt et du bois
19, avenue du Maine
75 732 Paris cédex 15
France
Tel: (33) 1 49554232
Fax: (33) 1 49554073
Email: alain.chaudron@agriculture.gouv.fr

Eric Collin
CEMAGREF
U.R. Ecosystème Forestiers
Domaine des Barres
45290 Nogent-sur-Vernisson
France
Tel: (33)238950968
Fax: (33)238950346
Email: eric.collin@cemagref.fr

Alexis Ducousso
Genetic team UMR BIOGECO
INRA
69 route Arcachon
33612 Cestas cedex
France
Tel: (33)557122828
Fax: (33)557122881
Email: ducousso@pierroton.inra.fr or alexis.ducousso@pierroton.inra.fr

Bruno Fady
Unité des Recherches Forestières Méditerranéennes, INRA
Domaine Saint-Paul
Site Agroparc
84914 Avignon cedex 9
France
Tel: (33) 4 32722908
Fax: (33) 4 32722902
Email: fady@avignon.inra.fr

Nathalie Frascaria-Lacoste
ENGREF
Université de Paris XI – Sud
Laboratoire ESE
Bât 360
91405 Orsay cédex
France
Tel: (33) 1 69156342
Fax: (33) 1 69154697
Email: nathalie.frascaria@ese.u-psud.fr

Sabine Girard
Institut pour le Développement Forestier
175 Cours Lafayette
69003 Lyon
France
Tel: (33) 4 37240408
Fax: (33) 4 78522053
Email: sabine.girard@cnppf.fr

Jean-Marc Guehl
INRA
Route d'Amance
54280 Champenoux
France
Tel: (33) 383394036
Fax: (33) 383394069
Email: guehl@nancy.inra.fr or delvig@nancy.inra.fr

Luc Harvengt
AFOCEL, Bioctech Laboratory
Domaine de l'Etançon
77370 Nangis
France
Tel: (33) 1 60670032
Fax: (33) 1 60670256
Email: luc.harvengt@afocel.fr

Antoine Kremer
INRA - Laboratoire de génétique et amélioration des arbres forestiers
Domaine de l'Hermitage
69 Route d'arcachon
33612 Cestas
France
Tel: (33) 57 122832
Fax: (33) 57 122881
Email: antoine.kremer@pierroton.inra.fr

François Lefèvre
Unité des Recherches Forestières Méditerranéennes, INRA
Domaine Saint-Paul
Site Agroparc
84914 Avignon cedex 9
France
Tel: (33) 4 32722901
Fax: (33) 4 32722902
Email: francois.lefevre@avignon.inra.fr

Brigitte Musch
ONF-DR Conservatoire Génétique des Arbres Forestiers
Centre INRA
2163 avenue de la pomme de pin - BP 20619
Ardon
45166 Olivet cedex
France
Tel: (33)2 38414808
Fax: (33)2 38414800
Email: musch@orleans.inra.fr or brigitte.musch@onf

Eric Teissier du Cros
11 Rue du Dr René Dayot
22430 Erquy
France
Tel: (33) 2 96635218
Email: eric.teissier-du-cros@wanadoo.fr

Alain Valadon
ONF - Conservatoire Génétique des Arbres Forestiers,
Centre INRA - Ardon
Avenue de la pomme de pin
BP 20619 Ardon
45160 Olivet
France
Tel: (33) 2 38414808
Fax: (33) 2 38414800
Email: alain.valadon@onf.fr

Anke Höltermann
Federal Agency for Nature Conservation
Konstantinstr. 110
53179 Bonn
Germany
Tel: (49) 228 8491417
Fax: (49) 228 8491480
Email: Anke.Hoeltermann@bfn.de

Ralf Kätzel
Forest Research Institute Eberswalde
Moeller strasse 1
16225 Eberswalde
Germany
Tel: (49) 3334 65230
Fax: (49) 3334 65239
Email: ralf.kaetzel@lfe-e.brandenburg.de

