IBFRA: International Boreal
Forest Research Association

Climate Change, Biodiversity and Boreal Forest Ecosystems

Edited by E. Korpilahti, S. Kellomäki and T. Karjalainen



The Finnish Forest Research Institute
The Finnish Society of Forest Science
The Finnish Research Programme
on Climate Change – SILMU

Climate Change, Biodiversity and Boreal Forest Ecosystems

METSÄNTUTKIMUSLAITOS
Jaostusosasto

Climate Change, Biodiversity and Boreal Forest Ecosystems

Peer-reviewed papers selected from the International Boreal Forest Research Association Conference held in Joensuu, Finland, 30 July–5 August, 1995

Edited by

Eeva Korpilahti, Seppo Kellomäki and Timo Karjalainen

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Contents

Preface 7
Acknowledgement 11
Statement of the Joensuu IBFRA 1995 Conference 13

Part I Climate Change

Mika Aurela, Tuomas Laurila & Juha-Pekka Tuovinen: Measurements of O_3, CO_2 and H_2O fluxes over a Scots pine stand in eastern Finland by the micrometeorological eddy covariance method. 17

F.G. Hall, P.J. Sellers & D.L. Williams: Initial results from the boreal ecosystem-atmosphere experiment, BOREAS. 29

Virpi Palomäki, Kaisa Laitinen, Toini Holopainen & Seppo Kellomäki: First-year results on the effects of elevated atmospheric CO_2 and O_3 concentrations on needle ultrastructure and gas exchange responses of Scots pine saplings. 43

Oddvar Skre & Knut Nes: Combined effects of elevated winter temperatures and CO_2 on Norway spruce seedlings. 55

Jonathan J. Ruel & Matthew P. Ayres: Variation in temperature responses among populations of *Betula papyrifera*. 65

Ilkka Leinonen, Tapani Repo & Heikki Hänninen: Testing of frost hardiness models for *Pinus sylvestris* in natural conditions and in elevated temperature. 79

Tarmo Virtanen, Seppo Neuvonen, Ari Nikula, Martti Varama & Pekka Niemelä: Climate change and the risks of *Neodiprion sertifer* outbreaks on Scots pine. 89

Päivi Lyytikäinen, Pirjo Kainulainen, Anne Nerg, Seppo Neuvonen, Tarmo Virtanen & Jarmo K. Holopainen: Performance of pine sawflies under elevated tropospheric ozone. 99

Robert A. Monserud, Nadja M. Tchebakova, Tatyana P. Kolchugina & Olga V. Denissenko: Change in Siberian phytomass predicted for global warming. 105

Dina I. Nazimova & N.P. Polikarpov: Forest zones of Siberia as determined by climatic zones and their possible transformation trends under global change. 121

Vadim V. Gorshkov, Irene J. Bakkal & Natalie I. Stavrova: Postfire recovery of forest litter in Scots pine forests in two different regions of boreal zone. 129

Jouko Silvola & Urpo Ahlholm: Effects of CO_2 concentration on the nutrition of willows *(Salix phylicifolia)* grown at different nutrient levels in organic-rich soil. 141

Heikki Hänninen, Ilkka Leinonen, Tapani Repo & Seppo Kellomäki: Overwintering and productivity of Scots pine in a changing climate. 149

Egbert Beuker, Marja Kolström & Seppo Kellomäki: Changes in wood production of *Picea abies* and *Pinus sylvestris* under a warmer climate: comparison of field measurements and results of a mathematical model. 159

Ari Talkkari: Regional predictions concerning the effects of climate change on forests in southern Finland. 167

Malle Mandre, Hardi Tullus, Vaike Reisner & Jaan Klõšeiko: Assessment of CO_2 fluxes and effects of possible climate changes on forests in Estonia. 179

Anssi Niskanen, Olli Saastamoinen & Tapio Rantala: Economic impacts of carbon sequestration in reforestation: examples from boreal and moist tropical conditions. 189

R.A. Fleming: A mechanistic perspective of possible influences of climate change on defoliating insects in North America's boreal forests. 201

Renaat S.A.R. van Rompaey: Need for integrated policy oriented national research programmes: the second phase (1995–2001) of the Dutch National Research Programme on Global Air Pollution and Climate Change NRP. 215

Part II Biodiversity

John C. Brissette: Effects of intensity and frequency of harvesting on abundance, stocking and composition of natural regeneration in the Acadian forest of eastern North America. 221

Timo Kuuluvainen, Antti Penttinen, Kari Leinonen & Markku Nygren: Statistical opportunities for comparing stand structural heterogeneity in managed and primeval forests: an example from boreal spruce forest in southern Finland. 235

Vadim V. Gorshkov & Irene J. Bakkal: Species richness and structure variations of Scots pine forest communities during the period from 5 to 210 years after fire. 249

Anton K. Chtchoukine: North European platyphyllous forests: biodiversity dynamics and climate changes in northwest European Russia. 261

Jari Parviainen: Impact of fire on Finnish forests in the past and today. 273

Valentin Strakhov and Anatoly Pisarenko: Development and utilization of Russian forest resources. 281

Jari Parviainen: Tasks of forest biodiversity management and monitoring deriving from international agreements. 293

Nigel Dudley, Jean-Paul Jeanrenaud & Adam Markham: Conservation in boreal forests under conditions of climate change. 299

List of Participants 305

List of Reviewers 315

Preface

Projections concerning future population growth on the global level indicate that there will be an increase from the current 5.7 billion to 11 billion by the year 2100 (Source: World Bank). Predictions concerning the world's population growth do, however, vary from 6.4 to 17.6 billion in scenarios produced by the United Nations. Compared with the time horizons of the boreal forests, this is about the same time that it takes for a pine seedling to grow into a mature tree. With increasing numbers of people demanding higher standards of living and with increasing urbanisation taking place, it is likely that greater amounts of greenhouse gases than hitherto will be produced and these will also influence the demand for forest products. International conventions on decreasing emissions of greenhouse gases are important in the endeavour to slow down the build-up of these gases in the atmosphere. Since many greenhouse gases have relatively long lifespans in the atmosphere, the concentration of these gases will increase even if the current level of emissions is retained. Recent scenarios predict increases of 1.0–3.5 °C in the global mean surface temperature by the year 2100. The expected increase depends, for example, on which one of the emissions scenarios for energy production and consumption one is referring to. Complicated climate models have succeeded in simulating the development of the mean temperature of the earth starting from a reference year in the late 18th century. Models including the effects of greenhouse gases give overestimates of the increase in mean temperature. If the effects of aerosols are included, the simulations are closer to the measured mean temperature. Scientific knowledge about this complex and difficult atmosphere-ocean-land system has improved and simulated predictions are coming closer to the measured temperature.

The boreal zone has experienced climate changes in the past when the ice sheets retreated before the present inter-glacial period. This period created major changes in ecological communities and the distribution of species. A drastic difference in the climatic warming in the beginning of the present inter-glacial and the predicted climate change is the rate of the temperature increase, which could be in the order of ten or more times faster than the temperature increase that the boreal ecosystem have experienced so far. Succession in the boreal ecosystem is a slow process and hence rapid changes in the environment could generate complex responses by the ecosystem. It is of utmost importance to

increase scientific knowledge about how the species and interaction of species in the ecosystem may respond to environmental changes. An understanding of these responses should be achieved at all hierarchical levels of ecosystems and covering long enough periods of time.

During the 1980s public concern was expressed over the future of forests and it led to universal changes in the attitude to forests. The UNCED Earth Summit conference held in Rio de Janeiro in 1992 and the commitment of governments to sustainable development made biodiversity of ecosystems into a basic element of sustainable management of forests. Biodiversity is coupled to the global change in complex ways, including direct, interactive and long-term impacts of human activities on ecosystems. European and international processes are in progress for promoting the implementation of the UNCED resolutions in the field of management, conservation and sustainable development of forests. The broad objectives of these processes are to develop sustainable management of forests, to enhance international research concerning forestry, and to develop appropriate criteria and indicators for sustainable forest management in order to monitor and evaluate sustainability. Although a lot of scientific research is available about species diversity and the successional development of boreal forests, research is needed for tackling the matter of development of ecosystems under changing environments, human impacts, and different management strategies.

The International Boreal Forest Research Association (IBFRA) was founded in 1991 with the mission to "promote and co-ordinate research to increase the understanding of the role of the circumpolar boreal forests in the global environment and effects of environmental change". The Second International Science Conference of IBFRA was held between 30 July and 5 August, 1995, in Joensuu, Finland, on the theme of "*Climate Change, Biodiversity and Boreal Forests*". IBFRA's endeavour is that research results and the synthesis of knowledge produced by its activities are presented and published in recognised scientific forums and publications. The speakers at the Joensuu Conference were invited to submit manuscripts expanding their presentations at the meeting for inclusion in a special edition of the journal *Silva Fennica*. The manuscripts were subject to peer review by the journal. This special edition of *Silva Fennica* contains nearly thirty articles from a global group of experts providing scientific, economic, and policy perspectives on climate change and biodiversity in context of boreal forests. The papers cover a wide range of topics on how boreal forests may respond to the changing environment and how the productivity and biodiversity of boreal forests may develop under various managing practices. In addition to the global perspective of boreal forests, this issue of *Silva Fennica* includes research results obtained in the course of the Finnish Research Programme on Climate Change (SILMU). Results of special interest are those pertaining to research focusing on the boreal forests of Russia.

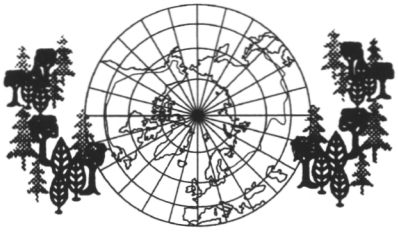
We hope that this issue will be a source of new knowledge in the endeavour to outline the wide range of the potential consequences that global change may have for boreal forests. Our intention is that the

research results published in this issue will serve to complement the scientific basis for the sustainable management of boreal forest resources and provide new perspectives for the development of constructive policies to improve management strategies for preserving the vitality of the boreal forests and their potential as a source of economic and social well-being. Progress in the scientific understanding of and knowledge on the boreal forests and their responses to global change will help in constructing and assessing decisions. An integral element of scientific progress is that it stimulates research to tackle challenging problems of international relevance.

Helsinki, Finland, June 1996

Eeva Korpilahti
Editor

Seppo Kellomäki
Timo Karjalainen
Sini Niinistö
Conference Secretariat



IBFRA: International Boreal Forest Research Association

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SILMU

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We would like to thank Professor Erkki Annila, Dr Markku Kanninen, Professor Eino Mälkönen, Professor Eljas Pohtila, and Dr Risto Päivinen for their valuable work in planning and setting up the conference as members of the steering committee of the IBFRA 1995 conference.

Seppo Kellomäki
Timo Karjalainen
Sini Niinistö
Conference Secretariat

Statement of the Joensuu IBFRA 1995 Conference

Boreal Forests

The world's forested ecosystems are a vital link in the exchange of carbon dioxide between the atmosphere and the biosphere. In this context, the boreal forests of Eurasia and North America have a special role in controlling the global carbon cycle, since boreal forested ecosystems and peatlands account for more than one-third of the carbon accumulated in the biosphere. However, these boreal forests also provide economic, environmental and social benefits, thus making the northern regions habitable.

The predicted global climate change is among the major factors affecting future economic and social development in the boreal zone. Research and international collaboration are needed to create a solid knowledge base for, (1) the assessment of the ability of boreal forests to mitigate the effects of global change, and (2) on the growth and development of boreal forests under a changing climate.

Conservation of biodiversity has become one of the major issues of public concern. Population pressure on forests in the boreal zone is less than elsewhere, but forests in the boreal zone are, nevertheless an important source of well-being. The concept of biodiversity, and measuring and applying it in forest management, is currently an important research gap.

Changes in tropical forests were the first to attract interest all over the world. Since boreal forests are now also a subject of major interest, the different processes in these two large ecosystems should be emphasized.

International Boreal Forest Research Association

The International Boreal Forest Research Association (IBFRA) was founded in 1991, and consists of the six boreal zone countries: Canada, Finland, Norway, Russia, Sweden and the U.S.A. The three major areas of interest within IBFRA are the effects of global climate change, monitoring and classification of boreal forests, and biodiversity and forest management.

Although excellent research has been carried out on the effects of global climate change on boreal forests, more research and funding are urgently needed since the boreal forests are predicted to undergo more changes than tropical or temperate forests within the coming decades. It is also important to use monitoring as an important tool in studying changes in boreal forests.

The Joensuu Conference

IBFRA met for the 6th time in Joensuu, Finland, 30th July–5th August 1995, and the theme was "Climate Change, Biodiversity and Boreal Forest Ecosystems". One hundred participants attended this scientific conference, representing 13 countries; this indicates the broad research interest in boreal forest issues even outside the boreal countries themselves. Information was presented in 79 presentations (45 oral and 34 posters), which highlighted the recent progress in research aimed at increasing our understanding of climate change and biodiversity related to boreal forest ecosystems. Atmospheric prediction models increasingly agree on the fact that the greatest magnitude of warming will be in boreal forest zones. Evidence was also presented that both temperature and growth enhancing effects of elevated CO_2 are already affecting the boreal forests.

As we look in to the future, IBFRA is pleased that the importance of boreal forests to the well being of the Earth and its people is being increasingly recognized. At the same time, researchers are concerned that the boreal forest resource is changing more rapidly than we are developing the knowledge needed for sustainable management. IBFRA will continue to strive for enhancement of this necessary knowledge base and to facilitate international scientific cooperation regarding boreal forest ecosystems. The countries participating in IBFRA should have a special responsibility in this respect.

Next IBFRA Conference

The next IBFRA conference will be held in Russia in 1996. Interest and participation in the IBFRA conferences in 1994 (Saskatoon, Canada) and this year in Joensuu show that IBFRA has a promising future and the association looks forward to continuing its activities in support of boreal forest research.

Eljas Pohtila
President of the International
Boreal Forest Research Association

Part I
Climate Change

Measurements of O_3, CO_2 and H_2O Fluxes over a Scots Pine Stand in Eastern Finland by the Micrometeorological Eddy Covariance Method

Mika Aurela, Tuomas Laurila and Juha-Pekka Tuovinen

The eddy covariance technique is a novel micrometeorological method that enables the determination of the atmosphere-biosphere exchange rate of gases such as ozone and carbon dioxide on an ecosystem scale. This paper describes the technique and presents results from the first direct measurements of turbulent fluxes of O_3, CO_2 and H_2O above a forest in Finland. The measurements were performed during 15 July–5 August 1994 above a Scots pine stand near the Mekrijärvi research station in Eastern Finland. The expected diurnal cycles were observed in the atmospheric fluxes of O_3, CO_2 and H_2O. The data analysis includes interpretation of the O_3 flux in terms of the dry deposition velocity and evaluation the dependency of the net CO_2 flux on radiation. The eddy covariance method and the established measurement system has proved suitable for providing high-resolution data for studying ozone deposition to a forest as well as the net carbon balance and related physiological processes of an ecosystem.

Keywords eddy covariance technique, ozone deposition, net carbon balance, micrometeorology, Scots pine stands

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1 Introduction

An understanding of the gas and energy exchange at the atmosphere/biosphere interface plays an increasingly important role in studies on air pollution and climate dynamics. As an example, the tropospheric ozone problem has been recently addressed by the UN-ECE Convention on the Long-Range Transport of Air Pollutants by adopting new air quality standards to protect crops and forests that are based on the critical level concept (Fuhrer and Achermann 1994). The critical levels are derived from experimental data on the dependency of ozone-induced effects on plants under exposure to atmospheric ozone. By defining more specifically the circumstances when the damage is likely to occur (i.e. elevated concentrations, growing season, daylight hours), the present approach introduces a major improvement over employing simple long-term mean concentrations as indices of air quality. However, the ultimate relation between the atmospheric concentrations (exposure) and the actual effect-inducing dose (deposition flux) experienced by the receptors is not considered explicitly. Another recent issue is that of climate change, in which the surface exchange of greenhouse gases, such as CO_2 and O_3, has been identified as a key research area for reducing the uncertainty in climate scenarios (Houghton et al. 1995).

Micrometeorological methods provide a means of quantifying the gas and energy exchange at the surface on an ecosystem scale. The most sophisticated of these methods is the eddy covariance technique, in which the high-frequency fluctuating components of the vertical wind velocity and, for example, the gas concentration are measured and correlated to produce a direct measurement of the vertical flux density of the component at the surface. The need for fast-response analyzers has been a problem, but during the last decade suitable instruments have become available for several compounds, e.g. for ozone (Güsten et al. 1992) and carbon dioxide (LI-6262... 1991). In addition, general micrometeorological requirements exist regarding statistical stationarity and horizontal homogeneity of the near-surface atmospheric flow (e.g. Businger 1986). These features make the eddy covariance method rather laborious and less suitable for the continuous monitoring of atmospheric deposition, but highly useful for providing data for studying processes (e.g. Erisman et al. 1994a). Recently, however, long term flux measurement campaigns based on the eddy covariance technique have been conducted successfully.

The processes of interest within this study are related to the deposition of ozone and the carbon balance in a boreal forest. In a previous study (Aurela 1995), the eddy covariance facility of the Air Quality Department of the Finnish Meteorological Institute was used for measuring ozone fluxes above an agricultural field. This paper describes results from the first direct measurements of turbulent fluxes of O_3, CO_2 and H_2O above a forest in Finland. The measurements were performed above a Scots pine stand at the Mekrijärvi research station in Eastern Finland in collaboration with the Faculty of Forestry of Joensuu University (Kellomäki 1994).

2 Material and Methods

2.1 Eddy Covariance Method

The general approach adopted in micrometeorological methods is to measure the turbulent flux above the surface assuming the flux divergence below the measuring height to be negligible. The eddy covariance method is the most direct approach to measuring turbulent fluxes of different compounds. Taking the time averages as area averages it offers an excellent tool for estimating fluxes on an ecosystem scale. In this method, the high-frequency fluctuating components of the vertical wind velocity (w) and, for example, the gas concentration (c) are measured and correlated to give a direct measurement of the flux density

$$\overline{F_c} = \overline{w' c'} \qquad (1)$$

where the primes denote deviations from mean values and the overbars denote means over periods of typically 30 min. Similarly, by observing the fluctuations in the horizontal wind velocity, u, temperature, T, and specific humidity, q, the turbulent fluxes of momentum, sensible heat and latent heat can be measured. (In Eq. 1, c is then

replaced by ρu, $\rho c_p T$ and $\rho \lambda q$, respectively, where ρ is the density of dry air, c_p the specific heat of air at constant pressure and λ the latent heat of vaporization of water.)

The fundamental requirement in flux measurements with the eddy covariance technique is to get the contributions from all sizes of turbulent eddies, implying a typical sampling frequency of no lower than 5 observations per second. In practice, however, the limiting factor is the frequency response of the sensors. Furthermore, general micrometeorological requirements exist regarding the statistical stationarity of the near-surface atmospheric flow and the horizontal homogeneity of the surface. The homogeneity requirement imposes stringent conditions with respect to the measurement site and the measurement height. In practice, flow conditions with an adequate fetch to provide equilibrium with the surface are often obtained only in limited wind sectors. The measurement height should be low enough to conform with the limited fetch, but still uninfluenced by the local inhomogeneity of the surface. The minimum height is also limited by the height-dependence of the size of the turbulent eddies. According to Businger (1986) the minimum operating height is $6\pi p$, where p is the path length of the sensor.

Even under ideal flow conditions there is a need for the addition in Eq. 1 of the small mean vertical velocity produced by the sensible heat and water vapour fluxes with their associated density fluctuations, if these are conserved in the sampling system (Webb et al. 1980).

2.2 Measurement Site

The measurement site (62°52'N, 30°55'E, elevation 175 m a.s.l.) is located near the Mekrijärvi research station of Joensuu University in eastern Finland, not far from the Russian border. The terrain is heathland mainly covered by Scots pine (*Pinus sylvestris*) having a height of 6 to 7 metres. An adequate fetch is obtained in wind directions from 160 to 340 degrees. To the south there is a narrow bog area at a distance of 150 m beyond which the forest continues at the same height, but not as dense. In directions from 80° to 160° the fetch varies from 50 to 100 m and the associated data should be taken as uncertain. To the north, there is a logging area that limits the useful measurement sector. In the wind sector used, the fetch varies from 200 to 400 metres, which can be considered satisfactory. The aerodynamic roughness length (z_0) of 0.5 m was calculated from the wind measurements by assuming the zero-plane displacement (d) to be 3/4 of the average height of the roughness elements (Thom 1971).

2.3 Instrumentation

2.3.1 Eddy Covariance Instruments

The eddy covariance measurements were performed on an elevatable platform at a height of 10 m. The measurement system consisted of an ATI SWS-211 sonic anemometer, a LI-COR LI-6262 CO_2/H_2O analyzer and a GFAS OS-2 ozone analyzer (see Table 1). The SWS-211 is a three-axis acoustic anemometer which also works as a fast-response thermometer, providing an accurate measurement of the virtual temperature, $T_v = T(1 + 0.61q)$ (Kaimal and Gaynor 1991). The measurements with the LI-6262 are based on the difference in absorption of infrared radiation passing through two gas sampling cells (LI-6262... 1991). The OS-2 is based on surface chemiluminescense reactions of ozone with an organic dye (Güsten et al. 1992). The relative accuracy of the OS-2 is adequate for eddy covariance measurements, but it has no absolute accuracy, so we used a slow-response ozone monitor based on UV-absorption for calibrating the OS-2 every half-an-hour.