Monika Konnert
Bayerisches Amt fuer forstliche Saat- und Pflanzenzucht (ASP)
Forstamtsplatz 1
83317 Teisendorf
Germany
Tel: (49) 8666 988313
Fax: (49) 8666 988330
Email: Monika.Konnert@asp.bayern.de

Werner D. Maurer
SGD Sued, Research Institute for Forest Ecology & Forestry (FAWF)
Schloss
67705 Trippstadt
Germany
Tel: (49) 6306 911134
Fax: (49) 6306 911200
Email: werner.maurer@wald-rlp.de

Astrid Thyssen
Federal Ministry for the Environment, Nature conservation and Nuclear Safety
Robert Schuman Platz 3
53175 Bonn
Germany
Tel: (49) 228 3052654
Fax: (49) 228 3052695
Email: Astrid.Thyssen@bmu.bund.de

Georg von Wühlisch
Bundesforschungsanstalt für Forst- und Holzwirtschaft (BFH)
Institut für Forstgenetik und Forstpflanzenzüchtung
Sieker Landstrasse 2
22927 Grosshansdorf
Germany
Tel: (49-4102) 696106
Fax: (49-4102) 696200
Email: wuehlish@holz.uni-hamburg.de

Paraskevi Alizoti
Aristotle University of Thessaloniki
School of Forestry and Natural Environment, Lab. of Forest Genetics and Tree Improvememnt
54124 Thessaloniki
Greece
Tel: (30) 2310 992769
Fax: (30) 2310 992777
Email: alizotp@for.auth.gr

Csaba Mátyás
Inst. Env. Science, Faculty of Forestry
University of West Hungary
P.O. Box 132
9401 Sopron
Hungary
Tel: (36-99) 518395
Fax: (36-99) 329840
Email: cm@emk.nyme.hu

John Fennessy
COFORD (National Council for Forest Research and Development)
Arena House
Arena Road
Sandyford, Dublin 18
Ireland
Tel: +(353) 1213 0725
Fax: +(353) 1213 0611
Email: john.fennessy@coford.ie

Fulvio Ducci
CRA - Consiglio per la Ricerca e Sperimentazione in Agricoltura
Istituto Sperimentale per la Selvicoltura
Viale Santa Margherita 80
52100 Arezzo
Italy
Tel: (39) 0575 353021
Fax: (39) 0575 353490
Email: ducci.fulvio@ricercaforestale.it and fulvio.ducci@entecra.it

Giovanni Giuseppe Vendramin
Istituto di Genetica Vegetale, Sezione di Firenze CNR
Polo Scientifico Sesto Fiorentino
Via Madonna del Piano 10, Edificio D
50019 Sesto Fiorentino, Firenze
Italy
Tel: (39-055) 5225725
Fax: (39-055) 5225729
Email: giovanni.vendramin@igv.cnr.it

Zbignev Glazko
Ministry of Environment
A. Jaksto st. 4/9
01105 Vilnius
Lithuania
Tel: (370) 52 727813
Fax: (370) 52 722029
Email: z.glazko@am.lt

Tor Myking
Norwegian Forest Research Institute
Fanaflaten 4
5244 Fana
Norway
Tel: (47) 5511 6229
Fax: (47) 55916245
Email: tor.myking@skogforsk.no

Tore Skrøppa
Norwegian Forest Research Institute
Høgskoleveien 8
1432 Ås
Norway
Tel: (47) 64 949067/ 64 949000
Fax: (47) 64 942980
Email: tore.skroppa@skogforsk.no

Jan Kowalczyk
Forest Research Institute
Dpt. Genetics and Forest Tree Physiol Bitwy Warszawskiej 1920 St. No 3
00 973 Warsaw
Poland
Tel: (48-22) 7150473
Fax: (48-22) 7150313
Email: j.kowalczyk@ibles.waw.pl

Maria Helena Almeida
Instituto Superior de Agronomia
Universidade Tecnica de Lisboa
Tapada da Ajuda
1349 017 Lisbon
Portugal
Tel: (351) 21 3653348
Fax: (351) 21 3645000
Email: nica@isa.utl.pt