The sonic anemometer was mounted at the end of a rotatable bar 2.5 m in length, directed manually towards the prevailing wind direction. The mouth of the inlet tubes for the OS-2 and the LI-6262 was attached 0.3 m away from the vertical wind component path of the sonic anemometer, resulting in a small lateral separation of the sensors. The length and the radius of the tube of the OS-2 were 0.7 m and 1 cm, respectively, and the flow rate was 100 l/min. For the LI-6262, the air was sampled through a tube of 1.55 mm in radius and 4 m in length. The flow rate was kept at 6 l/min, as controlled by a critical orifice. This

Table 1. Instrumentation at the Mekrijärvi site.

Component	Sensor	Height (m)	Data collection frequency (Hz)
Eddy covariance data			
CO_2	LI-6262, LI-COR, USA	10	5
H_2O	LI-6262, LI-COR, USA	10	5
O_3	OS-2, Gesellschaft für Angewandte Systemtechnik, Germany	10	10
O_3	Model 49, Thermo Environmental Instruments Inc., USA	10	0.1
3-D Wind	SWS-211, Applied Technologies Inc., USA	10	10
Air temperature	SWS-211, Applied Technologies Inc., USA	10	10
Meteorological data			
Air temperature	HMP35D, Vaisala, Finland	1, 3	
Surface temperature	DTS12G, Vaisala, Finland	0	
Humidity	HMP35D, Vaisala, Finland	1, 3	
Net radiation	Suomi-Franssila	3	
PAR	LI-190SZ, LI-COR, USA	3	

design guarantees a turbulent flow in the inlet tubes and consequently a small attenuation of fluctuations. A sampling rate of 10 Hz was used for the sonic anemometer and the OS-2. The LI-6262 data was collected through the serial port with an output rate of 5 Hz.

2.3.2 Supporting Meteorological Instruments

Additional meteorological data were obtained from a weather station situated 10 metres north of the eddy covariance tower. Temperature and humidity were measured at two heights (1 and 3 m). Temperature was also measured at the surface. Photosynthetically active radiation (PAR) and net radiation were measured at 3 m. Regarding radiation measurements, we had some tree shadowing problems in the afternoon, so all the afternoon radiation data had to be disqualified. The instrumentation of the meteorological tower is shown in Table 1.

2.3.3 Data Collection

Sonic wind and temperature data were input digitally from the SWS-211 to a personal computer (PC 386). The data from both O_3 monitors were digitized by the A/D converter in the SWS-211 and combined with wind and temperature data. The LI-6262 data were input directly to the PC through a second serial port. The collection was carried out by a modified version of a program due to McMillen (1986), using an averaging period of 30 min. The lags between the time series resulting from the air tubes and the lateral displacement of sensors were taken into account in the on-line calculation of the flux quantities. The lag time was determined by maximising the covariances between the vertical wind speed and the gas concentration. The drifts and trends not associated with turbulent transport were removed by using a 200-s running mean filter, and the coordinate frame was rotated to correct for a possible misalignment of the sensor (McMillen 1988). This procedure also provides a correction for non-optimal terrain. Ozone fluxes were corrected for the density fluctuations related to heat and water vapour fluxes (Webb et al. 1980). For the LI-6262 data this was not found necessary. By measuring simultaneously the carbon dioxide and water vapour concentrations the LI-6262 is capable of correcting the CO_2 concentrations proportional to dry air (LI-6262... 1991). Due to the damping of the temperature fluctuations in the inlet tube, the

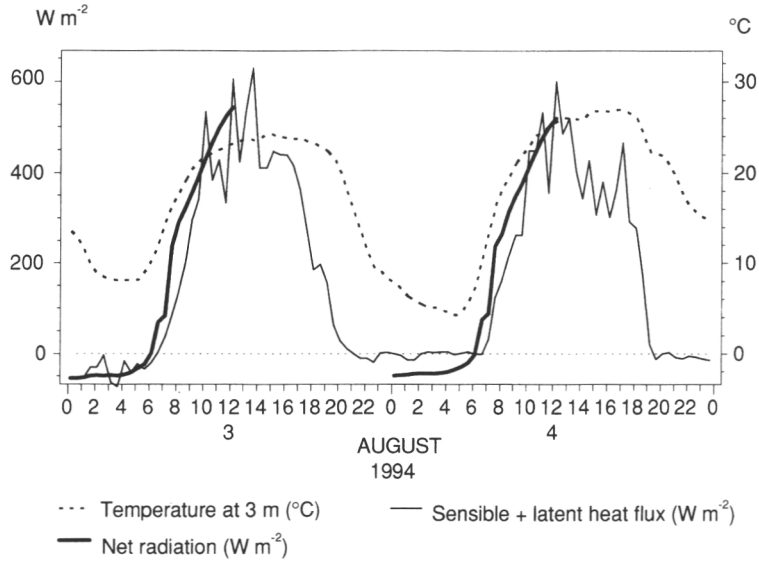


Fig. 1. The net radiation, the sum of the sensible heat and latent heat fluxes, and the temperature at the Mekrijärvi research site over a two-day period. The zero-level for all variables is marked with a dashed line.

corresponding heat-originated density fluctuations are assumed to be negligible.

All the supporting meteorological data were collected into a Vaisala QLI50 data-logging front end and archived by the PC 286. Data were saved as 10-min averages together with minima and maxima for each period.

3 Results

The measurement campaign was performed over the period 15 July to 5 August 1994. Due to the limited wind sector for acceptable flow conditions and some technical problems, part of the data obtained had to be discarded. Presented here are some results from the longest undisturbed period 3–4 August 1994.

3.1 Meteorological Conditions

On the selected days, 3–4 August 1994, the weather was fair, being almost cloudless on the 3rd but becoming partly cloudy at noon on the 4th. During the daytime the wind direction was in the sector 160° to 280°, with wind speeds varying mainly from 1.5 to 2.5 m s^{-1}. During the night before 3 August the wind direction was between 90 and 100 degrees. The night between 3 and 4 August was quite calm and the wind direction was unstable. The relative humidity was typically 50 % during the days, reaching almost 100 % during the night.

Time series of temperature, net radiation and the sum of the sensible heat flux and the latent heat flux are presented in Fig. 1. At 3 m the temperature varied from 5 to 27 °C, the fluctuation being somewhat smaller at 10 m. Net radiation is only presented for the forenoon because of the shadowing problems with the radiometers in the afternoon. Observed maximum PAR values on these two days were about 1300 µmol m^{-2} s^{-1}, corresponding to maximum net radiation values of 600 W m^{-2}. Fig. 1 shows that the total heat flux is very similar in magnitude to the net radiation. The components, the sensible and latent heat flux, are close to each other in magnitude, both having a maximum of 300 W m^{-2} in

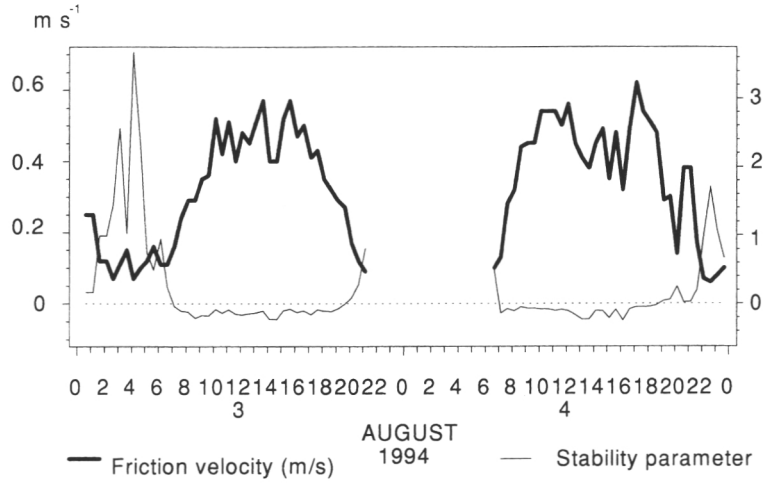


Fig. 2. The friction velocity and the dimensionless stability parameter at 10 m at the Mekrijärvi research site over a two-day period. The zero-level for all variables is marked with a dashed line.

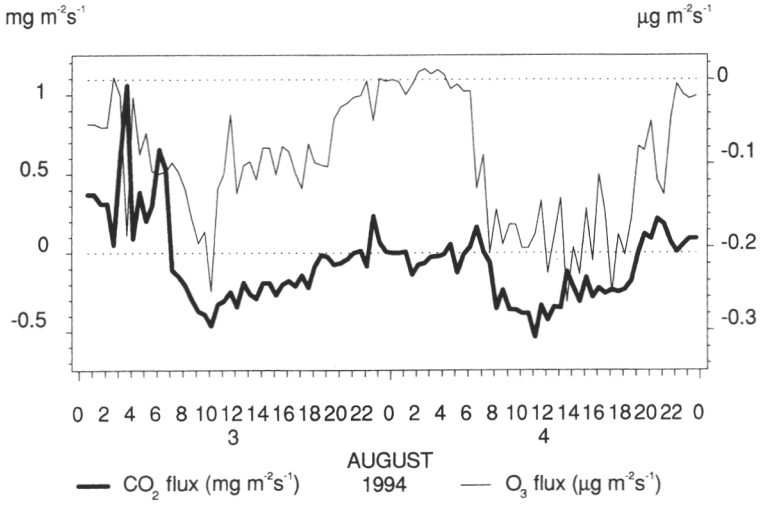


Fig. 3. CO_2 and O_3 flux densities measured at the Mekrijärvi research site. The zero-levels for the fluxes are marked with dashed lines.

the afternoon. In the forenoon, from 6 to 10 o'clock, the surplus of net radiation is converted into warming of the ground and biomass.

The turbulent properties of the flow can be characterised by two further quantities, the friction velocity and the stability parameter (Fig. 2). The friction velocity, $u_* = (-\overline{u'w'})^{1/2}$ represents the vertical flux of momentum and can be taken as a measure of mechanical turbulence. An appropriate measure of the surface-layer stability is the dimensionless height, $\zeta = (z - d) / L$, where z is the height above the ground, d the zero-plane

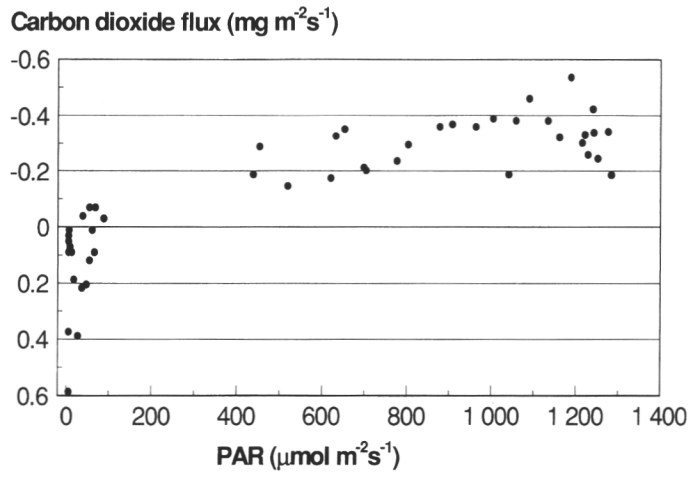


Fig. 4. CO_2 flux density versus PAR at the Mekrijärvi research site 3–4 August 1994. All afternoon observations have been discarded due to uncertain radiation measurements. Negative values represent downward flux.

displacement height and L the Obukhov length (the ratio of the turbulence production by buoyancy and shear forces, $L = -u_*^3 \overline{T_v} / (\kappa g \overline{w' T_v'})$, where $\kappa = 0.4$ is the von Kármán constant and g the acceleration due to gravity).

The strong diurnal cycle depicted in Fig. 1 is also present in the friction velocity and the stability parameter. During the daytime, the surface layer is moderately unstable ($\zeta \approx -0.2$ at z = 10 m) as a result of strong buoyancy, but it is rapidly stabilised as radiative heating is diminished. At the same time the mean wind and mechanical turbulence are reduced, and highly stable conditions prevail during the night (the data are discarded in Fig. 2 as the turbulent quantities become ill-defined).

3.2 CO_2 and O_3 Fluxes

Soil and vegetation can act both as a source and a sink for atmospheric constituents. The decomposition of organic matter releases carbon dioxide from the soil into the atmosphere, whilst for vegetation the fluxes are bi-directional (photosynthesis/respiration). For ozone, vegetation and the soil constitute a powerful sink, and no emission of ozone takes place. Ozone and carbon dioxide fluxes for the measurement period are shown in Fig. 3. Negative fluxes indicate deposition to the forest surface.

Both the daytime photosynthesis and the nocturnal respiration are observed in the atmospheric CO_2 fluxes. The ozone flux has a clear diurnal cycle having its maximum around midday and effectively vanishing for the duration of the night. Both fluxes are controlled by turbulent mixing and physiological processes. The effect of the atmospheric turbulence is seen clearly in the short-term co-variation between the fluxes in Fig. 3. During the daytime the variations in the curves are well correlated, while at night, when CO_2 is emitted from the soil and vegetation, they are anticorrelated.

The daytime changes in CO_2 fluxes can be explained by the variations in photosynthetically active radiation (PAR), which drives the assimilation. In addition, PAR largely controls the opening of leaf stomata, which form the primary pathway for respiration and the uptake of CO_2 by plants. Fig. 4 presents the observed relationship of the net CO_2 flux to PAR. The CO_2 uptake increases strongly with increasing radiation until a threshold value of 400 µmol m^{-2} s^{-1} is reached.

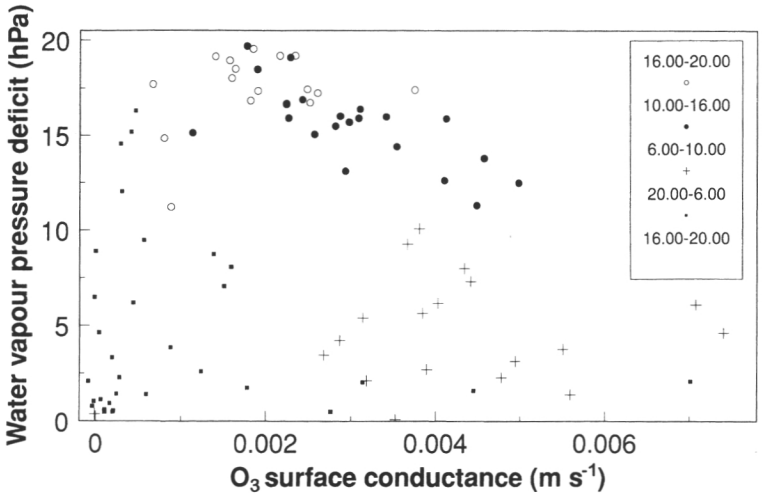


Fig. 5. Surface conductance of O_3 and water vapour pressure deficit. Symbols represent half-hour averages during the period from 3 August 00.40 to 5 August 9.40 (local time).

The direction of the net flux is reversed from net release to net uptake at a low PAR value of less than 100 μmol m^{-2} s^{-1}. At the higher end, increasing radiation does not much affect the carbon dioxide flux. All afternoon values have been discarded from this data set due to tree shadows on the radiometers, and therefore it is not possible to evaluate if the behaviour remains monotonous at higher PAR.

3.3 Dry Deposition Velocity of Ozone

Scaling the ozone flux densities by the mean concentrations produces a quantity, the deposition velocity $v_d = \overline{F_c} / \bar{c}$ of ozone, that can be used as a generalized measure of the deposition rate. Although the ozone concentration and the ozone flux both exhibit a diurnal cycle, they are not proportional by a constant value. Thus v_d also exhibits a diurnal cycle, which is governed by both the physiological functioning of the leaf stomata and the turbulent transport above the canopy.

The effect of the atmospheric processes can be differentiated by assuming the deposition process to be controlled by three series resistances, of which the surface resistance, r_s (or its inverse, the surface conductance), represents solely the biological and chemical affinity between the depositing component and the receptor surfaces. The surface resistance can be obtained from the flux measurements as a residual in the total resistance after subtracting the other two resistances, namely the atmospheric resistance r_a and the molecular resistance r_b, for which standard micrometeorological formulations exist (Garratt 1992, Hicks et al. 1987):

$$r_a = \frac{1}{\kappa u_*}\left[\ln\left(\frac{z-d}{z_0}\right) - \Psi_h(\zeta)\right] \quad (2)$$

and

$$r_b = \frac{2}{\kappa u_*} Le^{2/3} \quad (3)$$

where z_0 is the roughness length, Ψ_h is the diabatic influence function for heat and Le is the Lewis number (the ratio of diffusion coefficients for heat and gas). The bulk surface resistance obtained thus represents all the possible sinks of ozone, the most important of these being via stomata (e.g. Erisman et al. 1994b).

The surface resistance depends on a number of factors, including the dependence of the stomat-

al conductance on PAR, temperature, water vapour pressure deficit and water potential. Fig. 5 shows the surface conductance ($1 / r_s$) as a function of the vapour pressure deficit, VPD, which is defined as the difference between the temperature-dependent saturation vapour pressure and the water vapour pressure in the ambient air. Assuming that the leaf temperature equals the ambient air temperature, the VPD can be taken as a difference of water vapour pressures outside and inside the leaf and it can be used as a measure of the drying power of the air. A clear diurnal cycle is seen in the surface conductance, organized here as a circular shape that results from simultaneous cycles of humidity and radiation-derived forcings. The different times of the day are clustered in a way that shows higher conductances in the forenoon than in similar radiation conditions in the afternoon. This is most likely due to differences in the air humidity. In the forenoon the humidity is higher and and plants keep their stomata wider open. In the afternoon, when the air gets drier, plants try to save water and partly close their stomata, resulting in a decrease in the surface conductance.

Concerning the deposition velocity, the surface resistance constitutes the major part of the total resistance during most of the period considered in Fig. 3. Similar results have been obtained by e.g. Lamaud et al. (1994). Exceptions to this are periods with low wind speed and high hydrostatic stability, when the total resistance to deposition is dominated by the atmospheric resistance. A daytime (06-18 local time) mean value of 0.25 cm s^{-1} was obtained for the dry deposition velocity of ozone during the 2-day period, the 30-min averages ranging from 0.1 to 0.5 cm s^{-1}. Night values were typically less than 0.05 cm s^{-1}.

3.4 Accuracy of the Fluxes Measured by the Eddy Covariance Method

There are several sources of uncertainty involved in eddy covariance measurements, both of theoretical and practical origin, as summarised e.g. by Businger (1986). These are briefly discussed in this section. Theoretically, the assumptions justifying the use of Eq. 1 are never completely fulfilled, but the effects of horizontal advection and entrainment from above the boundary layer, for instance, are difficult to quantify. Chemical reactions below the measurement height potentially affect the flux divergence of chemically-active species like ozone. At Mekrijärvi this is not very probable, as the measurement site is not close to any significant NO sources.

In deriving Eq. 1, it is assumed that the mean vertical wind velocity is zero. Even in ideal flow conditions, non-homogenous terrain and misalignment of the anemometer may produce an apparent vertical wind component. These are corrected for in the applied acquisition programme by defining the coordinate system with respect to the streamlines of the flow (McMillen 1988).

In contrast with the other popular micrometeorological technique, the gradient method, the absolute accuracy is normally not a problem with the eddy covariance method. However, the averaging time being a compromise for stationarity, there remains a relatively large statistical uncertainty in the flux measurements because of the intermittency of the turbulent transport. With the averaging time of 30 min used here, an accuracy of 20 % can be expected for an individual flux value (van Pul 1992).

A part of the actual flux may be lost as a result of incomplete representation of the real turbulent spectrum. A small loss is due to the digital high-pass filter used to remove the non-turbulent motions which also depletes the low-frequency end of the covariance spectrum. The time constant of 200 s used here may cause a maximal flux reduction of 5 % in unstable conditions (McBean 1972). A more serious removal of contributing frequencies and the corresponding flux is likely to take place at the high end of the spectrum, if the response time of the analyzer is not adequate. Likewise, a small attenuation of high frequencies may be attributed to the separation of the gas sampling inlets from the wind sensor.

High frequencies may also be attenuated in the inlet tube especially if the tube flow is laminar (e.g. Leuning and Moncrieff 1990). In the present system, turbulent flow is maintained (the Reynolds number is 2800 for the LI-6262 tube flow), which results in a negligible attenuation of high-frequency concentration fluctuations, as calcu-

lated according to the theory presented by Lenschow and Raupach (1991). The damping of temperature fluctuations can still be important for the CO_2/H_2O measurements. In this study all fluctuations are assumed to have vanished and thus no density correction (Webb et al. 1980) is made. A proper way would be to take this correction into account partly depending on the portion of the remaining temperature fluctuations.

The time response of the fast ozone analyzer used in this study is better than 0.1 s (Güsten et al. 1992) and that of the CO_2/H_2O instrument proved to correspond to its sampling rate of 5 Hz when tested in the laboratory before the field campaign. Therefore, no frequency response corrections, as proposed e.g. by Moore (1986), were found necessary for the ozone data, though they might be appropriate for CO_2 and H_2O. Nevertheless, the analog filter applied to remove the aliased energy resulting from the noisy performance of the A/D converter may have lead to an average flux loss <~10 %. This was estimated on the basis of spectrum analysis of the Mekrijärvi data and the universal co-spectra developed for momentum and heat by Kaimal et al. (1972). The loss depends on the importance of the smallest turbulent eddies in the transport process, thus being least during unstable flow (daytime conditions).

With micrometeorological methods, measurements can be taken above the surface of interest without disturbing the surface itself. Instrumentation may, on the other hand, disturb the atmospheric flow. If not taken into account this may lead to considerable errors (Wyngaard and Zhang 1985), especially due to transducer shadowing of the acoustic anemometer. In the ATI instrument used in this study, the shadowing effect is corrected for internally. However, there remains the danger of flow disturbances by the measurement mast and individual surface elements.

Errors may also be introduced in the results inferred from the flux observations on account of necessary further assumptions, for instance, with respect to flux-gradient relations. Within the parameters presented here, the roughness length and the aerodynamic resistance are affected by the presumed flux-gradient profiles. The traditional profiles used also in this study have been shown to fail in the so-called roughness sublayer close enough to the roughness elements of the surface (Garratt 1992). It is possible that the aerodynamic resistances obtained in this study are somewhat overestimated as a result of this effect. However, as the aerodynamic part seldom dominates the total resistance, only small relative errors are introduced into the surface resistance.

4 Conclusions

Surface fluxes of O_3, CO_2 and H_2O were measured over a Scots pine stand by the eddy covariance technique. Results from a 2-day period were presented here. The eddy covariance method and the established measurement system has proved suitable for providing high-resolution data for studying ozone deposition to a forest and the net carbon balance and related physiological processes of an ecosystem.

Clear diurnal cycles were observed in the atmospheric fluxes of O_3, CO_2 and H_2O. Daytime changes in CO_2 fluxes are primarily caused by variations in photosynthetically active radiation. Ozone flux is interpreted here by calculating the deposition velocity and the surface conductance, the latter providing a measure of the purely biological and chemical part of the deposition process. It was observed that conductances in the forenoon are higher than in similar radiation conditions in the afternoon. This is most likely due to differences in the air humidity. This should be taken into account, for example, when evaluating the overstepping of critical levels from monitored ozone concentrations. The same concentration in the same radiation conditions can cause different doses depending on the environmental conditions.

In future the measurement system will be developed further, focusing especially on data screening procedures based on spectrum analysis. The parameterisation of the ozone flux will be extended to include a multi-path surface resistance so that the performance of suggested general parameterisation schemes (e.g. Erisman et al. 1994b) can be evaluated.

Acknowledgements

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Initial Results from the Boreal Ecosystem-Atmosphere Experiment, BOREAS

F.G. Hall, P.J. Sellers and D.L. Williams

BOREAS is a four-year, regional-scale experiment to study the forested continental interior of Canada. The objective of BOREAS is to improve our understanding of the interaction between the earth's climate system and the boreal forest at short and intermediate time scales, in order to clarify their role in global change.

During the winter, spring and summer of 1994, five field campaigns were conducted. About 85 investigation teams including nearly 300 scientists participated, including forest ecologists and ecophysiologists, atmospheric physicists, boundary-layer meteorologists, hydrologists, biochemists, atmospheric chemists and remote sensing specialists. Data from the field campaigns is being placed into a central archive at the Goddard Space Flight Center for immediate access by all participating scientists, and eventually by the outside scientific community.

Analysis of the data began in mid-summer as the data were being collected and continues at a rapid pace. The findings so far have been significant in terms of their implications for global change. The boreal ecosystem, occupying roughly 17 percent of the vegetated land surface and thus an important driver of global weather and climate, absorbs much more solar energy than is assumed by operational numerical weather prediction models. Albedo measurements in BOREAS shows that this forest absorbs nearly 91 percent of the sun's incident energy. Additionally, while it is known that much of the boreal ecosystem consists of forested wetlands, numerous lakes, bogs and fens, tower and aircraft measurements during 1994 show that the atmosphere above was extremely dry; humidity and deep boundary layer convection (3000 m) mimicked conditions found only over deserts. Physiological measurements of the trees during BOREAS show that this atmospheric desiccation was a result of the forest's strong biological control limiting surface evaporation. The data further show this tight control was linked to the low soil temperatures and subsequently reduced rates of photosynthesis.

BOREAS measurements also focused on net ecosystem carbon exchange. Data acquired during the late spring and summer, showed the boreal forest to be a net carbon sink. However, no measurements were taken in the early spring following thaw, and in the late fall, where the balance between photosynthesis and respiration is poorly understood. During 1996 additional data will be acquired to resolve the annual carbon budget and how it might depend on interannual climate differences.

Keywords BOREAS, boreal ecosystems, climate change, carbon exchange, Canada
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1 Introduction

The boreal ecosystem girdles the Earth above about 48 degrees north latitude and covers about 17 % of the earth's land surface (Whittaker 1975). It consists primarily of aspen and coniferous forests and is second in areal extent only to the world's tropical forests.

The role of the boreal ecosystem in influencing global climate and weather patterns is not well understood. It is well accepted now that variations in the ratio of sunlight reflected to that absorbed by land surface vegetation is a major driver of local and global atmospheric circulation. Light reflected back to space has little effect on atmospheric dynamics. On the other hand, light absorbed by vegetation, either heats the surface, in turn heating the lower atmosphere (sensible heat), or is released as evaporation (latent heat) which eventually condenses into clouds; the ratio of heat energy release to evaporative energy release can have very different effects on the dynamics of the lower atmosphere.

The role that the boreal ecosystem plays in global carbon dynamics, is also just emerging. Theoretical studies suggest that these forests play a strong role in cleansing the earth's atmosphere of excess carbon dioxide, by removing nearly 20 % of the annual emissions from fossil fuel combustion yearly (Tans et al. 1990). The exact mechanisms involved and the spatial contributions to this sink are as yet unknown, but the implication is that carbon is being stored in either living tissue or in the soil.

Other studies suggest however, that the areal extent and composition of the boreal forests might be greatly affected by rapid climatic change resulting from global warming (Davis and Botkin 1985, Solomon and Webb 1985) altering the vast stores of carbon accumulated since the last ice age. Such changes would alter the rate at which the boreal ecosystem accumulates or releases carbon thus accelerating or mitigating global warming. Such changes may also have feedback effects on the near-surface climatology, i.e. temperature, humidity, precipitation and cloudiness fields (Sato et al. 1989).

BOREAS was instigated to improve the understanding of the above interactions in order to clarify their roles in global change. BOREAS is a large scale, international investigation focused on improving our understanding of the exchanges of radiative energy, sensible heat, water, CO_2 and trace gases between the boreal forest and the lower atmosphere. A primary objective of BOREAS is to collect the data needed to improve computer simulation models of the important processes controlling these exchanges so that scientists can anticipate the effects of global change on the biome, in particular the effects of altered temperature and precipitation patterns.

2 Experiment Design

As shown in the accompanying graphic, BOREAS employed a multi-scale experiment design (see Fig. 1), permitting physiological, ecological and other information obtained at the leaf, plot and study area level, to be translated, via remote sensing and process models, to regional, and ultimately global scales.

BOREAS was designed to measure and verify what was known at the leaf and plot level about ecophysiology and the biophysics of nutrient cycling, and what was known at the mesoscale and global levels about surface/atmosphere interactions and atmospheric circulation dynamics. The design permitted knowledge at one scale to be translated and compared to knowledge and data at different scales. The goal of experiment design was to permit understanding of the regional scale well enough to simulate various scenarios of global change, and their consequences; thus, BOREAS was not a program of strictly monitoring to observe change over a long period, but rather to develop the understanding necessary to simulate processes over a wide range of scales.

For example, general circulation models run at very coarse spatial resolutions on the order of hundreds of kilometers; thus, one required scale of investigation in BOREAS was the 1000×1000 km scale. Since it is impractical, even with aircraft, to measure these energy/water/carbon fluxes over areas larger than about 40 km, another scale of investigation is about 50×50 km. This scale is small enough to permit ground and aircraft characterization, yet large enough to test scaling hypotheses with models and remote sens-

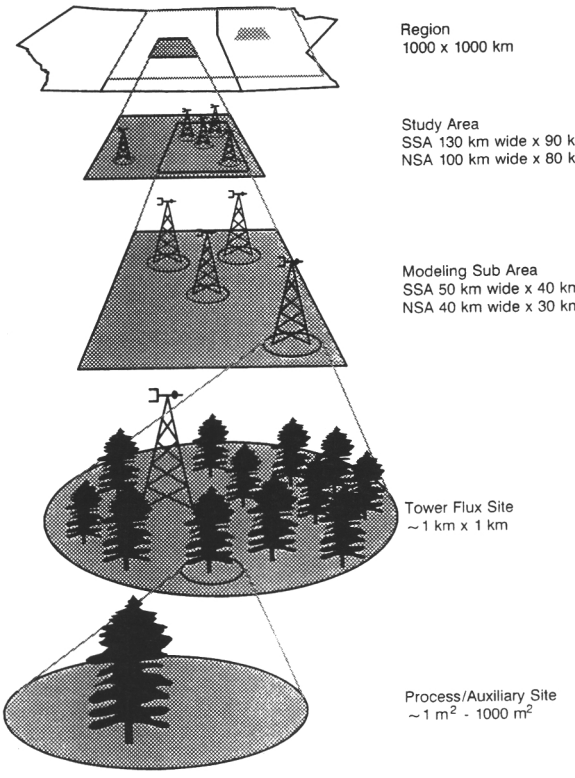


Fig. 1. Multiscale measurement strategy in BOREAS.

ing images. To verify the aircraft measurements of surface energy, water and carbon flux, and remote sensing estimates of biophysical parameters, measurements at a scale of about 1 km were utilized where towers were used to measure water, heat and CO_2 fluxes over relatively homogeneous patches. To characterize the ecophysiology, and biophysical characteristics these patches were subsampled with plots and within plots, measurements were made of site-level biomass density, leaf area index, light absorption, photosynthetic rate, litter decomposition and quality, soil moisture and temperature etc, all the variables needed to drive stand-level ecophysiological models.

A key tool that permits translation of this knowledge among scales is remote sensing, which in BOREAS was done at all scales from the leaf level using laboratory spectrometers, to the regional scale using satellite data such as the National Oceanic and Atmospheric Administration (NOAA) satellite series Geostationary Orbit Environmental Satellite (GOES) and the NOAA satellite series carrying the Advanced High Resolution Radiometer (AVHRR).

3 Implementation of the Experiment Design

To accomplish the measurements and modeling at the different scales required a large team of scientists, trained in the several disciplines involved. As shown in Fig. 2 over 85 teams were chosen through a competitive solicitation, and began work in 1993. These nearly 300 scientists were supported by a staff of about 11 people at the Goddard Space Flight Center (GSFC), who set up infrastructure, calibrated instruments, man-

Team	Team Name	Number of Teams
AFM	Aircraft Fluxes, Meteorology	14
TF	Tower Flux	10
TE	Terrestrial Ecosystems	21
HYD	Snow and Hydrology	10
TGB	Trace Gas and Biogeochemistry	10
RSS	Remote Sensing Science	21

Fig. 2. BOREAS science teams.

aged operations, did all the satellite data acquisition and analysis, and the very important job of building and maintaining a data system BOREAS Information System (BORIS) to distribute data to all BOREAS investigators as it becomes available. In BOREAS, every investigator has access to every other investigator's data, so BORIS serves the central function of acquiring the data from each investigator, putting it into a uniform format, working with the PI to document it, and putting it on line so that every one has access to it. In the end, the BOREAS data will be packaged, along with the documentation, and made available to the general science community.

In BOREAS many of the measurements were continuous or at least periodic. Some towers ran continuously, and some teams were in the field all summer. Certainly, satellite data were collected continuously. But to sustain an effort of this magnitude on a continuous basis is not possible, so periods were defined for intensive visits to the field by all investigators called intensive field campaigns. Experiment operations began in August of 1993 with an intensive field campaign (IFC) designed primarily to test equipment and operations procedures, but the major focus was the winter, spring, and three summer periods of 1994, of approximately two weeks each. The IFC's were spaced to catch the major phenological events, including a snow hydrology campaign in the winter, spring thaw, greenup, peak greenness, and beginning of senescence.

A variety of instrumentation was in place at the various scales. Beginning with the 1000 × 1000 km BOREAS region the existing operational meteorological network in Canada was augmented with nine automated meteorological stations acquiring the data needed to drive both the mesoscale and GCM models. In addition, satellite data was also collected or the entire region and aircraft transects flown between the Southern Study Area (SSA) and Northern Study Area (NSA) to characterize a transect between the two study areas.

At the study area level, two approximately 50 × 50 km study areas were located on the northern and southern edge of the boreal ecotone to capture a wide range of conditions for the driving variables (see Fig. 3). To characterize the study area energy, water and CO_2 flux, aircraft were used to fly flight lines at the edges of the study areas, and in grids over the study areas, using eddy correlation probes which permitted a computation of the area-averaged surface flux over a region, as well as the flow in and out the sides and boundary layer top of a three-dimensional box covering the area. A large part of the project operational management responsibility was to schedule these aircraft between the two study areas, and within the study areas, where often as many as eight aircraft operated at similar altitudes.

In each study area three boreal forest dominants were characterized by plot level measurements: black spruce, jack pine and aspen. Within each of these classes both mature and young regenerating stands were instrumented, as well as two wetland fens, one in the NSA and one in the SSA. Because the nine tower sites could not capture the range of variability in the region, an additional 70 auxiliary sites were also allocated, stratified by species type, productivity and age. In these approximately 100 × 100 m sites biometry and optical techniques were used to measure biomass density, leaf area index, NPP, litter

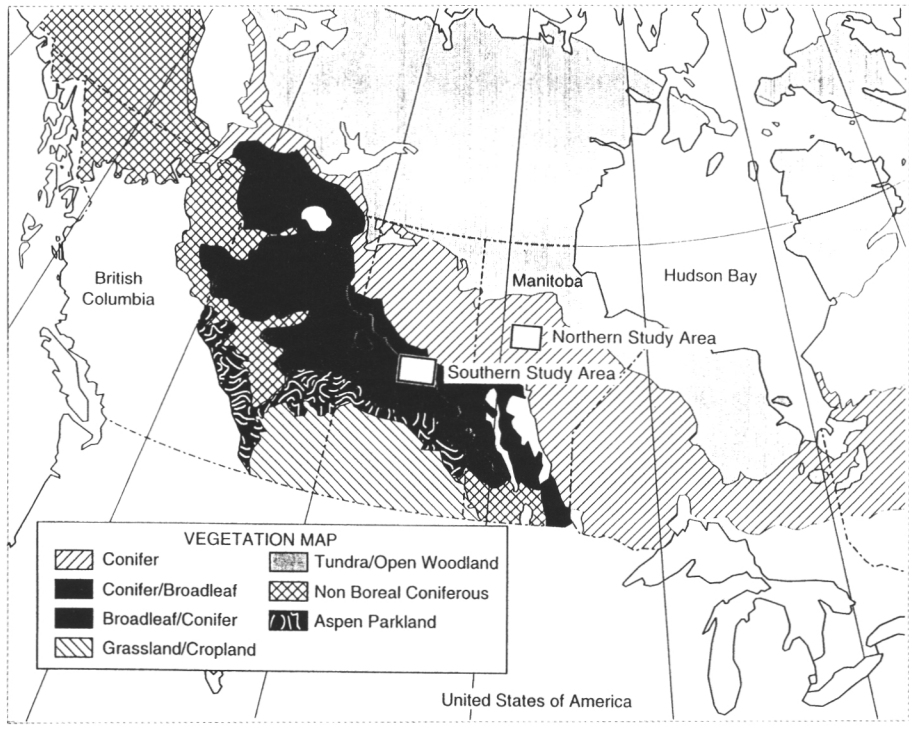


Fig. 3. Map of Canada showing location of the two BOREAS Study Areas and the major vegetation formations of the biome.

fall etc. While the models will be tuned primarily on the tower flux sites, the auxiliary sites will be used as independent test sites for model predictions.

In the NSA, where trace gas studies were concentrated, a number of beaver pond sites and a collapsed palsa were also instrumented to measure methane flux.

At all these sites a remote sensing science program was implemented to characterize the optical properties from the leaf level, using lab spectroradiometers, to the canopy and stand level using tower and helicopter mounted spectrometers, to the study area and regional level using aircraft and satellite platforms.

To fund and obtain the international cooperation required for a project of this scale required the collaboration of several US and Canadian agencies and other organizations from around the world. The US National Aeronautics and Space Administration (NASA) and the Canadian Center for Remote Sensing CCRS led the study, with support also from the National Oceanic and Atmospheric Administration (NOAA) and the National Science Foundation and Canadian agencies, the National Science and Engineering Research Council of Canada, Environment Canada, Agriculture and Agri-Food Canada, Canada Forest Service, and the National Research Council of Canada. There is also significant support from research agencies in the United Kingdom and France.

4 Operations

In August 1993, many of the BOREAS investigators and staff were in the study areas as part of an operational test, IFC-93. This 21-day IFC was used to test the experiment infrastructure and investigator's instruments as well as to re-

fine coordination and communication procedures. All of these experiences were pooled to rewrite the four volume experiment plan which served as the basis for running operations in 1994. During IFC-93 and the 1994 field campaigns, operations were coordinated out of two centers, one in the NSA and one in the SSA. Each center was equipped with ground-to-ground and ground-to-air radio links, telephones, fax machines, etc. to maintain real-time management of the airborne operations and related surface work. Nightly BOREAS Operations Group meetings analyzed the results of the days completed operations and set up the next day's activities. Weekly science meetings provided a useful forum for sharing scientific results and reviewing recent progress. In addition to Landsat and SPOT images, data were acquired from GOES; AVHRR and ERS-1 (European Resource Satellite) over the BOREAS region throughout the field year.

The last field campaign ended in September of 1994, and the first science workshop was held in December and the initial summary of results is presented in Sellers et al. (1995). Even at this early stage in the experiment, a fascinating picture is emerging of the energy, water and carbon dynamics of the boreal ecosystem and its strong coupling to the boreal soils and forest species types.

5 Results

A fundamentally new realization from BOREAS is that the composition of the boreal forests and soils may be as much a determinant of boreal climate as the boreal climate is of the nature of the boreal ecosystem. In addition, the parameters of the interaction between the boreal ecosystem and the atmosphere are quite different than previously believed.

Much of the boreal forest of central Canada grows on a nearly flat terrain composed of mineral soils deposited by glaciers and lakes during the last ice age. These soils are overlain by a thin layer of live and decomposed moss to which the tree's root systems are largely confined. Because annual precipitation exceeds evaporation, the moss layer and soil surface generally stays saturated, even throughout the summer. With an abundant water supply and the warm summer temperatures of central Canada, trees should be capable of sustaining large growth rates, and a correspondingly large capacity to transpire water to the atmosphere, humidifying the atmospheric boundary layer.

Instead, BOREAS tower and aircraft measurements of evaporation and heat release showed that the forest behaves more like a desert than a wetland. The transpiration rates observed from the coniferous forests were low on most days (< 2 mm/day) throughout the growing season. Figs. 4 and 5 show time-series of midday evaporative fractions (latent heat flux divided by the sum of the latent and sensible heat fluxes) and CO_2 fluxes, respectively, as reported by some of the TF sites during the intensive field campaigns. Again, we see some very low evaporative fractions (corresponding to high Bowen ratios) over most of the sites most of the time. These are associated with much lower CO_2 fluxes than are commonly observed over temperate forests (Verma et al. 1986). The exception to this generalization are the aspen and fen sites which after a rapid leaf-out in IFC-1 maintained the highest evapotranspiration and carbon draw down rates of all the sites. By contrast, the SSA Old Jack Pine site and the SSA Old Black Spruce site reported mean growing season evapotranspiration rates of around 1.3 to 2.0 mm/day, respectively. These two sites more or less bracket the range of wet (black spruce) and dry (jack pine) conditions over most of the BOREAS sites and present us with a new and unexpected picture of the partitioning of energy at the surface in this region. These data are consistent with those measured from eddy-correlation aircraft flying patterned grids over the study area.