Maria Moise
Forestry Department
Ministry of Agriculture, Forests and Rural Development
24 Carol I bvd. Sector 3
020921 Bucharest
Romania
Tel: (40-21) 3072 338
Fax: (4021) 3079803
Email: maria.moise@maa.ro

Ciprian Pahontu
Ministry of Agriculture, Forests and Rural Development
24 Carol Blvd
Bucharest
Romania
Tel: (40-21) 3079801
Fax: (40-21) 3079803
Email: ciprian.pahontu@maa.ro

Ljiljana Sovilj
Ministry of Agriculture, Forestry and Water Management
Forest Directorate of Serbia
Omladinskih brigada str. 1
11000 Belgrade
Serbia
Tel: (381-11) 3117566; (381-63) 8369444
Fax: (381-11) 3117611
Email: ljsovilj@ptt.yu

Ladislav Paule
Faculty of Forestry
Technical University
T.G. Masaryka 24
960 53 Zvolen
Slovakia
Tel: (421-45) 5206221
Fax: (421-45) 5332654 or 5350608
Email: paule@vsld.tuzvo.sk

Gregor Bozic
Dept. of Forest Physiology and Genetics
Slovenian Forestry Institute
Vecna pot 2
1000 Ljubljana
Slovenia
Tel: (386-1) 2007821
Fax: (386-1) 273589
Email: gregor.bozic@gozdis.si

Hojka Kraigher
Department for Forest Physiology and
Genetics, Slovenian Forestry Institute
Vecna pot 2
1000 Ljubljana
Slovenia
Tel: (386-1) 2007820
Fax: (386-1) 2573589
Email: hojka.kraigher@gozdis.si

Ricardo Alía
Centro Investigacion Forestal, INIA
Apdo. 8111
28080 Madrid
Spain
Tel: (34-91) 3473959
Fax: (34-91) 3572293
Email: alia@inia.es

Josefa Fernández-López
Xunta de Galicia
Carretera de Marín km 4 - Apartado 127
36080 Pontevedra
Spain
Tel: (34-986) 805002
Fax: (34-986) 856420
Email: ffina.cifal@siam-cma.org

Santiago C. González-Martínez
Center of Forest Research
Department of Forest Systems and
Resources
Carretera de la Coruña km 7,5
28040 Madrid
Spain
Tel: (34) 913471499
Fax: (34) 913572293
Email: santiago@inia.es

María A. Prada
Conselleria de Territoti I Habitatge
Generalitat Valenciana
Avda. Comarques del Paìs Valencia, 114
46930 Quart de Poblet - Valencia
Spain
Tel: (34) 961 920 300
Fax: (34) 961 920258
Email: gis_banco@gva.es

Jonas Bergquist
Swedish Forest Agency
Skogsstyrelsen
55183 Jönköping
Sweden
Tel: (46-36) 155720
Fax: (46-36) 166170
Email: jonas.bergquist@skogsstyrelsen.se or
jonas.bergquist@svo.se

Per G. Broman
Per B Konsult
Promenaden 27
SE 79130 Falun
Sweden
Tel:
Fax:
Email: perbkonsult@bromans.net

Hillevi Eriksson
Swedish Forest Agency
Skogsstyrelsen
551 83 Jönköping
Sweden
Tel: (46) 36 155560
Fax: (46) 36 166170
Email: Hillevi.Eriksson@skogsstyrelsen.se

Johan Sonesson
Skogforsk, the Forestry Research Institute of Sweden
Uppsala Science Park
75183 Uppsala
Sweden
Tel: (46) 1818589
Fax: (46) 18188600
Email: Johan.Sonesson@Skogforsk.se

Koen Kramer
ALTERRA
Droevendaalsesteeg 3 - P.O. Box 47
6700 AA Wageningen
The Netherlands
Tel: (31) 317 477894
Fax: (31) 317 424988
Email: koen.kramer@wur.nl