For example, the National Research Council Twin Otter flux aircraft flew a total of 22 double-grid patterns (9 in the SSA, 13 in the NSA), during the 1994 IFCs. These patterns consisted of a series of nine 16-km parallel tracks with a spacing of 2.0 km. Three of the flux tower sites were contained within this grid. Many of the Twin Otter grid patterns were flown in coordination with the University of Wyoming King Air, which flew a 32×32 km grid that encompassed both the Twin Otter grid and another of the flux

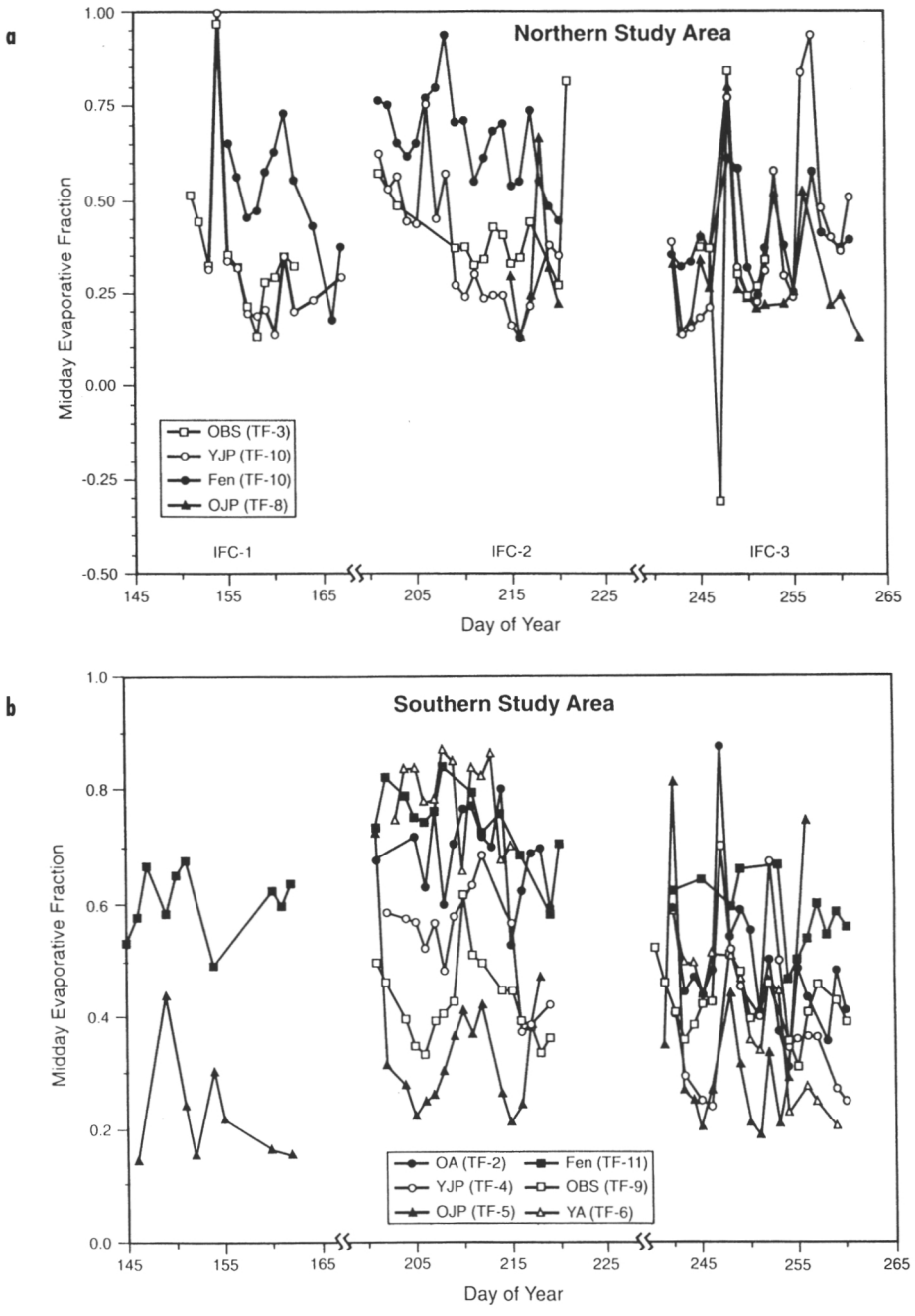


Fig. 4. Time-series of evaporative fractions (LE / (H + LE)). These were calculated from preliminary analyses of flux measurements averaged over a one-hour period centered on midday for each day of the IFC. (a) Northern Study Area, (b) Southern Study Area.

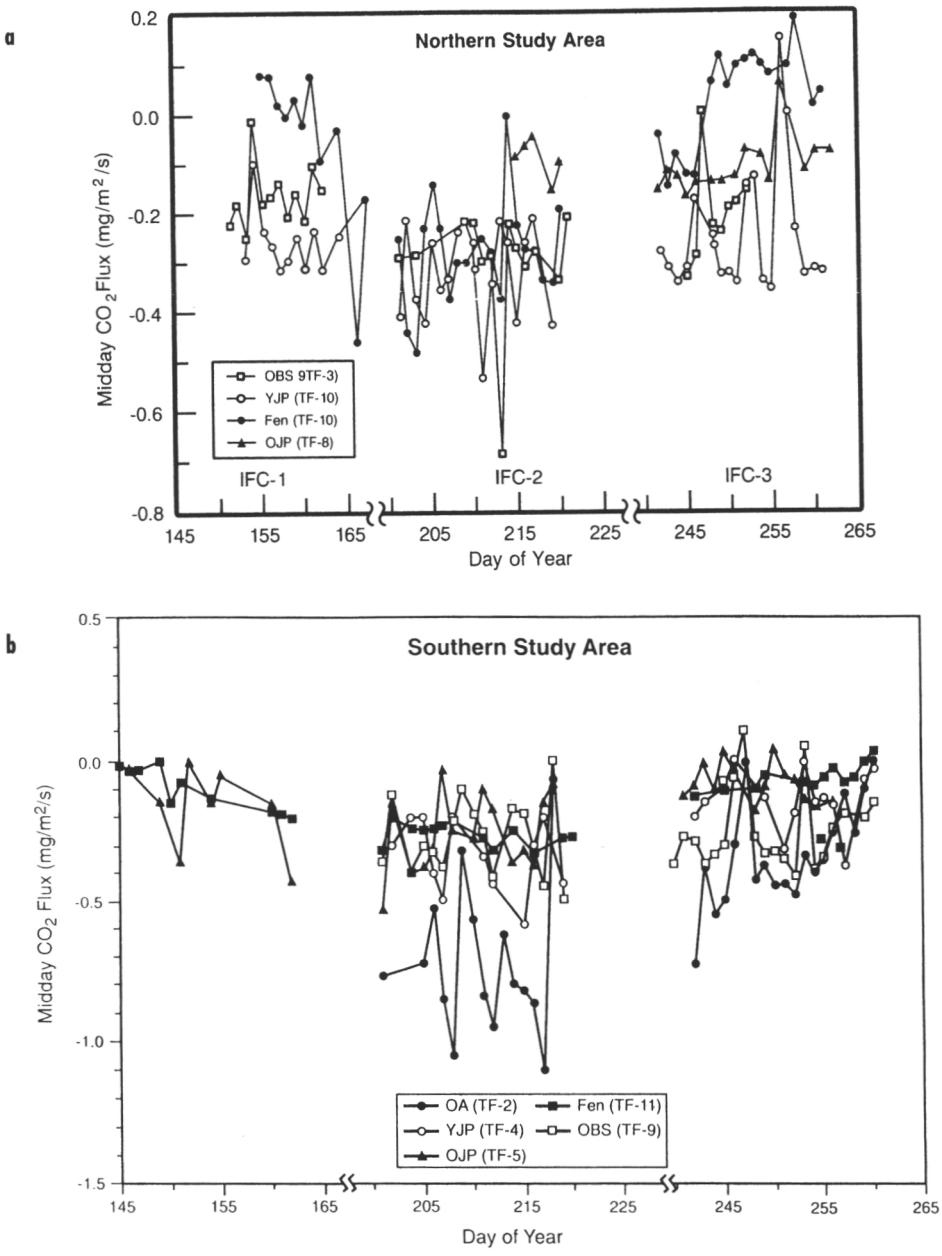


Fig. 5. Time-series of total (above canopy) CO_2 flux. These were calculated from preliminary analyses of flux measurements averaged over a one-hour period centered on midday for each day of the IFC. (a) Northern Study Area, (b) Southern Study Area.

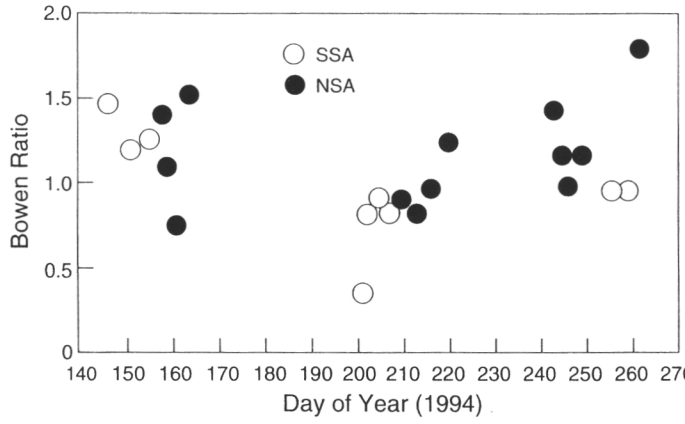


Fig. 6. Seasonal pattern of Bowen ratios for the SSA and NSA grid patterns as flown by the Twin Otter in BOREAS.

tower sites (Old Black Spruce). The Twin Otter was flown at an altitude of approximately 35 m, while the King Air operated at 60 m. On each occasion, the grid was flown twice, with the second pass flown in the opposite direction to the first. This procedure ensures that each pair of legs flown are time-centered on the same reference time, a technique designed to remove time trends from the data. Fig. 6 shows the Bowen Ratio (H/LE) computed from the sensible (H) and latent (LE) heat flux measured by the Twin Otter and averaged over all 18 runs of each double grid pattern.

Two points are worth noting: first, the SSA is generally associated with lower Bowen ratio values (i.e. higher latent heat fluxes) over the period and; second, the values are consistently high, that is the area-averaged daytime sensible heat flux is greater than the latent heat flux (Bowen ratio greater than one). These data were acquired under a wide range of radiation conditions, from smoky and cloudy through to clear-sky. Bowen ratios were consistently higher under clear-sky conditions. These high Bowen ratios suggest significant stomatal control by the vegetation. Other data collected in the experiment support this and indicate that under warm, clear-sky conditions, the stomata of coniferous trees tend to close down in response to the associated high atmospheric vapor pressure deficit, presumably a self-protective mechanism to prevent desiccation of the foliage and embolisms in the conducting tissue. By mid-morning stomata were responding to falling humidity as the atmospheric boundary layer expanded and dried from solar heating. The boundary layer expansion was accelerated by the evaporative shutdown of the vegetation. This positive feedback between the vegetation physiology and lower atmosphere resulted in deep convection by mid-morning, creating boundary layer heights greater than 3000 m, similar to those observed over deserts.

The key to understanding this somewhat unexpected picture of an atmospherically arid wetland ecosystem appears to lie with the low photosynthetic capacity observed for the boreal vegetation. Measurements showed that the boreal species have considerably less photosynthetic capacity than temperate forests to the south. This is reflected in low rates of annual carbon dioxide exchange with the atmosphere, and associated low carbon fixation rates. Low photosynthetic capacities in turn may be related to the limited root volumes of the forests and low soil temperatures with correspondingly low rates of nutrient cycling. Because transpiration of water from boreal vegetation is strongly coupled to photosynthetic rates, the boreal soils themselves and the adaptation of boreal vegetation to these harsh conditions, may provide a key to understanding boreal climatology and the effects of future climate change.

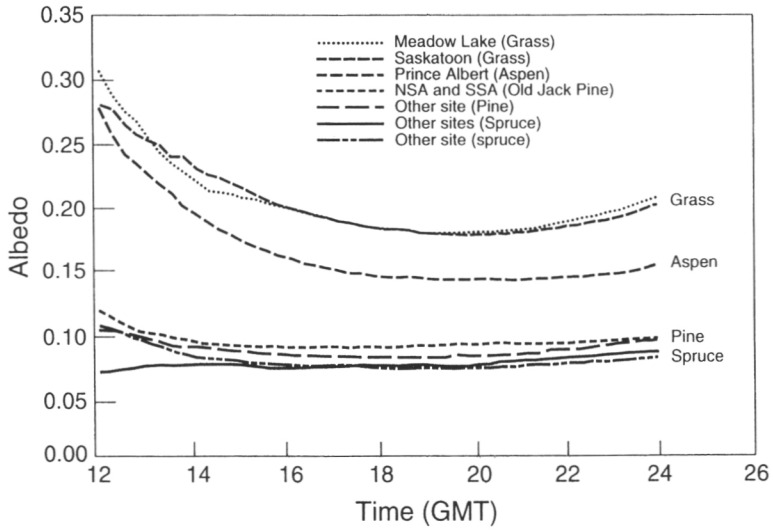


Fig. 7. Surface albedos for different vegetation covers found in the BOREAS region. The data were obtained from the BOREAS automatic meteorological station (AMS) network.

Another somewhat unexpected result is the very low albedos measured for the surface of the boreal forest. Fig. 7 was produced from analyses of the short wave radiation measurements made by the mesoscale network of automatic meteorological stations (AMS). Each AMS is equipped with upward and downward looking radiometers which allows for the direct calculation of albedos for the different vegetation covers found in the BOREAS region. The European Center for Medium Range Forecasting (ECMWF) model assumes that the boreal winter-time albedo prior to snowmelt is that of a bare snow-covered surface, i.e. about 0.8. However, the BOREAS AMS measurements show that during the winter, the coniferous canopy cover obscures the snow background almost completely, reducing the albedo of snow cover by an order of magnitude to about 0.08. The erroneous value for winter-time albedo in the ECMWF model causes large errors in the ECMWF predictions of surface air temperature by as much as 18 °C. During the non-winter months the ECMWF albedos are also higher than those measured in BOREAS. The grassland areas in the 1000 × 1000 km BOREAS study region show albedos of between 0.19 and 0.26, depending on solar angle, while the coniferous covers (Jack Pine and Spruce) show almost constant albedos of between 0.07 and 0.11 during the day. The fully foliated aspen cover with a total (canopy plus understory) leaf area index of between 4 and 5 has intermediate values. The variation in albedo with solar angle is a function of the heterogeneity of the surface cover and hence the amount of shadowing in the canopy: the spire-shaped crowns of the black spruce canopies generate a large proportion of shadowed area while the relatively diffuse deciduous and grass canopies behave more like classical turbid media with regard to radiative transfer and are therefore characterized by relatively strong variations in albedo with solar angle.

These and later findings should have significant implications for our understanding of how this important ecosystem influences weather, climate and other global processes. In an earlier similar study of the grassland prairies of the US called FIFE (Sellers and Hall 1992, Hall and Sellers 1995), scientists showed that more correctly accounting for the stored soil moisture and evaporative heat release in operational weather forecast models, permitted much more accurate predictions of the 1993 floods that inundated portions of the US Central Plains. Current

Table 1. Aerial fractions of landcover type as estimated from classification of composited AVHRR data over the BOREAS 1000 × 1000 km region.

Landcover type	% of total
Wetland conifer	27.0
low density	(5.0)
medium density	(14.5)
high density	(7.5)
Upland conifer	5.5
Mixed coniferous/deciduous	22.7
coniferous dominated	(8.1)
coniferous, deciduous codominant	(8.7)
deciduous dominated	(5.9)
Bare/very sparsely vegetated	6.5
Recent burn (< 5 years)	4.4
Visible regeneration from fire/logging	16.2
Open water	13.3
Unidentified	4.4

weather models do not realistically represent the boreal ecosystem; thus it is anticipated that the BOREAS results, when incorporated into operational forecast models, will greatly improve weather forecasts in the short term, as well as longer term climate simulations.

As mentioned in Section 3, to permit scaling the results from the plot level to regional and global levels, the BOREAS experiment design incorporated a remote sensing science component that utilized ground, aircraft and satellite remote sensing to provide a self-consistent set of vegetation biophysical properties (landcover type, LAI, biomass density, Fapar, etc.) at all geographic scales. These properties, along with their desired spatial and temporal precision were defined and prioritized by the scientific questions at stake in BOREAS. While the ultimate use of the remote sensing products will be as drivers of the carbon/energy/water process models at the various scales, a number of interesting findings have already emerged.

Beginning at the 1000 × 1000 km scale, AVHRR analyses by Steyaert et al. (personal communication) have shown the boreal biome in the BOREAS study area to be dominated by wet land and upland conifer (Table 1). The classes wetland conifer, upland conifer and coniferous dominated mixed class, occupy nearly 40 % of the region. Conifers in these classes are characterized by shallow rooting systems, and in general can be expected to display the same seasonal behavior observed for the black spruce and jack pine flux tower sites; i.e. low evaporation and carbon storage rates. Another interesting observation from Table 1 is that only about 14 % of the study region is deciduous forest, and is located mostly in the southern edge of the region. Finally, nearly 11 % of the region is relatively recently disturbed (< 25 yrs), primarily from naturally occurring forest fires. A majority of this disturbance occurs in the mid to northern reaches of the study region, which is sparsely settled and fire suppression is not practical. Open water will also play a significant role in regional energy balance since over 13 % of the region is in lakes. While these results are preliminary, they are being carefully evaluated by comparison to TM analyses over the BOREAS southern and northern study areas. The TM classifications are in turn thoroughly evaluated by comparison to auxiliary site data, thus permitting data collected at the plot scale to be extrapolated to the total BOREAS study region.

In addition to the optical remote sensing analyses, ERS-1 C-band imaging radar data were collected continuously during 1994 and will continue to be collected in 1995 on 3-day repeat intervals. Preliminary analyses show a large shift in backscatter between winter frozen and summer thawed conditions. The spring thaw transition shows a sharp rise in backscatter with the first early thaw and less pronounced shifts for subsequent freeze/thaw transitions. These data are being correlated with the onset of transpiration as indicated by in situ tree xylem flux measurements and other observations, see also Rignot and Way (1994).

6 Conclusions

In terms of data acquisition, and early science results, the 1993–1994 BOREAS field year must be considered a success with the collection of comprehensive surface, airborne and satellite data sets.

An unexpected picture of the energy, water and carbon dynamics of the boreal ecosystem is emerging, even at this early stage in the experiment. Observations show that the root zone of the wetland conifers, which comprise the bulk of these boreal forests, is very thin (< 40 cm deep) and is contained entirely within the live/decomposed moss (moss/humus) layer. As a result the boreal ecosystem often behaves like an arid landscape. Early in the growing season, the low soil temperatures inhibit the uptake of water by vegetation, while later in the growing season a combination of xylem (stem) resistance and vapor pressure deficit feedback responses act to strongly control the evapotranspiration rate. Most of the incoming solar radiation is intercepted by the vegetation canopies rather than by the moist underlying moss/soil surface which generally makes only a small contribution to the total sensible and latent heat fluxes. In addition, many areas have low water holding capacities so that much of the summer precipitation penetrates through the moss and soil to the underlying semi-impermeable layer and runs off. These strong controls on evapotranspiration result in the dissipation of much of the intercepted radiation as sensible heat. Consequently, a deep (> 3000 m) and turbulent atmospheric boundary layer can often develop over this ecosystem. These insights into the partitioning of the surface energy should have a significant impact on the development of climate and weather models, most of which currently characterize the boreal landscape as a freely evaporating surface.

Importantly, it would appear that the moisture level in the moss/humus layer does not get low enough to induce moisture stress in the overlying foliage. This implies that root zone moisture, a difficult variable to quantify over large spatial scales, does not exert a major control on the surface energy balance. Rather, the more important variables controlling photosynthesis and evaporation appear to be soil temperature in the spring, and atmospheric relative humidity and air temperature in the summer and fall.

This new understanding of controls on regional evaporation rates is relevant to the issue of whether the boreal ecosystem is a sink or source of carbon, but until the analysis is further along this question will remain unresolved. We have learned that sequestration of carbon by conifers, the largest component of the boreal ecosystem, is limited in the spring by frozen or cold soils, and in the summer by hot temperatures and dry air. In the fall, the conifers were observed to have the largest carbon uptake of the season; presumably as soils are warmed, the air temperatures are not so hot, and the air is not so dry. Leaf-level measurements suggest that the end of the growing season may be induced by flow air temperatures. Measurements show that at temperatures between –5 to –10 °C, black spruce needles do not photosynthesize. Measurements conducted throughout the winter indicate that the soils are a sustained source of respired CO_2 during the cold season.

Acknowledgements

As pointed out in the text, a large number of scientists, staffers participated in BOREAS. The results synopsized herein are the result of their hard work, creativity and dedication.

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First-Year Results on the Effects of Elevated Atmospheric CO_2 and O_3 Concentrations on Needle Ultrastructure and Gas Exchange Responses of Scots Pine Saplings

Virpi Palomäki, Kaisa Laitinen, Toini Holopainen and Seppo Kellomäki

The effects of realistically elevated O_3 and CO_2 concentrations on the needle ultrastructure and photosynthesis of ca. 20 year-old Scots pine (*Pinus sylvestris* L.) saplings were studied during one growth period in open-top field chambers situated on a natural pine heath at Mekrijärvi, in eastern Finland. The experiment included six different treatments: chamberless control, filtered air, ambient air and elevated O_3, CO_2 and $O_3 + CO_2$. Significant increases in the size of chloroplast and starch grains were recorded in the current-year needles of the saplings exposed to elevated CO_2. These responses were especially clear in the saplings exposed to elevated $O_3 + CO_2$ concentrations. These treatments also delayed the winter hardening process in cells. In the shoots treated with O_3, CO_2 and combined $O_3 + CO_2$ the P_{max} was decreased on average by 50 % (ambient CO_2) and 40 % (700 ppm CO_2). Photosynthetic efficiency was decreased by 60 % in all the treated shoots measured under ambient conditions and by 30 % in the CO_2 and $O_3 + CO_2$ treated shoots under 700 ppm. The effect of all the treatments on photosynthesis was depressive which was probably related to evident accumulation of starch in the chloroplasts of the pines treated with CO_2 and combined $O_3 + CO_2$. But in O_3 treated pines, which did not accumulate starch in comparison to pines subjected to ambient air conditions, some injuries may be already present in the photosynthetic machinery.

Keywords CO_2, O_3, Scots pine, needle ultrastructure, gas exchange, climate change
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List of symbols

P_n Net photosynthesis rate, μmol m^{-2} s^{-1}
θ Convexity of light response curve; dimensionless parameter with values of $0 \leq \theta \leq 1$
α initial slope of light response curve; photosynthetic efficiency, mol mol $photon^{-1}$
I photon flux density, μmol m^{-2} s^{-1}
I_c light compensation point of photosynthesis, μmol m^{-2} s^{-1}
P_m maximum rate of photosynthesis at saturating photon flux density, μmol m^{-2} s^{-1}
I_s light saturation point, μmol m^{-2} s^{-1}

1. Introduction

The concentrations of atmospheric CO_2 and O_3 are forecasted to rise to levels approximately double the present by the year 2100 (Dickinson 1986). The incorporation of ozone studies into climate change research has proved to be necessary since the ozone concentrations measured in Finland (Laurila and Lättilä 1994), especially in spring and early summer, momentarily exceed the levels believed to be harmful to sensitive forest vegetation. The effects of elevated CO_2 and O_3 concentrations on the photosynthesis of plants have been widely studied and they have been reported to be either stimulative or depressive depending on the dose, exposure time and environmental conditions (Bazzaz 1990, Bunce 1992, Weber et al. 1993, Ceulemans and Mousseau 1994, Flagler et al. 1994, Runeckles and Krupa 1994). Ultrastructural study of needles has proved to be a sensitive method revealing early stimulative or harmfull effects of ozone in several conifer species (Sutinen et al. 1990, Rantanen et al. 1994, Anttonen et al. 1995, Holopainen et al. 1996), but very little is so far known on the effects of elevated CO_2 alone or in combination with O_3.

The objective in this research is to study the effects of realistically elevated O_3 and CO_2 concentrations alone and in combination on the needle ultrastructure and photosynthesis of Scots pine saplings grown in open-top field chambers situated on a natural pine heath in eastern Finland.

2. Materials and Methods

2.1 Experimental Area

The experimental area is situated in a naturally regenerated stand of Scots pine (*Pinus sylvestris* L.) close to the Mekrijärvi Research Station (62°47'N, 30°58'E, 145 m a.s.l.) of the University of Joensuu in Finland. The heights of the saplings chosen for the experiment varied between 2.5 m and 3.4 m (mean 3.0 m) and their ages between 14 years and 24 years (mean 19). The mean stem diameter at 1.3 m above ground level was 5 cm and the number of stems was 2500 per hectare. The stand had not been fertilised during the lifespan of the experimental pines. The forest type of the site is of *Vaccinium* type (Cajander 1949) and soil is sandy moraine.

2.2 Experimental Design

Each experimental pine (20) was surrounded by an open-top chamber (about 10 m^3 volume, width 1.7 m and height 3.5 m) made of plastic sheet. A circular tube of perforated PVC membrane (diameter 250 mm) was located at the bottom of each chamber for distribution of air and experimental gases. The total air volume in the chambers changed once a minute. Five different treatments (four replicates) were arranged in the chambers: filtered air, ambient air, elevated O_3, elevated CO_2, elevated O_3 + CO_2. In addition five similar saplings serve as chamberless controls. Saplings for each treatments were selected randomly. CO_2 concentrations approx. doubled (ranges between 600 ppm and 800 ppm) compared to the ambient, and O_3 concentrations between 40 ppb (September) and 70 ppb (June) were maintained in the chambers. The total O_3 doses received by the saplings during the growth period and critical doses exceeding 40 ppb threshold concentration (AOT 40) are shown in Table 1. The exposure and controlling systems for the gases are computer-controlled. Exposure was started on 2 June and ended on 23 September in 1994. The time of exposure was 16 h per day (from 6.00 to 22.00).

Table 1. The total doses (>0 ppb) and critical doses exeeding 40 ppb (AOT 40) of O_3 in O_3 exposed chambers, filtered chambers and ambient air over the growth period of 1994.

Treatment	Total dose	Critical dose AOT 40
O_3	109 651	16 499
Filtered air	59 243	203
Ambient air	80 977	1 274

2.3 Needle Sampling and Microscopical Studies

Needle samples for microscopical studies were collected three times (9 August, 19 September, and 1 November) during the study year of 1994, from the first-order laterals on the fourth whorl from the stem apex both from current and previous year shoots separately from each sapling. The samples were directly placed in 2 % glutaraldehyde fixative prepared in phosphate buffer (pH 7.0, 0.1 M). Approx. 1 mm piece was cut from a region 1/3 behind the tip of each needle and prefixed for 20 h in glutaraldehyde fixative followed by postfixation in 1 % OsO_4 solution for 6 h at +6°C. After fixation, samples were dehydrated in a graded ethanol series and embedded in epon LX-112. Blocks were polymerized for one day at +37°C followed by three days at +60°C. Sections for electron microscopy (2 replicates) were stained with uranylacetate and lead citrate. Observations on the condition of cell organelles and cytoplasm were made using an electron microscope (JEOL JEM 1200 EX). The size of the starch grains and chloroplasts in the mesophyll cells were measured from electron micrographs (×10 000, 20–25 per series).

2.4 Gas Exchange Measurements

The gas exchange measurements were conducted using a portable open gas analysing system ADC LCA-4 (Analytical Development Co. Ltd. UK.) and employing a Parkinson leaf chamber for conifers (PLC4) with a portable light unit (PLU-002) and neutral density filters. The gas exchange results are given according to the silhouette shoot area (m^2) determined from still-video images (model Canon ION Still Video C-Camera RC-260, PAL High-Band). The images of the shoots were taken in the field in the direction parallel to the light beams from the light source.

Photosynthesis in saturated light was measured simultaneusly with needle sampling in August and September. The measurements were made under ambient CO_2 concentration (310–350 ppm) of the current-year shoots, i.e. of the same shoots as the needle samples prior to needle sampling.

The light response curves for fully developed current-year shoots, one shoot in each pine, were measured during the period 10–29 August, after one growing season of exposure to the treatments. The gas exchange measurements were conducted on the first-order laterals of the fourth whorl from the stem apex. The temperature of the shoot cuvette during measurements varied between 16 and 20°C. The measurements for each shoot were done under 350 ppm (ambient) and 700 ppm concentrations of CO_2. The CO_2 concentrations for the measurements were obtained from standard cylinders of CO_2 (AGA Ltd. Sweden).

2.5 Analysis of Gas Exchange Measurements

The non-rectangular hyperbolic equation (1) presented by Thornley and Johnson (1990) was fitted to the light response curve measurements conducted of a single shoot for each tree for the purpose of obtaining the values for the parameters.

$$P_n = \frac{1}{2\Theta}\left\{\alpha(I-I_c)+P_m-\sqrt{(\alpha(I-I_c)+P_m)^2-4\Theta\alpha P_m(I-I_c)}\right\} \quad (1)$$

Respectively, the light saturation point was calculated using the following equation (2).

$$I_s = \frac{P_m}{\alpha}\left[\frac{\rho-\Theta}{1-\rho}+\Theta(1+\rho)\right]+I_c \quad (2)$$

$\rho = P_n / P_m$ with the fixed value 0.7. The dark respiration was also calculated from the data.

2.6. Statistical Analysis

The data of the size of the starch grains and chloroplasts were subjected to analysis of variance (ANOVA). The individual means were compared by the Duncan's multiple range test and using general factorial ANOVA test (SPSS-PC programmes).

The means and standard deviations for the sampling of photosynthetic values and for the values of the different parameters were calculated. Furthermore, the photosynthetic values connected to sampling of needles and the model parameters were tested using the SPSS general factorial ANOVA test and the non-parametric Mann-Whitney U-test.

3. Results

3.1 Needle Ultrastructure

In the beginning of August, a significant increase in the size of chloroplasts in the saplings exposed to filtered air, elevated CO_2 and elevated $O_3 + CO_2$ concentrations compared to ambient air were measured (Table 2). Correspondingly starch grain size increased in saplings exposed to filtered air, elevated CO_2 and elevated $O_3 + CO_2$ concentrations in the current-year needles of the saplings (Fig. 1). In September, the starch grains were small or absent, and significant differences between treatments were no longer observable. In November, some delay in the appearance in the structural changes related to winter-hardening in the needles were observed. Especially in the needles of ambient air treatment and O_3 exposed saplings, chloroplasts were aggregated together and small vacuoles appeared in the cytoplasm, which is typical in winter condition. In the treatments, which caused accumulation of starch in summer (CO_2 and $O_3 + CO_2$), the chloroplasts were situated adjacent to the cell wall which is characteristic in summer condition (Fig. 2).

Table 2. The area of chloroplasts (mm^2) and starch grains (means±SD) measured from EM- photographs taken from the mesophyll tissue of current-year needles in saplings treated with elevated O_3 and CO_2 alone and in combination, filtered air, ambient air (air) and open air (out control) in August 1994 (a) and the main effects and interactions of the elevated O_3 and CO_2 (b).

2a.

Treatment	Chloroplast area	Starch grain area
O_3	10.6±2.5ab	5.6±2.6ab
$O_3 + CO_2$	15.9±5.9c	11.9±5.8c
CO_2	11.6±4.4ab	7.8±3.9b
Filtered air	12.4±3.6b	7.9±3.8b
Air	10.8±3.9ab	6.0±4.4ab
Out control	9.9±1.9a	4.9±3.9a
F	7.3001	10.1737
P	0.0000	0.0000

Means in the same column followed by different letters are significantly different ($P<0.05$).

2b.

	df	SS	F	P
Chloroplast area				
O_3	1	1335.067	5.433	.022
CO_2	1	2661.191	10.830	.001
$O_3 + CO_2$	1	1564.882	6.368	.013
Residual	92	22607.111		
Starch grain area				
O_3	1	1173.241	4.803	.031
CO_2	1	4896.553	20.047	.000
$O_3 + CO_2$	1	1686.082	6.903	.010

3.2 Photosynthesis Measurements During Sampling of the Needles

Compared to the chamber control (AIR = ambient air), the light saturated photosynthesis (P_{max}) decreased in all of the exposed pines, both in August and in September (Fig. 3, Table 3 and 4). The decrease was greatest in the shoots exposed to the filtered air and O_3 treatments and varied from 45 % and 40 % in August to 31 % and 17 % in September, respectively. In the CO_2 exposed shoots, the decrease was 27 % and 14 %, but in the $O_3 + CO_2$ exposed shoots only 6 % and 1 %, respectively.

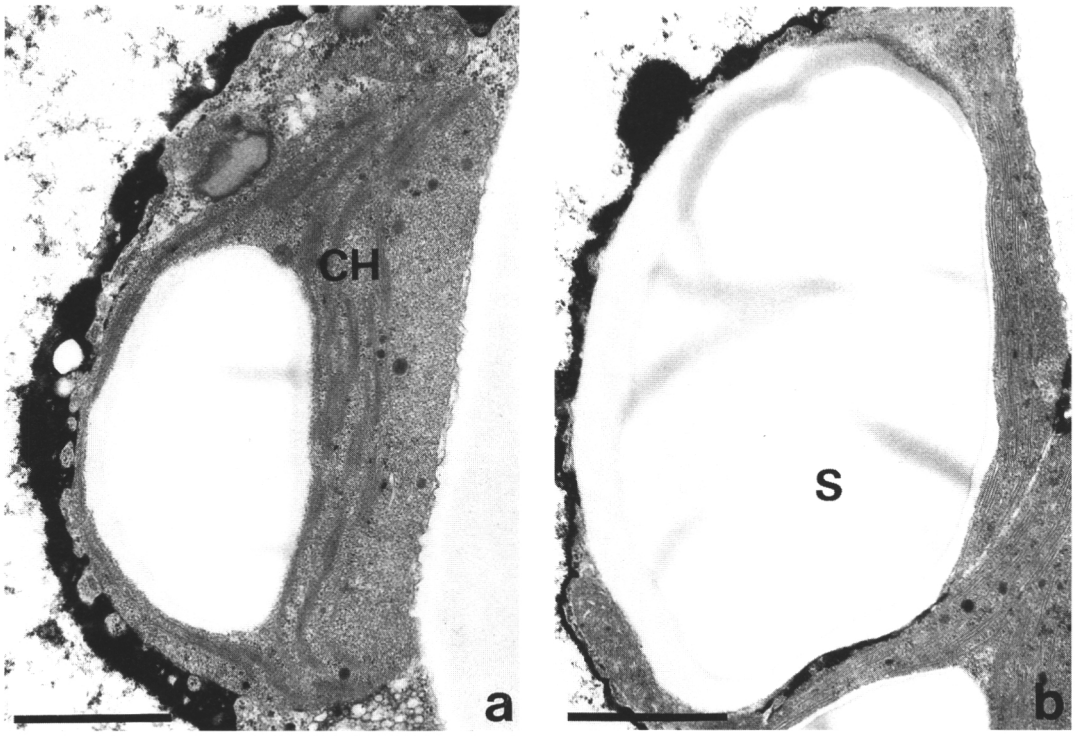


Fig. 1. (a) Normal structure of mesophyll chloroplasts (CH) in the needles of saplings subjected to ambient air treatment in August. (b) Accumulation of starch (S) in a chloroplast in the needles of elevated O_3 + CO_2 treatments in August.

3.3. Light Response Curves

In the O_3, CO_2 and combined O_3 + CO_2 treated shoots the *maximum rate of photosynthesis* (Fig. 4a) decreased by 44–59 % measured under ambient and 30–47 % under 700 ppm of CO_2 as compared to the chamber control (AIR = ambient air) (Tables 5 and 6). Respectively, the decrease was 12 % and 44 % in the filtered air treatment of shoots.

Compared to the values of the chamber control (AIR), *dark respiration* (Fig. 4b) decreased by 39–67 % in the shoots exposed to O_3, O_3 + CO_2, CO_2 and filtered air treatments when measured under the ambient CO_2 level. Respectively, under CO_2 concentration of 700 ppm, dark respiration increased by 13–84 % in shoots subjected to the O_3 + CO_2, CO_2 and filtered air treatments as was also the case with the chamberless control (out control) shoots (Table 5 and 6). In the O_3 exposed shoots under the 700 ppm concentration of CO_2, the dark respiration rate decreased by 48 %.

Compared to the values of the chamber control *light compensation* (Fig. 4c) increased by 115 % and 130 % when measured under the ambient and by 63 % and 163 % when measured under the concentration of 700 ppm of CO_2 in O_3 + CO_2 and CO_2 exposed shoots (Table 4). In the O_3 exposed shoots there was a great increase in the parameter value (287 %) measured under the ambient but a decrease (76 %) measured under 700 ppm concentration of CO_2. In the filtered air treatment there was an increase of 88 % in light compensation when measured under the 700 ppm CO_2 concentration.

Light saturation increased in the O_3, O_3 + CO_2, CO_2 and filtered air treated shoots. The increase was 24–90 % when measured under the ambient and 16–105 % when measured under a CO_2 concentration of 700 ppm (Fig. 4d, Table 4).

Photosynthetic efficiency i.e. the initial slope

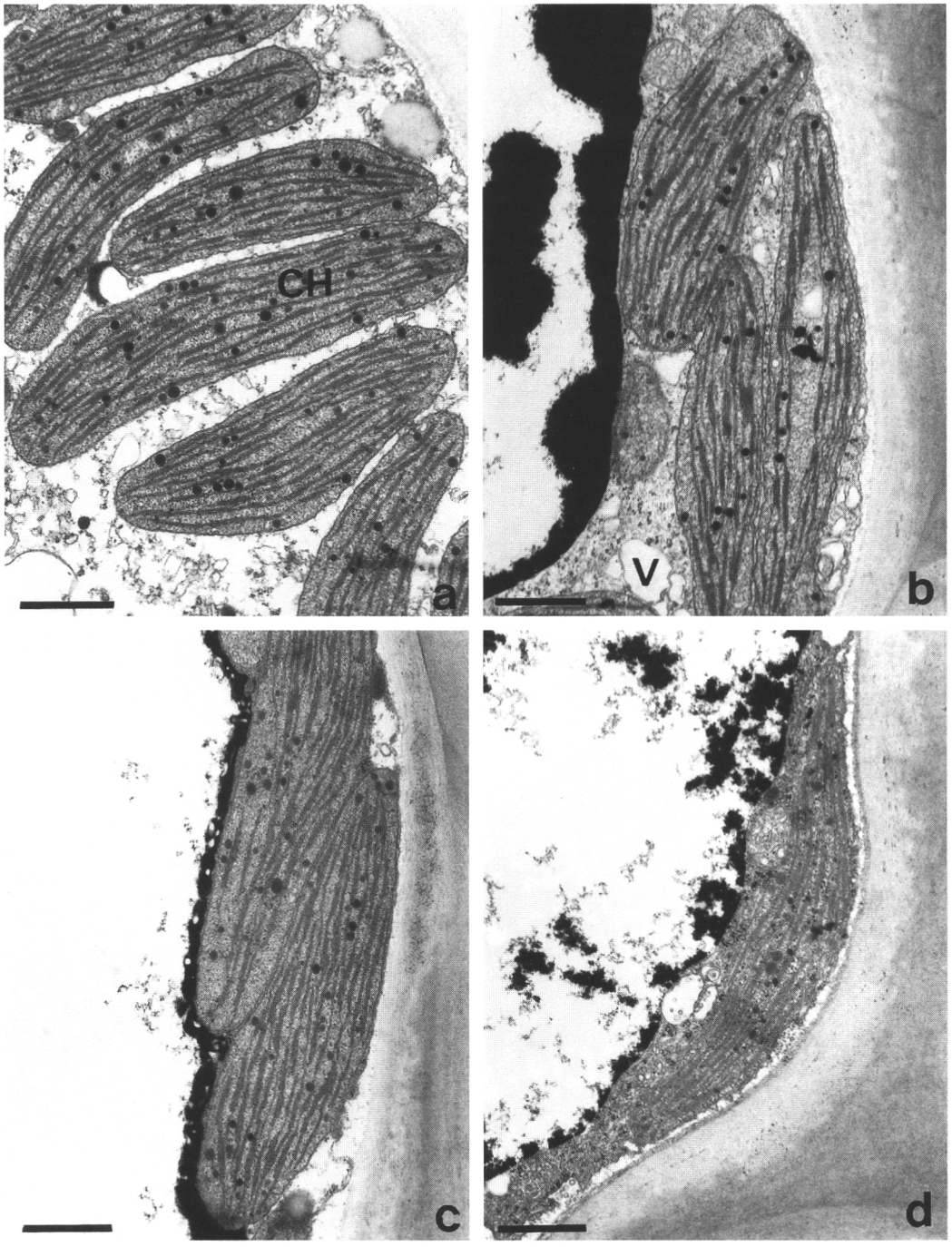


Fig. 2. Mesophyll cell from the needles of samples subjected to different treatments and sampled in November. a–b. The chloroplasts (CH) in needles treated with ambient air (a) and O_3 (b) have aggregated and small vacuoles (V) have appeared in the cytoplasm; this is typical for the winter situation. c–d. The chroloplasts are situated adjacent to the cell wall in needles treated with elevated CO_2 (c) and $O_3 + CO_2$ (d); this is typical in summer.

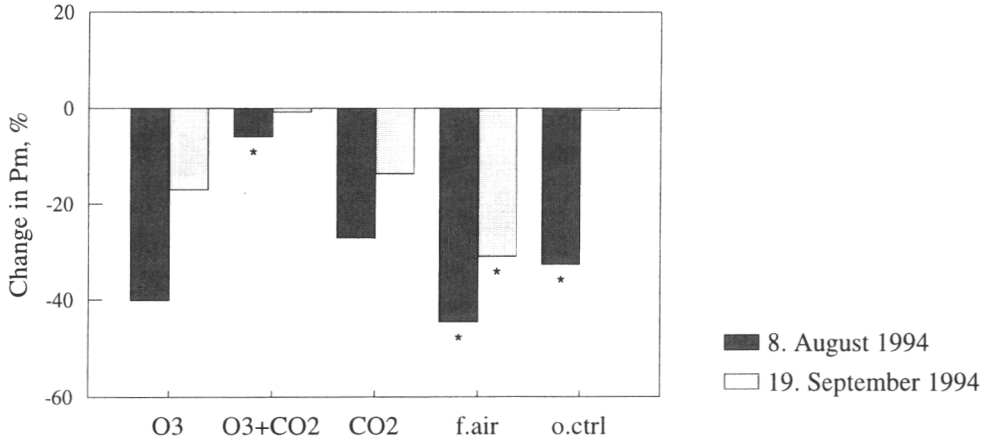


Fig. 3. The relative change (%) in the maximum rate of photosynthesis as compared to the value for the chamber control in August and September; * denotes a statistically significant difference ($p<0.05$).

Table 3. The maximum rate of photosynthesis ($\mu mol\ m^{-2}\ s^{-1}$, means±SD) measured in connection with needle sampling in August and September.

Treatment	August	September
O_3	16.67± 2.79	12.83±7.91
$O_3 + CO_2$	26.19±11.76	15.35±5.21
CO_2	20.29±11.34	13.35±6.49
Filtered air	15.46± 5.42	10.67±2.08
Air	27.85± 6.15	15.47±4.34
Out control	18.73± 8.52	15.41±5.52

(Fig. 4e), decreased in the O_3, $O_3 + CO_2$, CO_2 and filtered air treated shoots. Compared to the chamber control, the decrease was 52–62 % when measured under the ambient CO_2 concentration (Table 4a). When measured under a concentration of 700 ppm, the decrease was 8–38 % (Table 4b).