Sven M.G. de Vries
Centre for Genetic Resources the Netherlands, Wageningen University and Research
c/o ALTERRA
P.O. Box 47
6700 AA Wageningen
The Netherlands
Tel: (31-317) 477841
Fax: (31-317) 424988
Email: sven.devries@wur.nl

Jeff Burley
Director Emeritus
Oxford Forestry Institute
Woodside, Friford Heath
OX13 5QG Abingdon
United Kingdom
Tel: (44) 1865 390754
Fax:
Email: jeff.burley@plants.ox.ac.uk

Jo Clark
Northmoor Trust
Little Wittenham
OX14 ARA Abingdon
United Kingdom
Tel: (44) 0 865 407792
Fax: (44) 0 1865 407131
Email: jo.clark@northmoortrust.co.uk

Jason Hubert
Broadleaved Tree Improvement and Genetic Conservation
Forest Research
Northern Research Station, Roslin
EH25 9SY Midlothian
United Kingdom
Tel: (44-131) 445 6947
Fax: (44-131) 445 2176
Email: jason.hubert@forestry.gsi.gov.uk

Adrian Parr
Sustainable Development Attaché
British Embassy Paris
35 rue du Faubourg St Honoré
75008 Paris
France
Tel: (33) 1 44513256
Email: adrian.parr@fco.gov.uk

International organizations

Bioversity International

Michele Bozzano
Bioversity International
Via dei Tre Denari 472/a
00057 Maccarese, Rome
Italy
Tel: (39) 066118221
Fax: (39) 0661979661
Email: m.bozzano@cgiar.org

Jarkko Koskela
Bioversity International
Via dei Tre Denari 472/a
00057 Maccarese, Rome
Italy
Tel: (39) 066118223
Fax: (39) 0661979661
Email: j.koskela@cgiar.org

Barbara Vinceti
Bioversity International
Via dei Tre Denari 472/a
00057 Maccarese, Rome
Italy
Tel: (+39) 06 6118412
Fax: (+39) 06 61979661
Email: b.vinceti@cgiar.org

EFI

Marcus Lindner
European Forest Institute
Torikatu 34
80100 Joensuu
Finland
Tel: (358-13) 2520240
Fax: (358-13) 124393
Email: marcus.lindner@efi.int

ELO

Paula Bortlová
ELO- European Landowners' organization
Rue de Trèves, 67
1040 Bruxelles
Belgium
Tel: (32) 2 2343000
Fax: (32) 2 2343009
Email: elo@elo.org

IUFRO

Alexander Buck
International Union of Forest Research Organizations
Hauptstrasse 7
1140 Vienna-Hadersdorf
Austria
Tel: (43-1) 8770151 ext 13
Fax: (43-1) 877 0151 ext 50
Email: buck@iufro.org

MCPFE

Roman Michalak
Ministerial Conference on the Protection of Forests in Europe
Liaison Unit Warsaw
Ul. Bitwy Warszawskiej 1920 nr 3
00973 Warsaw
Poland
Tel: (48-22) 3317031
Fax: (48-22) 3317032
Email: r.michalak@lu-warsaw.pl

EUFORGEN

Conservation and use of forest genetic diversity are cornerstones of sustainable forest management. Genetic diversity ensures that forest trees can survive, adapt and evolve under changing environmental conditions. Bioversity International and the International Union of Forest Research Organizations (IUFRO) organized a workshop in Paris, France, on 15 and 16 March 2006 to discuss the role of forest genetic diversity in mitigating the effects of climate change and in maintaining sustainable forest management in Europe. The workshop was organized in collaboration with the European Forest Genetic Resources Programme (EUFORGEN), the Liaison Unit Warsaw of the Ministerial Conference on the Protection of Forests in Europe (MCPFE), the Ministry of Agriculture and Fisheries of France, and Ecole Nationale du Génie Rural et des Eaux et des Forêts (ENGREF), France.

This publication contains invited papers presented during the workshop, summaries of the outputs of working group discussions and recommendations for further action. The content provides an up-to-date review of knowledge on how forest trees will cope with and adapt to climate change, the implications for forest management and conservation of forest genetic diversity, and how regional and national strategies should address these challenges.