Convexity of the curve (Fig. 4f) decreased in the O_3, $O_3 + CO_2$, CO_2 and filtered air treated shoots compared to the chamber control. The decrease was 10–52 % when measured under the ambient concentration and 11–67 % under a CO_2 concentration of 700 ppm (Table 4).

Table 4. The statistical analysis for the needle sampling photosynthesis data. The main effects and interactions (ANOVA) of the treatments elevated O_3 and CO_2 (a) and the Mann-Whitney U -test for chamber control (air) vs. out control and filtered air (b). * denotes a statistically significant difference ($p<0.05$).

4a.

	df	SS	F
August			
O_3	1	85.26	1.08
CO_2	1	11.71	0.15
$O_3 + CO_2$	1	892.54	11.26*
Within and residual	45	3566.82	
September			
O_3	1	0.85	0.02
CO_2	1	0.34	0.01
$O_3 + CO_2$	1	45.22	1.15
Within and residual	30	1179.89	

4b.

vs. air	Time	Z	2-Tailed P
Out control	August	–2.4398*	0.0147
	September	–0.2407	0.8098
Filtered air	August	–3.6373*	0.0003
	September	–2.5019*	0.0124

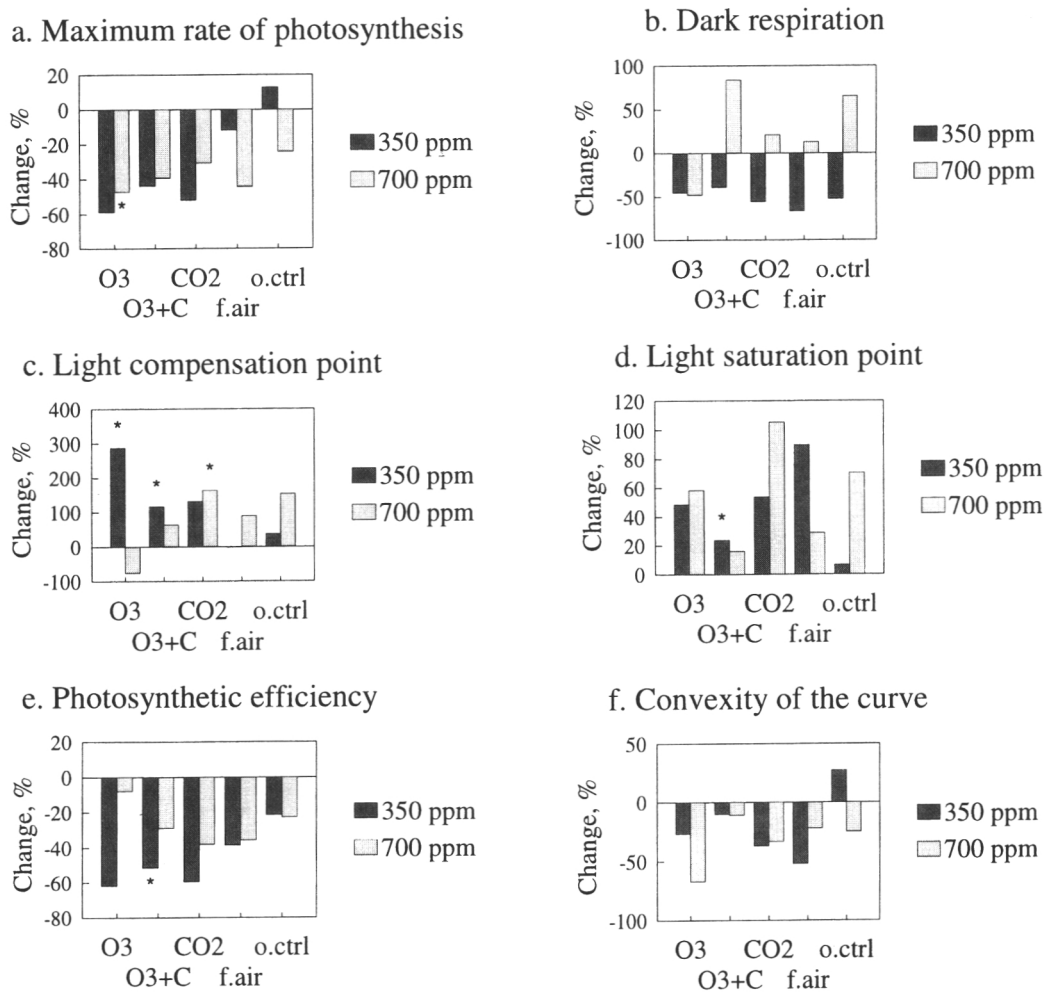


Fig. 4. The relative change (%) in the parameter value as compared to the value in the chamber control (AIR) under 350 ppm and 700 ppm; a) maximum photosynthesis, b) dark respiration rate, c) light compensation point, d) light saturation point, e) photosynthetic efficiency, f) convexity of light response curve; * denotes a statistically significant difference ($p<0.05$).

4. Discussion

The effects of elevated concentration of CO_2 and O_3 on different species of plants have been widely studied in different exposure levels and durations (Barnes et al. 1990, Bunce 1992, Ceulemans and Mousseau 1994, Flagler et al. 1994, Clark et al. 1995). In this study we report the effects of elevated CO_2, O_3 and their combination to the needle ultrastructure and photosynthesis of Scots pine after one growing season exposure.

The effects of elevated CO_2 and O_3 and their combination on photosynthesis appeared to be depressive. The reduction could be related to the accumulation of starch in chloroplasts in plants subjected to the CO_2 and combined O_3 + CO_2 treatments, because chloroplasts may have been saturated by starch earlier in the summer (e.g. Carmi and Shomer 1979). However, the reduction of net photosynthesis was lowest and starch accumulation most clear in combined O_3 + CO_2 exposure in the simultaneous photosynthesis and microscopical studies. In earlier studies Carmi

Table 5. The values for the parameters (meansSD), P_m = maximum photosynthesis, R_d = dark respiration rate, I_c = light compensation point, I_s = light saturation point, α = photosynthetic efficiency, θ = convexity of the light response curve, under the treatments measured under 350 ppm (a) and 700 ppm (b).

5a. 350 ppm Treatment	P_m	R_d	I_c	I_s	α	θ
O_3	12.57± 3.04	1.97±0.91	156±30	969±247	0.0248±0.0077	0.378±0.175
$O_3 + CO_2$	17.16±10.48	2.19±1.20	87±60	807±145	0.0315±0.0170	0.463±0.205
CO_2	14.67± 9.10	1.60±0.78	93±23	1072±227	0.0263±0.0133	0.324±0.119
Filtered air	26.95±11.89	1.20±0.32	40±14	1237±268	0.0399±0.0044	0.248±0.080
Air	30.53±10.92	3.58±4.33	40±34	652±224	0.0650±0.0253	0.515±0.321
Out control	34.40±12.66	1.72±0.57	55±36	695±128	0.0510±0.0137	0.665±0.173
5b. 700 ppm Treatment	P_m	R_d	I_c	I_s	α	θ
O_3	33.83±12.67	1.02±0.76	8± 6	875±550	0.0843±0.0523	0.257±0.343a
$O_3 + CO_2$	38.88± 3.81	3.59±2.47	52±33	640±157	0.0650±0.0276	0.700±0.023ab
CO_2	44.40± 9.74	2.36±1.29	84±19	1134±798	0.0566±0.0033	0.525±0.369ab
Filtered air	35.67± 1.32	2.21±0.84	60±27	713±342	0.0589±0.0089	0.612±0.278ab
Air	64.03±13.71	1.96±1.24	32± 5	553± 99	0.0914±0.0079	0.785±0.042b
Out control	48.39±21.30	3.23±1.88	81±39	941±669	0.0707±0.0197	0.588±0.225ab

and Shomer (1979) reported accumulation of starch in bean exposed to elevated CO_2 concentration but Robertson and Leech (1995) measured reduction in starch accumulation in wheat.

Our results indicating depression of photosynthesis after one growing season under elevated CO_2 concentration are contrary to what is reported in an earlier study with long-term exposure (Wang et al. 1995) made in the same area in the open top chambers with the same species using the same measuring technique. Wang et al. (1995) reported slightly enhanced photosynthesis (14 %) and decreased dark respiration (20 %) for a Scots pine grown for two years under doubled CO_2 concentrations compared to the chamber control. In general, variable results have been obtained when studying the effect of elevated CO_2 concentrations, but down-regulation in photosynthesis and decrease in dark respiration after long-term exposure has often been reported (Bunce 1992, 1995, Ceulemans and Mousseau 1994) in deciduous species. In conifers both increase or no acclimation of photosynthesis has been reported in long-term studies. In seedlings of *Pinus radiata* Hollinger (1987) reported no difference in assimilation after 120 days at 340 or 640 ppm of CO_2. Correspondingly, Teskey (1995) reported no change in assimilation of *Pinus taeda* after 157 days under elevated CO_2, as also a decrease in respiration after elevated CO_2 treatment. Tissue et al. (1993) studied *Pinus taeda* seedlings after two years under elevated CO_2 and reported an increase in assimilation, but only when the seedlings received supplemental nitrogen.

In the present study, O_3 exposure did not induce initial starch accumulation to the chloroplasts, which has been observed in several other fumigation studies with slightly elevated O_3 concentrations (e.g. Luethy-Krause and Landolt 1990, Rantanen et al. 1994). Environmental conditions e.g. limited nutrient availability may have reduced the stimulative effect of low O_3 concentration in the present experiment (Wallin et al. 1990, Rantanen et al. 1994). In the present study the depression of photosynthesis may be an early indication of the harmful effect of O_3, although the O_3 exposure did not cause advanced injury symptoms like increased density of chloroplasts stroma and clearly decreased size of chloroplasts and starch grains (e.g. Sutinen et al. 1990) in the needle ultrastructure during the study

Table 6. The statistical analysis for the light response parameters (P_m = maximum photosynthesis, R_d = dark respiration rate, I_c = light compensation point, I_s = light saturation point, α = photosynthetic efficiency, θ = convexity of the light response curve) measured under 350 ppm and 700 ppm. The main effects and interactions (ANOVA) of the treatments elevated O_3 and CO_2 (a) and the Mann-Whitney U-test for chamber control (air) vs. out control and filtered air (b). * denotes a statistically significant difference ($p<0.05$).

6a.

Treatment	df	P_m SS	P_m F	R_d SS	R_d F	I_c SS	I_c F	I_s SS	I_s F	α SS	α F	Θ SS	Θ F
350 ppm													
O_3	1	205.01	2.35	0	0	10349.28	5.99*	12612.01	0.29	0	3.23	0	0
CO_2	1	109.88	1.25	1.06	0.30	232.04	0.13	30317.01	0.69	0	2.70	0.01	0.18
O_3+CO_2	1	356.61	4.11	1.18	0.33	12793.22	7.40*	224960.5	5.13*	0	5.44*	0.07	1.25
Within and residual	10	872.53		35.56		17282.54		438571.1		0		0.53	
700 ppm													
O_3	1	850.59	10.99*	0.02	0.01	2106.96	5.02	19415.76	0.07	0	0	0.08	1.13
CO_2	1	141.88	1.83	6.49	2.68	6188.72	14.74*	80460.93	0.29	0	1.93	0.02	0.31
O_3+CO_2	1	406.32	5.25	2.98	1.23	37.41	0.09	444253.0	1.61	0	0.16	0.33	4.51
Within and residual	7	541.76		16.96		2938.93		1935782		0.01		0.51	

6b.

vs. air	P_m Z	P_m 2-Tailed P	R_d Z	R_d 2-Tailed P	I_c Z	I_c 2-Tailed P	I_s Z	I_s 2-Tailed P	α Z	α 2-Tailed P	Θ Z	Θ 2-Tailed P
350 ppm												
Out control	–0.5774	0.5637	–0.2887	0.7728	–0.5774	0.5637	–0.2887	0.7728	–0.8660	0.3865	–0.8660	0.3865
Filtered air	–0.4629	0.6434	–0.9258	0.3545	–0.9258	0.3545	–1.8516	0.0641	–0.9258	0.3545	–0.9258	0.3545
700 ppm												
Out control	–0.3873	0.6985	–0.7746	0.4386	–1.5492	0.1213	–0.3873	0.6985	–1.5492	0.1213	–1.5492	0.1213
Filtered air	–1.8516	0.0641	0	1	–1.8516	0.0641	–0.4629	0.6434	–1.8516	0.0641	–1.3887	0.1649

period, which lasted over one summer. The early decrease in assimilation may be associated with changes in Rubisco functioning as reported by Pell et al. (1992), who also reported a decline in photosynthetic efficiency in several species after exposure to O_3.

In long-term O_3 exposures a reduction in assimilation rate has been a common response as reported by Barnes et al. (1990) and Wallin et al. (1990) in *Picea abies* and by Flagler et al. (1994) in *Pinus echinata* and by Weber et al. (1993) and Clark et al. (1995) in *Pinus ponderosa*. Both Barnes et al. (1990) and Wallin et al. (1990) found increased dark respiration in *Picea abies* after long-term O_3 exposure. As in this study Barnes et al. (1990) reported an increase in light compensation in *Picea abies* after long-term O_3 exposure.

In the present study the elevated CO_2 concentration alone and in combination with O_3 appeared to delay the structural winter-hardening process (e.g. Soikkeli 1980) in the cells of Scots pine needles, which needs further attention involving frost tolerance measurements. If winter hardening process is continuously delayed, this may have serious consequences for the frost tolerance of the trees in harsh continental climate, like in Eastern Finland.

The results presented in this study are rather preliminary, since the experiment is planned to last at least two more years and the tree responses will be studied with several methods in the future. The results already available indicate, however, that slightly elevated ozone concentrations may have negative effects on the photosynthetic efficiency of naturally growing young Scots pines. After longer duration of O_3 exposure, decreased photosynthesis may be followed by structural injuries of chloroplast (Sutinen et al. 1990, Wallin et al. 1990) also in the present experiment. Although the accumulation of starch was increased in new needles of the seedlings grown at higher CO_2 level , there was no direct evidence that elevated CO_2 provided additional protection against harmful effects of O_3. This is in agreement with the observations of Barnes et al. (1995) dealing with Norway spruce.

Acknowledgements

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Total of 28 references

Combined Effects of Elevated Winter Temperatures and CO_2 on Norway Spruce Seedlings

Oddvar Skre and Knut Nes

A total of 1800 3-year old seedlings of Norway spruce (*Picea abies* (L.) Karst.) from two Norwegian and one German provenance were treated with two different nitrogen levels during the 1992 growth season. The plants were kept during the following winter at two different temperature levels. In the spring of 1993 the nutrient application was resumed, and the plants were divided between three different treatments, 350 and 650 p.p.m. in open top chambers and a control plot outside the chambers. This treatment was repeated also during the following 1994 growth season.

The growth and primary production was studied by photosynthesis experiments and by non-destructive growth measurements.

The results indicate that raised winter temperatures may lead to increased needle loss and reduced growth the following season, particularly in northern provenances.

Carbon dioxide significantly influenced growth in addition to nutrient level and winter temperature. High CO_2 also seemed to cause increased photosynthesis at early season, and earlier budbreak and growth cessation than in control plants.

Keywords winter temperatures, carbon dioxide, spruces, growth, photosynthesis
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1 Introduction

One of the major topics of present-day research is the growing concern about the effects of the expected rise in greenhouse gases, particularly CO_2. According to climatological models (GCM) a doubling of the CO_2 concentration would cause a 3–4°C increase in winter temperatures and about 2°C in summer temperatures (Pedersen 1993). A side-effect of raised temperatures would be a more rapid decomposition and uptake rates of nitrogen in soil.

In the present study the emphasis has been placed on the combined effect of raised winter temperature and increased CO_2 level on trees.

As test plant has been chosen Norway spruce (*Picea abies* (L.) Karst.).

In spruce and other evergreens the excess of assimilated carbon is usually stored in evergreen leaves. The carbon reserves are mobilized next spring, and enable the plants to overcome the critical period with negative photosynthesis, and to produce new leaves, that eventually take over as carbon producer (Rutter 1957).

The induction of winter dormancy in fall takes place through photoperiodic reactions and is only slightly influenced by temperature (Håbjørg 1972, Heide 1974).

When the low temperature requirements for dormancy breaking are fulfilled, however, usually in January, high temperatures would lead to earlier budbreak, and induce higher metabolic activity in buds and needles (Ritchie 1982, Heide 1993). As a result of a longer growth period, plants would therefore increase their growth potential, but at the same time earlier budbreak would more easily expose plants to frost damages due to sudden cold periods in spring, particularly in continental areas and ecotypes (Jalkanen and Nikula 1993).

Another effect of high winter temperatures would be a longer period with negative carbon balance at mid-winter, due to high winter temperatures combined with low light intensities (Printz 1933) This could lead to a temporary shortage of carbohydrates in plants during the growth period in spring (Stewart and Bannister 1973). On the other hand earlier dormancy breaking would lead to increased photosynthesis in evergreen needles when light conditions are improving in February and March after dormancy breaking (Hagem 1947, Aalvik 1939). The overall effect on the carbon balance could therefore become positive in some woody species and negative in others.

In an earlier study (Skre 1995) high winter temperatures were found to cause a lower carbohydrate level in needles and heavy needle loss, particularly of old needles, the following spring. Consequently, a strong reduction was found in growth and biomass the following season.

The aim of the present study is to follow the growth processes in the investigated spruce plants, and to see to what extent the expected rise in CO_2 level would help resuming growth after a winter with exceptionally high temperatures, by increasing photosynthetic rates and biomass production.

2 Material and Methods

Three years old spruce seedlings, raised from mixed seed populations within three provenances, were transplanted into plastic containers (diameter 12 cm) with fertilized peat in the spring of 1992. For peat composition see Skre (1991). The provenances were as follows:

Harz, Germany (52°N), 420–470 meter (H5)
Östfold, Norway (59°N), 50–150 meter (C1)
Hedmark, Norway (61°N), 250–350 meter (B3)

The C1 provenance was intermediate in its responses between the B3 and H3 provenances (Skre 1995), and the actual results from the growth measurement are therefore not shown for the C1 plants, but they are included in the variance analysis.

The plants were placed under a birch canopy (light intensity 300–400 $\mu molm^{-2}s^{-1}$ PPFD) and added two strengths of SUPERBA nutrient solution, equivalent to 1 or 10 $gm^{-2}year^{-1}$ nitrogen once a week over the season (May-October). For composition of nutrient solution, see Skre (1991). The ratios between the concentrations of nutrients were kept unchanged. In late November the plants were moved into two greenhouse compartments, simulating ambient temperature conditions and 4°C raised winter temperature (see Fig. 1a). A constant temperature difference of about 4°C was achieved by means of a differential temperature controller.

In late April 1993 the plants were moved into six open top chambers with normal (350 p.p.m.) and high (650 p.p.m.) CO_2 level, and with control plants outside the chambers.

The CO_2 treatment continued until early November. The remaining plants, eight per replicate and with three replicates per treatment, were moved into the two greenhouse compartments, and the winter temperature treatment was repeated (Fig. 1b). In early May 1994 the plants

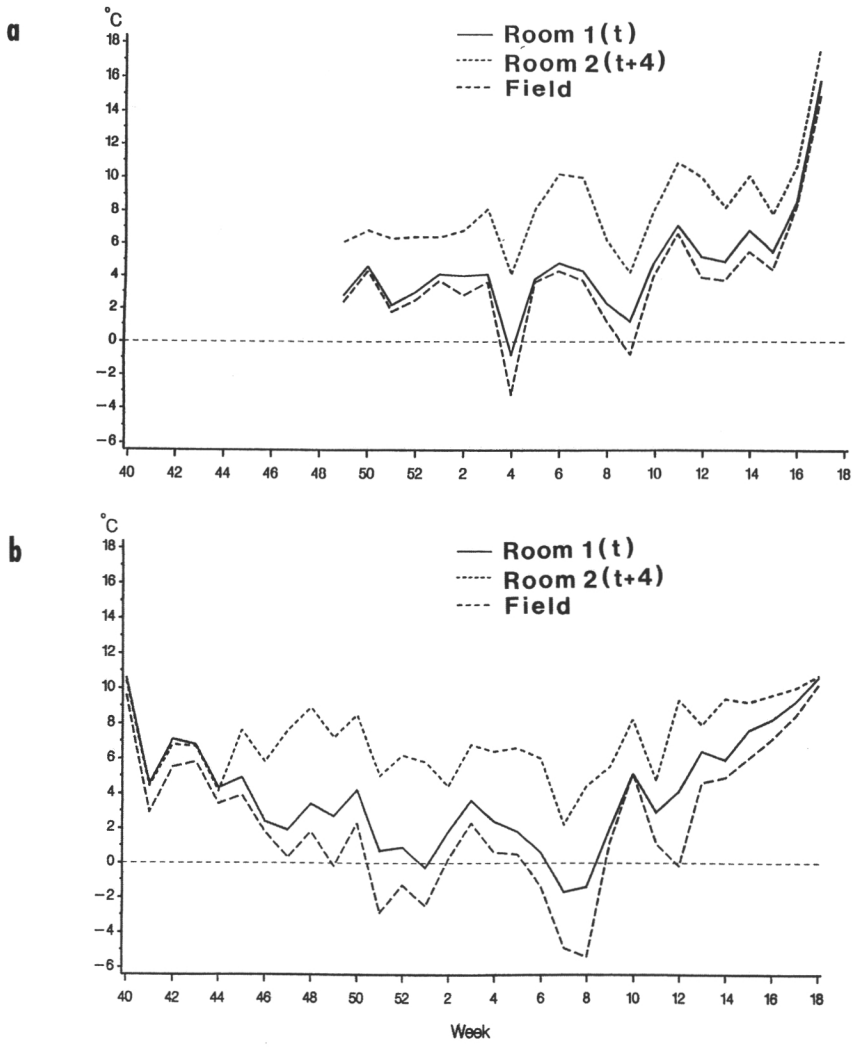


Fig.1. Weekly mean and extreme temperatures during the winter 1992/93 (a) and 1993/94 (b) in the low (t) and high (t+4) temperature rooms, and in field. Fig. 1a is a redrawn from Skre (1995).

were moved into open top chambers and the CO_2 treatment was repeated until late October.

Subsamples of plants and needles were taken for biomass determination throughout the experiment, and shoot length, stem base diameter and needle density were measured at intervals.

The temperature and CO_2 content in the open top chambers and in the greenhouse were monitored continuously and data stored in a datalogger. Also the data from one light probe (Lambda LI-185B quantum sensor) and the humidity probe were recorded, the probes were placed in one open top chamber during the summer and in the greenhouse during the winter season.

The CO_2 exchange measurements of net photosynthesis and respiration rates were made in a closed system using a Li-COR 6200 transportable system with a clear plexiglass chamber (volume 1190 cm^2) equipped with a Lambda Li-185B quantum sensor, thermocouple and humid-

ity sensors. 2-year-old shoots from the upper whirl were used. The total area of the shoot was estimated from the length and width of needles, needle density and shoot length. After an equilibration time, that was found to be three minutes for photosynthesis and ten minutes for dark respiration measurements, six measurements, once every 5 ppm subsequent drop in the CO_2 level, were taken at 10–40 seconds intervals.

The fitted light response curves at early and late season at a given temperature (16–20°C) were found according to Farquhar and Caemmerer (1982) and Leverenz (1994). The temperatures were close to the measured optimum temperatures at saturation light levels (Skre unpubl.). All variables were tested by GLM variance analysis (Goodnight 1976) in order to find significant effects and interactions.

Table 1. Variance ratios (F) and significance levels for needle density (cm^{-1}) of shoots from the 1991 age class (n_2), measured Dec. 28, 1992 and June 12, 1993, and shoots from the 1992 age class (n_3), measured June 12, 1993. The plants have been subjected to different nutrient levels and winter temperatures. Significant levels are * = $p < 0.001$; + = $p < 0.01$; ° = $p < 0.05$. DF = degrees of freedom. R_2 = square multiple correlation coefficient. SS = sum of squares.

Source	DF (n_2)	Dec. 28. (n_2)	June 12. (n_3)	June 12.
Provenance	2	102.5*	54.1*	10.6*
Nutrient level	1	0.2	3.0	11.6*
Winter temp.	1	0.0	125.4*	72.1*
Prov × nut	2	1.5	1.3	1.2
Prov × temp	3	1.2	14.5*	12.0*
Nut × temp	1	1.7	6.1°	9.4+
Prov × nut × temp	2	0.7	0.7	0.6
Block	9	0.7	3.2+	1.0
Error SS	99	116.2	422.3	407.7
Total SS	119	373.4	1718.8	1029.6
R^2		0.69	0.75	0.60

3 Results

The observations on needle density from the first winter (1992/93) were evaluated by running a three-way variance analysis on the observed values before and after the winter season on age class 1991. In addition a separate test was run on age class 1992 after the winter season. The results are presented in Table 1.

The stem base diameter underneath the lowest side branch (means of two measurements at right angels) was measured on October 27, 1994 after

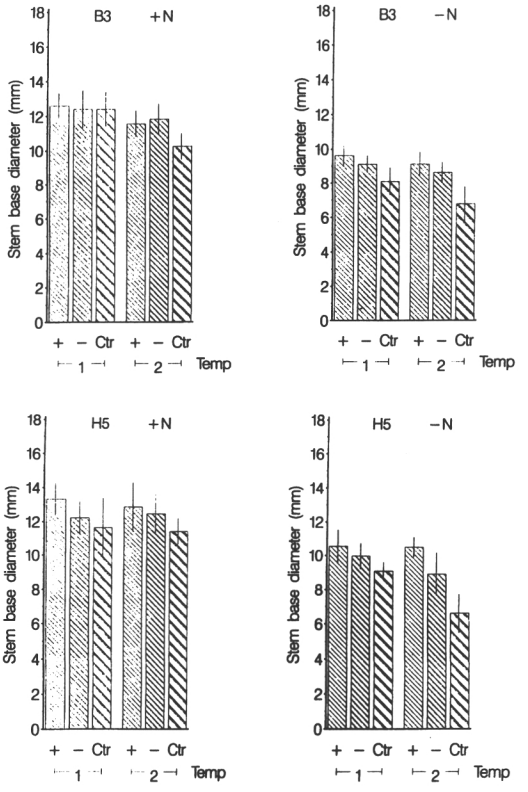


Fig. 2. Stem base diameter (mm) in October 1994 in fertilized (+N) and non-fertilized plants (–N) from a German (H5) and a Norwegian (B3) provenance, grouped according to CO_2 and winter temperature treatment, where the symbols are: high CO_2 (+), low CO_2 (–), outside open top chamber (Ctr.). High (2) and low (1) winter temperature. Means of 24 observations per treatment and provenance, with ±2 s.e.

two summers with normal and raised (650 ± 50 ppm) CO_2 level and two winters with normal and 4°C raised winter temperatures on the same plants. The stem base diameter is a measure of the accumulated growth during the whole 2-year period. Fig. 2 shows the results, as compared with measurements on control plants outside the open top chamber.

The needle density measurements of April 1994 presented in Fig. 3 are only shown for plants grown at normal CO_2 level, because CO_2 had only slight and hardly significant influence on this growth parameter. The needle densities are mainly influenced by nutrient levels and winter temperatures. The density in young 1993 needles (n_3) is influenced by the temperature during the preceeding 1993/94 winter (Fig. 1b), while the densities in the 1992 age class (n_2) are also influenced by the extremely mild 1992/1993 winter (Fig. 1a), that caused heavy needle loss the following spring (Skre 1995).

The length of the apical shoot at May 26, 1994 (Fig. 4) may be used as a measure of budbreak time. The result is only shown for fertilized Norwegian spruce plants.

The growth of annual shoots usually took place from May to July, after which there was a period with only secondary growth in stem and root, and bud development. In some plants, however, there was a new short period with apical growth in late August and early September. This is called Lammas growth. The length of these "Lammas shoots" may be used as a measure of the budset time, or time of growth cessation in shoots. Fig.

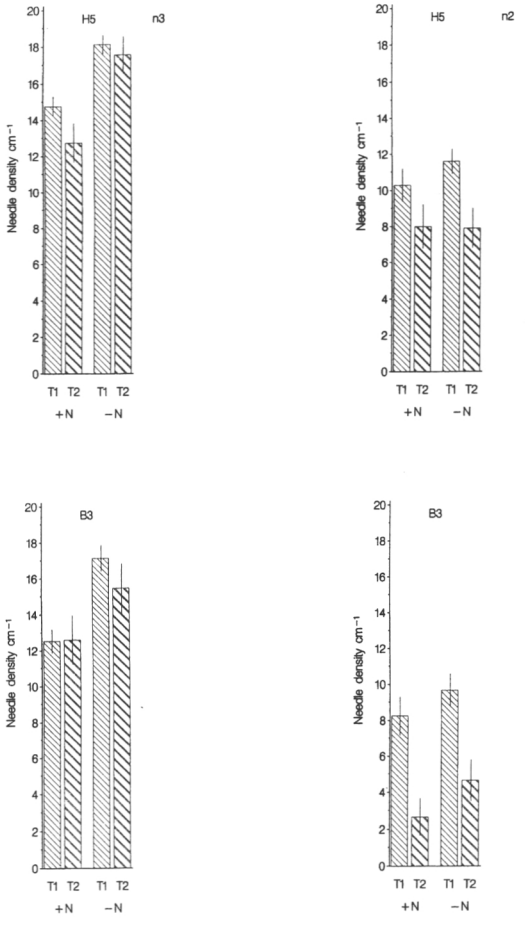


Fig. 3. Needle density (cm^{-1}) in the 1992 (n_2) and 1993 (n_3) needles measured in April 1994, grouped according to provenance, nutrient level and winter temperature treatment, symbols are: high (T_2) and low (T_1) winter temperature. High (+N) and low (–N) nutrient level. Means of 24 observations per treatment and provenance, with ±2 s.e.

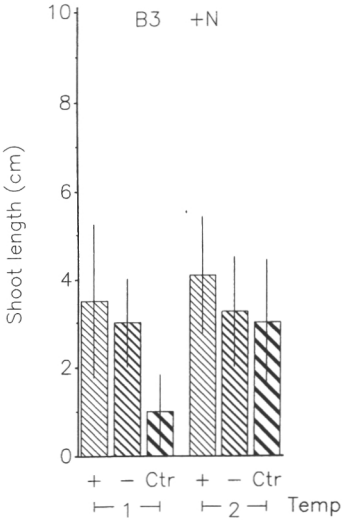


Fig. 4. Length of annual shoots (cm) on May 26, 1994 in fertilized seedlings of the Norwegian provenance (B3). The plants are grouped according to CO_2 and winter temperatures, where the symbols are: High CO_2 (+), low CO_2 (–). outside open top chamber (Ctr.). High (2) and low (1) winter temperatures. Means of 24 observations per treatment and provenance, with ±2 s.e.

Table 2. Variance ratios (F) and significant levels for annual shoot length (cm), measured May 26 (L_{41}) and August 3 (L_{42}), 1994. (L_{41}), length of Lammas growth (ΔL), and stem base diameter (d), measured October 27, 1994, in three Norway spruce provenances, as a function of winter temperature, nutrient level and CO_2 concentration of the previous summer. * = $p < 0.001$; + = $p < 0.01$; ° = $p < 0.05$. DF = degrees of freedom. Only significant interactions are included.

Source	DF	L_{41}	L_{42}	ΔL	d
Provenance	2	2.9°	10.0*	7.6*	11.1*
Temperature	1	8.0+	35.3*	26.8*	10.8*
Nutrient	1	9.3+	108.8*	1.0	215.4*
CO_2	1	16.6*	9.2+	19.8*	19.4*
Temp × CO_2	1	1.4	3.0+	2.7	3.2°
Model	23	2.2*	4.2*	3.0*	9.2*
Error m.s.	72	2.44	6.66	1.46	2.33
R^2		0.233	0.546	0.294	0.562

5 shows the length of "Lammas shoots" in fertilized plants on August 30, 1994 (control plants are not shown).

The measurements of apical shoot lengths on May 26 and August 3 (L_{41} and L_{42}), 1994, the length of the "Lammas growth" at August 30, 1994 and the stem base diameters October 27, 1994 of the total plant material were transformed to logarithmic values and subjected to a variance analysis. The result of this analysis is shown in Table 2.

In the presentation of net photosynthesis measurements in Tables 3–4 only the results from the fertilized plants are shown, and all three provenances are combined because there was no significant provenance effect on the photosynthesis values. The results are therefore based on measurements on net photosynthesis at temperatures close to optimum values, given in the tables. In Table 3 are shown the estimated maximum net photosynthesis rates in 2-year-old shoots at early (July) and late season (September) 1994, and the corresponding optimum temperatures and saturation light levels. At late season measurements were also made on spruce shoots grown in high CO_2 concentrations, but measured at normal CO_2 level. In Table 4 are shown the maximum net photosynthesis rates in dormant shoots January 1994, grown in normal and 4°C raised temperatures.

Table 3. Estimated maximum net photosynthetic rates, P_{max} (μmol $CO_2 m^{-2} s^{-1}$), saturation light intensity of photosynthesis, I_{max} (μmol m^{-2} s^{-1}) and temperature, T (°C) during measurements of light response in 2-year-old fertilized spruce shoots at early (July 4–7) and late season (September 2–4) 1994, measured at two different CO_2 levels (C_2). Optimum temperatures, T_{opt} and light intensity, I (μmol m^{-2} s^{-1}) during the measurements of temperature response. Means with ±2 s.e. are given on the P_{max} values. The mean CO_2 concentration (ppm), the month before (C_1) and during the measurements (C_2), and relative humidities RH (%) during the measurements are also given.

C_1	C_2	P_{max}	I_{max}	T	T_{opt}	I	RH
Early season							
668	614	4.5±0.5	500	16.5	22	600	60
355	373	1.5+0.4	300	19.0	19	450	59
Late season							
667	622	2.5±0.4	700	19.7	19	750	53
667	372	2.9±0.4	800	18.4	18	700	62
382	367	2.9±0.5	400	18.8	21	500	64

Table 4. Maximum net photosynthetic rates, P_{max} (μmol $CO_2 m^{-2} s^{-1}$), saturation light intensity of photosynthesis, I_{max} (μmol $m^{-2} s^{-1}$) and optimum temperatures, T_{opt} (°C) in daylight with supplementary light in fertilized 2-year-old spruce shoots at mid-January 1994 at ambient (T) and 4°C raised temperatures (T+4). All three provenances are combined. Seedlings were grown at ambient CO_2 concentration. Means with ±2 s.e. The mean CO_2 levels (ppm), temperatures T (°C), light levels I (μmol m^{-2} s^{-1}) and relative humidities RH (%) during the measurements are also given.

Temperature treatm.	CO_2	P_{max}	I_{max}	T	T_{opt}	I	RH
T	368	0.7±0.2	100	8.8	9.5	140	70
T+4	371	1.1±0.3	120	9.6	9.0	135	61

The saturation light is defined as the light level corresponding to a photosynthetic rate equal to 90 % of the estimated maximum value.

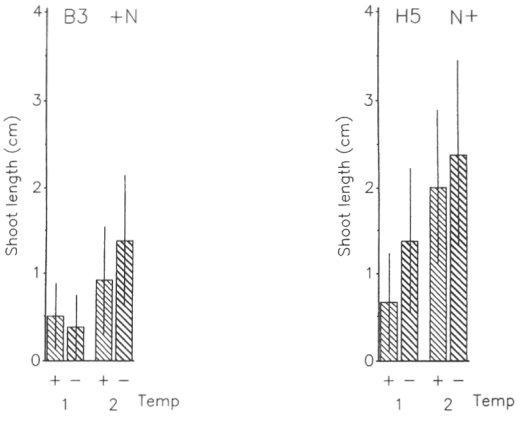


Fig. 5. Lammas growth (cm) on August 30, 1994 in fertilized spruce seedlings of a German (H5) and a Norwegian (B3) provenance. The plants are grouped according to CO_2 and winter temperature, where the symbols are: high CO_2 (+), low CO_2 (–). High (2) and low (1) winter temperatures. Means of 24 observations per treatment and provenance, with ±2 s.e.

Table 3 indicates a strong positive CO_2 effect on photosynthesis in spruce shoots at early season, while there was a slight negative effect at late season. In winter the photosynthetic rates were slightly higher at 4°C raised temperatures than at normal temperatures (Table 4).

4 Discussion

The nutrient level increased growth and biomass in both provenances (see Fig. 2). The reason is probably prolonged secondary growth in fall (Pümpel et al. 1975, Skre 1988) and partly earlier budbreak (Larsen 1976, Murray et al. 1994).

Because of high temperatures during the first winter, the needles suffered an increased carbon loss, as demonstrated by decreased C/N ratio (Skre 1995). At the same time heavy needle damages were observed in plants from the high temperature treatment. The damage was strongest in fertilized plants (Fig. 3). The damaged needles developed necrotic spots in March and eventually fell off. As a result of this needle loss the annual production during the 1993 season was lower in fertilized plants grown at high winter temperature than in low temperature (Skre 1995). This growth reduction was still significant also in 1994 (Fig. 2, Table 2).

The higher degree of needle loss in plants grown at high nutrient level than at low level, is another indication that the damage may be related to low C/N ratio and high dark respiration rates, as a result of stronger fertilization and growth (Skre 1992). Damages on spruce needles during winter storage in low temperatures above zero have been reported by e.g. Venn (1980). Sandvik (1968) found that dark respiration rates during winter storage of five year old Norway spruce were about twice as high at +0.5°C than at –2°C, and that the respiration increased in late April, probably due to increased metabolic activity (see also Ritchie 1982). Navratil and Dye (1978) studied white spruce and black spruce seedlings and found 12 % dry weight loss after 40–70 days of winter storage at +2.5–4.0°C, equivalent to about 50 % depletion of food reserves (Venn 1980).

The growth increase due to elevated CO_2 is often overestimated because of the CO_2 acclimation that takes place at the same time (Mortensen 1993). The reason for CO_2 acclimation may be attributed to limited pot volume (Kerstiens and Hawes 1994), substrate limitation (Poorter 1993) or enzymatic adaptations (Crawford 1989).

After two seasons with different CO_2 treatment a significant increase due to raised CO_2 level was found in the stem base diameter (Table 2), particularly in the German provenance (Fig. 2). This agrees well with the results of Mortensen (1994a, b) who also found that elevated CO_2 levels increased biomass and growth rates in *Picea abies*. There was a strong positive CO_2 effect on photosynthesis at early season, and a corresponding negative CO_2 effect at late season (Table 3). This down regulation of photosynthesis may be seen by comparing spruce shoots grown at high or normal CO_2 concentrations, measured at normal CO_2 level, but also by comparing shoots grown at high CO_2, but measured at high or normal CO_2 level. This so-called "CO_2 acclimation" may be attributed to sink limitation (Poorter 1993).

The strong increase in net photosynthesis rates at normal CO_2 level during the season is proba-

bly related to the development of new, photosynthetically active needles without any sink limitation as in the CO_2 treated needles.

In contrast to the extremely warm winter of 1992/93 the following winter 1993/94 was relatively cold, or about 2°C below the first winter (Fig. 1b). In accordance, needle densities were only slightly lower on annual shoots (n_3) from the high temperature treatment than in the corresponding shoots from the low temperature treatment (Fig. 3) in contrast to the 1-year-old needles (n_2).

High CO_2 seemed to induce early growth cessation as indicated by the significantly lower Lammas growth (Fig. 5). The early budbreak in CO_2 treated plants (Fig. 4) was confirmed by the F-values on the variance ratio (Table 2). This is in contrast to the results of Murray et al. (1994) in *Picea sitchensis*. According to some authors (Sandvik 1978, Heide 1974), however, plants that are induced by short days to early growth cessation would also have a tendency towards earlier budbreak next spring. The relatively early growth cessation in CO_2 treated plants, particularly in the German provenance (Fig. 5), may be a result of accumulation of photosynthetic products. Driessche (1969) concluded from experiments with Douglas fir (*Pseudotsuga menziesii*) that light promotes hardening (and early growth cessation) by synthesis of cryoprotective substances.

Early growth termination in spruce (*Picea abies*) might result in better bud development and stronger growth next year (Heide 1974). This is in good agreement with the present results (Fig. 2). The increased stem base diameter in CO_2 treated plants indicates higher root growth, since a close connection has been found between root biomass and stem base diameter (Rutter 1955).

The CO_2 level also seemed to increase apical growth, but the affect, as indicated by the F-values, was not as strong as for the stem base diameter (Table 2).

Photosynthesis measurements (Table 4) during the 1993/94 winter showed that spruce grown in elevated winter temperatures to a certain degree is able to balance the carbon loss due to increased respiration rates during dark periods, when grown at saturating light levels. This is in accordance with earlier long-term experiments on spruce seedlings (Hagem 1947). Further experiments are needed, however, to evaluate the effect of the predicted 4°C increase in winter temperatures on the carbon balance on Norway spruce in West Norway.

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Variation in Temperature Responses among Populations of *Betula papyrifera*

Jonathan J. Ruel and Matthew P. Ayres

How will global warming affect southern populations of boreal trees? In paper birch, *Betula papyrifera* (Betulaceae), alpine trees with an evolutionary history of relatively cool summers may be more sensitive to climate warming than valley populations. We evaluated this scenario by growing seedlings from different populations in four temperature treatments (mountain field site, valley field site, and two greenhouse rooms). Populations from low elevations germinated earlier and had higher germination success than populations from high elevations (16.8 vs. 22.0 d; 72 % vs. 11 %). At the valley site, seedlings from native populations grew faster than seedlings from higher elevations (mean ± SE = 0.25 ± 0.02 vs. 0.09 ± 0.04 mm · cm^{-1} · d^{-1}) while at the mountain site, all seedlings grew at similar rates. Seedlings grown in cooler environments had higher root : shoot ratios, perhaps to compensate for temperature limitations in nutrient uptake by roots. Leaf area varied among populations but was not affected by environmental differences across the field sites. Net photosynthetic rates at valley temperatures were higher for seedlings grown in the valley than for seedlings grown in the mountains or the warm greenhouse (12.0 vs. 10.3 and 5.8 µmoles · m^{-2} · s^{-1}), perhaps due to adaptive phenotypic adjustments. Climatic warming could rapidly produce important phenotypic changes in birch trees (e.g., decreased root : shoot ratio, reduced growth in alpine populations). On a longer time scale, warming could also result in genetic changes as natural selection favors valley genotypes in alpine sites where they are presently rare.

Keywords *Betula*, growth, photosynthesis, temperature, adaptation
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1 Introduction

Increases in atmospheric carbon dioxide, methane and other greenhouse gases are expected to result in increases of 2–4 °C in global mean temperatures during the next century (Schneider 1993). The cumulative effect of atmospheric changes on plant populations will be a complex combination of the effects of increased carbon dioxide, increased temperature, and changes in cloud cover, precipitation, and nutrient availability (Field et al. 1992). During the last 15 years, there has been extensive research on the direct effects of increased carbon dioxide (e.g., Eamus and Jarvis 1989, Bazzaz 1990, Pettersson and McDonald 1992, Rochefort and Bazzaz 1992), but comparatively little research on plant responses to temperature changes. Our understanding of plant responses to temperature is largely based on studies of graminaceous, herbaceous, and/or crop plants, as opposed to trees (e.g., Scott 1970, Wardlow 1979, Kemp and Williams 1980, Pollack et al. 1983, Marriot et al. 1988, Patterson 1990, Pollack 1990, Winter and Königer 1991, Ackerly et al. 1992, Coleman and Bazzaz 1992, Kirk and Marshall 1992, Baker and Allen 1993, Bowman and Turner 1993, Mozafar et al. 1993, Wall 1993, Williams and Black 1993, Chen et al. 1994, Krapp et al. 1994, Morse and Bazzaz 1994, Oechel et al. 1994, Wookey et al. 1994; but see Bonan and Sirois 1992, Jones 1993, Lord et al. 1993, Stoneman and Dell 1993, Bassow et al. 1994, Callaway et al. 1994, Clark et al. 1995, Mortensen 1995). We have found few studies that explored genetic variation in tree temperature responses (Sorensen 1983, Drew and Chapman 1992, Wang et al. 1994). Consequently, we have only limited ability to anticipate the consequences of climate change on forests.

How will projected changes in ambient temperature affect tree species and forest communities? One hypothesis is that southern genotypes will tend to extend their distributions northward and supplant cold-adapted genotypes. In mountainous regions, valley populations may extend their distributions into the mountains and supplant cold-adapted alpine populations. Changes could be particularly rapid in mountainous regions because of the potential for rapid dispersal across the geographically compressed climatic gradients. Our study evaluates the potential for climatically-induced changes in the distribution, morphology, and physiology of birch genotypes within the mountainous regions of the northeastern United States. We selected paper birch, *Betula papyrifera* Marsh. (Betulaceae), as a model species because it is an important component of forest ecosystems throughout northern North America in general and throughout the altitudinal gradients of New England in particular. We tested the following three hypotheses with a combination of field and greenhouse experiments. (1) Paper birch trees originating from populations at different elevations will differ in their growth, morphology, and photosynthesis when grown experimentally under the same conditions. (2) Trees from the same population will differ in their growth, morphology, and photosynthesis when grown at sites with different temperature regimes. (3) Temperature responses will differ among populations, in that trees from high altitude populations will tend to grow relatively better at cool temperatures while trees from low altitude populations will tend to grow relatively better at warm temperatures (i.e., trees are locally adapted to the temperature regimes of their native environments).

2 Methods

2.1 Overview

Seedlings from each of four *B. papyrifera* populations were placed at each of four treatment sites and monitored for one growing season. We measured seed mass, germination date, germination success, relative growth rates, root : shoot allocation, leaf area, and rate of photosynthesis.

2.2 Population Sampling

B. papyrifera seeds were gathered from mature, naturally established trees during October, November and December of 1993. New Hampshire populations were all from a similar latitude (43°40'–44°0' N), but were classed into three groups based on elevation. Eight trees, sampled

from scattered locations within a 15 km radius of Hanover, NH, comprised our Low elevation group (≈250 m a.s.l.) The Middle elevation group (350–530 m a.s.l.) was comprised of six trees from the lower slopes of Mt. Moosilauke near Warren, NH and three trees from lower Mt. Kancamagus near Lincoln, NH. Our High elevation group (> 1265 m a.s.l.) consisted of eight trees from upper Mt. Moosilauke. Upper elevation trees were probably *Betula cordifolia* Regel, a closely related species (Brittain and Grant 1965, 1969) or variety (Fernald 1945, Little 1979) that replaces *B. papyrifera* above ≈600 m in the White Mountains. Chromosome counts (L.C. Broughton and M.P. Ayres, unpublished data) indicated that our High population was 2n = 28 (as *B. cordifolia*) while the Low and Middle elevation populations were 2n = 70 or 84 (as *B. papyrifera*). Our study also included the progeny of fourteen *B. papyrifera* from Midland County, Michigan (43°38' N, 84°10' W , ≈200 m a.s.l.). Five to ten seeds from each of the 39 mother trees were individually weighed (± 1 µg) to test for differences in initial seed mass that might affect seedling growth. Seeds were kept at 5 °C for the winter.

On 9 May 1994, seeds were planted in growing medium in germination cell flats in the Murdough Greenhouse, Dartmouth College, Hanover, NH. Twenty cells, with approximately ten seeds per cell, were planted for each mother tree. In order to distribute possible micro-climate effects, we planted seeds from many mothers in each germination flat and periodically rearranged the flats in the greenhouse. The flats were watered twice daily. We conducted daily counts of germinated sprouts until 19 June.

The insect growth regulator Enstar® was applied, according to the manufacturer's directions, on 24 June and 30 June to control a white-fly infestation. On 5–6 July, seedlings were transplanted to individual 15 cm (6 inch) diameter pots with unamended topsoil from a valley site (clay loam) and fertilized with 201 mg of water soluble N-P-K (20-20-20) and 85 mg of trace elements. Fertilization was repeated on 18 August. All seedlings were watered to saturation twice weekly throughout the growing season.

2.3 Treatment Sites

The treatments consisted of two field sites and two greenhouse rooms. The Valley site was in a meadow near Etna, NH (43°43' N, 72°10' W) at approximately 250 meters above sea level. The Mountain site was in a clearing off U.S. Forest Service road FR 190 near Titus Brook in Glencliff, NH (44°3' N, 71°53' W) at 760 meters. The seedlings, in individual pots, were placed side by side in fenced enclosures to exclude vertebrate herbivores. Climate stations equipped with LI-COR Data Loggers (LI-1000) were placed at each site and programmed to record daily precipitation, and hourly means of ambient temperature and photosynthetically active radiation (PAR). Values from a NOAA weather station in Hanover, NH were used for some days when the Valley site climate station failed to record data.

Two greenhouse rooms provided an analogous pair of treatments (Warm Room and Cool Room). Different temperature regimes were produced by adjusting the ventilation settings. The Warm Room and Cool Room were identical with respect to light levels and other environmental conditions. Daily maximum and minimum temperatures were recorded in each room.

On 6 July, seedlings from mother trees in the Low, Middle and Michigan groups were placed in each of the greenhouse treatments. Seedlings were placed at the field sites on 20–21 July. Until then, they were kept in their original greenhouse room at a temperature intermediate between the two greenhouse treatments. Seedlings from the high population were only placed at the field sites (not in the greenhouse rooms) because low germination success resulted in reduced sample size.

2.4 Measuring Growth and Photosynthesis

Above-ground seedling growth was measured three times during the summer (7 July, 25 July, and 8 September). On each occasion, we measured height and number of leaves. The number of leaves per unit height (L_t / H_t) was calculated as a morphological descriptor at each sampling time. Relative growth rates (RGR) were calculated as:

$$RGR = [\ln(H_f) - \ln(H_i)] / t$$

where ln = natural logarithm, H_i = initial height, H_f = final height and t = time in days. Relative growth rates were calculated for two periods. RGR_1 describes pre-treatment growth rates, i.e., between the mean germination date (by mother tree) and 7 July. RGR_3 describes growth during the treatment period (25 July to 8 September).

In late October, following leaf senescence but prior to abscission, all leaves were collected from a subsample of Low, Middle and High seedlings at both field sites (1–9 seedlings for each of 3–8 mothers per population at each site). The area of each leaf was measured using computerized video-image capture and the program Optimas©. Fifty-five seedlings were sacrificed for examination of root and shoot allocation. The seedlings, without leaves, were severed at the stem base, oven-dried, and weighed.

On 10–20 September, we measured photosynthesis with a CID infrared CO_2 analyzer (model CI-301PS) with a leaf chamber of 11 cm^2 configured as an open system. A high intensity lamp (General Electric 75 watt 1300 lumen MR16) was attached at 27 cm above the leaf chamber to ensure light saturation (photosynthetically active radiation > 1200 $\mu moles \cdot m^{-2} \cdot s^{-1}$). The analyzer recorded leaf surface temperature, air temperature, evapotranspiration, stomatal conductance, and net photosynthetic rate. On 9 September, we moved seedlings from the Mountain site and the greenhouse to the Valley site so that on subsequent days the photosynthetic rates of trees from all sites could be measured at the same time and under the same environmental conditions.

2.5 Statistics

Statistical comparisons of *Betula* populations were based on the number of mother trees (seedling families) representing each population, and the variance among mother trees. Figures and tables show population means and standard errors calculated from mother-specific means. Pre-treatment relative growth rate (RGR_1), germination date, and seed mass were analyzed with a nested ANOVA model that included population as a fixed effect and mother trees within populations as a random effect. Percentage germination was analyzed with a one-way ANOVA testing for the effect of population on the percentage of cells with ≥ 1 seedling for each mother.

Analyses of leaf area and relative growth rate during the treatments (RGR_3) were based on individual seedling values (because not all mother trees were represented at all sites so the alternative nested model was intractable). Two sets of RGR_3 data (three populations across the two field sites and four populations across the two greenhouse treatments) and one set of leaf area data (three populations across the two field sites) were analyzed with a two-way ANOVA model that included population and site as fixed effects. Two models were used to test the root and shoot masses and the root : shoot ratios: (1) middle population seedlings were compared across the four sites with a two-way ANOVA model including site as a fixed effect and mother as a random effect; (2) Low, Middle, and Michigan seedlings grown at the Valley site were compared with a nested ANOVA including population as a fixed effect and mothers within population as a random effect. Photosynthetic data were converted to mother-specific means and analyzed as a partial factorial (Milliken and Johnson 1984) for effects of population, growing environment, and measurement day. All variables satisfied assumptions of normality and homoscedasticity. Analyses were conducted with the SAS general linear models procedure (SAS 1990).

3 Results

3.1 Germination

Middle, High, and Michigan populations had similar seed masses, but seeds from the Low populations weighed less than half as much (Table 1, $F_{3,35} = 71.33$, $p < 0.001$). Seed mass also varied significantly among mothers within populations ($F_{35,185} = 4.84$, $p < 0.001$). Germination success (% of germination cells with at least one seedling) varied from 11 % in the High population group to 90 % in the Michigan population group (Fig. 1a, $F_{3,35} = 23.17$, $p < 0.001$).

Table 1. Seed mass of four *Betula* populations (n = 8–14 mothers per population, with 5–10 seeds per mother).

	Seed mass (mg)		
Tree population	Mean	SE	n
Low elevation	0.121	0.019	8
Middle elevation	0.269	0.019	9
High elevation	0.285	0.009	8
Michigan	0.258	0.017	14

Among the New Hampshire populations, seeds from lower elevations had higher germination. Of cells with some germination, date of first germination (mean number of days after planting) varied across populations, with seeds from higher elevations germinating later (Fig. 1b, $F_{3,35} = 15.81$, $p < 0.001$). Date of first germination also varied among mothers within populations ($F_{35,433} = 3.10$, $p < 0.001$).

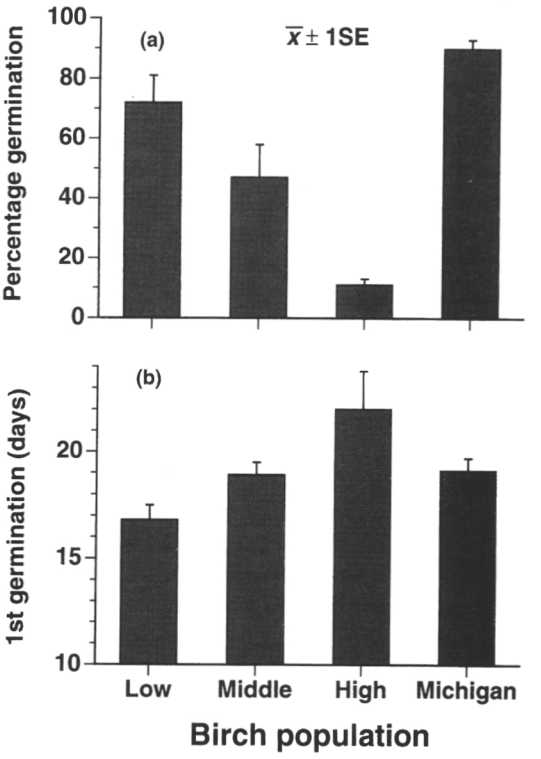


Fig. 1. (a) Germination success of four *Betula* populations (n = 20 germination cells per mother and 8–14 mothers per population). (b) Time from planting until germination in four *Betula* populations (n = 1–20 germinated cells per mother and 7–14 mothers per population).

3.2 Treatment Sites

The mean daily temperature at the Valley site averaged 2.1 °C greater than that at the Mountain site (from 20 June to 20 September, Fig. 2a). This was primarily due to differences in daytime temperatures; night-time temperatures were similar (Fig. 2b). The greenhouse Warm Room site had daily temperature maxima that averaged 13.6 °C warmer and mimima that averaged 2.4 °C warmer than those of the Cool Room treatment (from 1 June to 1 October, Fig. 3). The Warm Room was the warmest treatment overall; the Mountain site was the coolest, and the Valley and Cool Room treatments had similar temperature regimes.

Potted seedlings at the two field sites were exposed to natural precipitation in addition to the twice-weekly waterings. The Mountain site had 17 more days with measurable precipitation resulting in a cumulative growing season sum of 368 mm, which was slightly higher than the Valley's sum of 312 mm (Fig. 4). This difference was less than the equivalent of two waterings, so was very small in terms of total water received during the season. A comparison of light data at the two field sites for the periods 21 June–12 July and 3 September–19 September indicated very similar patterns of photosynthetically active radiation. (A failure of the data logger prevented comparisons of radiation during other times.)

3.3 Growth and Photosynthesis

In seedlings grown at the field sites, population of origin had a large effect on tree relative growth rate (RGR_3; $F_{3,52} = 7.92$, $p < 0.001$). Seedlings from the Low elevation population grew faster

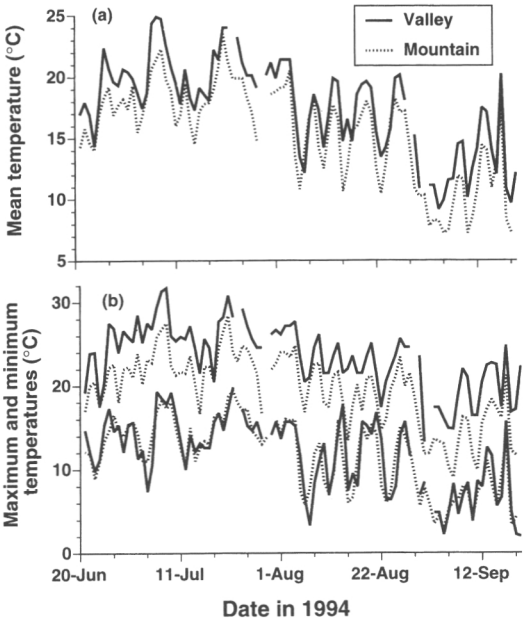


Fig. 2. (a) Daily mean temperature at valley and mountain field sites during the 1994 growing season. (b) Daily maxima and minima of hourly temperatures at the two field sites.

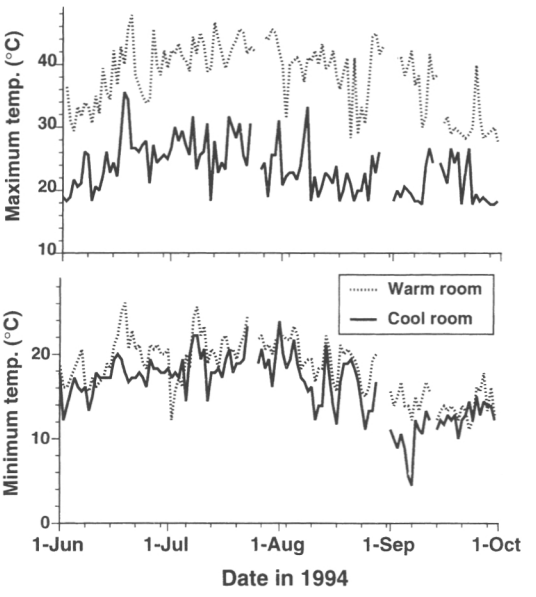


Fig. 3. Daily maximum temperatures (upper) and daily minimum temperatures (lower) in the two greenhouse rooms during the 1994 growing season.

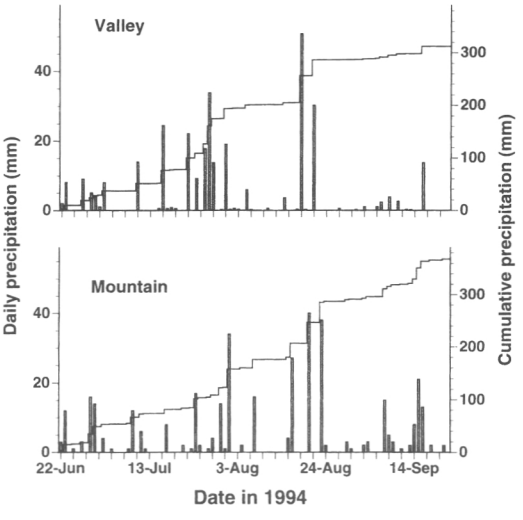


Fig. 4. Daily precipitation (columns) and cumulative sum of precipitation (line) at valley and mountain field sites during the 1994 growing season.

than seedlings from the Middle elevation population, which grew faster than High elevation population seedlings (Fig. 5; least square means $\pm$ SE = 0.23 ± 0.012, 0.19 ± 0.012, 0.13 ± 0.017 mm $\cdot$ cm^{-1} $\cdot$ d^{-1}, respectively). Michigan seedlings grew at rates similar to Low and Middle seedlings (mean $\pm$ SE = 0.21 ± 0.010 mm $\cdot$ cm^{-1} $\cdot$ d^{-1}). There was a significant population $\times$ growing site interaction because High seedlings grew faster at the Mountain site than at the Valley site, while Low and Middle seedlings tended to grow faster at the Valley site (Fig. 5, $F_{3,52} = 3.30$, $p < 0.03$). In the greenhouse, Middle population seedlings grew slower than the Low and Michigan seedlings (mean $\pm$ SE = 0.22 ± 0.01 vs. 0.25 ± 0.01 and 0.26 ± 0.01 mm $\cdot$ cm^{-1} $\cdot$ d^{-1}, respectively; $F_{2,42} = 4.12$, $p < 0.03$), but there was no site $\times$ population interaction ($F_{2,42} = 1.37$, $p > 0.26$). Relative growth rates during the pre-treatment period (RGR_1) did not differ across populations (grand mean $\pm$ SE = 0.78 ± 0.04 mm $\cdot$ cm^{-1} $\cdot$ d^{-1};

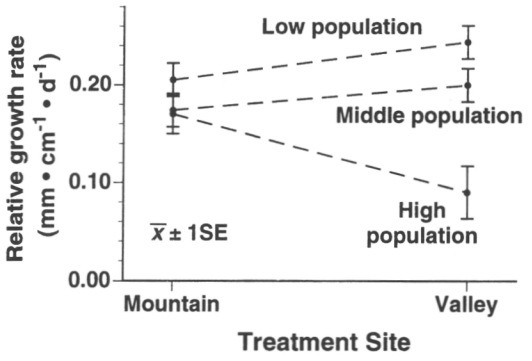


Fig. 5. Relative growth rates from 25 July through 8 September for seedlings from three New Hampshire birch populations grown at the mountain and valley sites (n = 3–10 mothers per population and 1–10 seedlings per mother).

$F_{3,28}$ = 1.87, p > 0.13), but did differ among mothers within populations ($F_{28,505}$ = 3.84, p < 0.001).

Neither root mass nor shoot mass of Middle seedlings varied significantly across sites (Fig. 6a, root: $F_{3,22}$ = 0.51, p > 0.5; shoot: $F_{3,22}$ = 1.03, p > 0.3) or among mothers ($F_{7,22}$ = 1.19, p > 0.3; $F_{7,22}$ = 0.92, p > 0.5). However, seedlings grown at cooler treatment sites had markedly higher root : shoot ratios (Fig. 6c, $F_{3,22}$ = 6.16, p < 0.003). There were no significant differences in root mass, shoot mass, or root : shoot ratios across Low, Middle, and Michigan seedlings grown at the Valley site (Fig. 6b, d; all F-statistics < 2.2, p > 0.11).

At the end of the growing season, the number of leaves per centimeter of height, a description of growth form, was highly dependent on seedling height (Fig. 7). Mean height at the end of the growing season ranged from the 4.4 ± 0.5 cm ($\bar{x}$ ± SE) in the High elevation trees at the Valley site to the 22.5 ± 1.1 cm in the Low elevation trees in the Cool Room (Fig. 8).

Among trees grown at the field sites, seedlings from higher elevation populations had smaller leaves (mean ± SE = 6.23 ± 1.32, 8.97 ± 0.85, 10.56 ± 0.80 cm^2 for High, Middle and Low populations; $F_{2,18}$ = 4.27, p < 0.05). There were no significant effects of site ($F_{1,117}$ = 2.99, p >

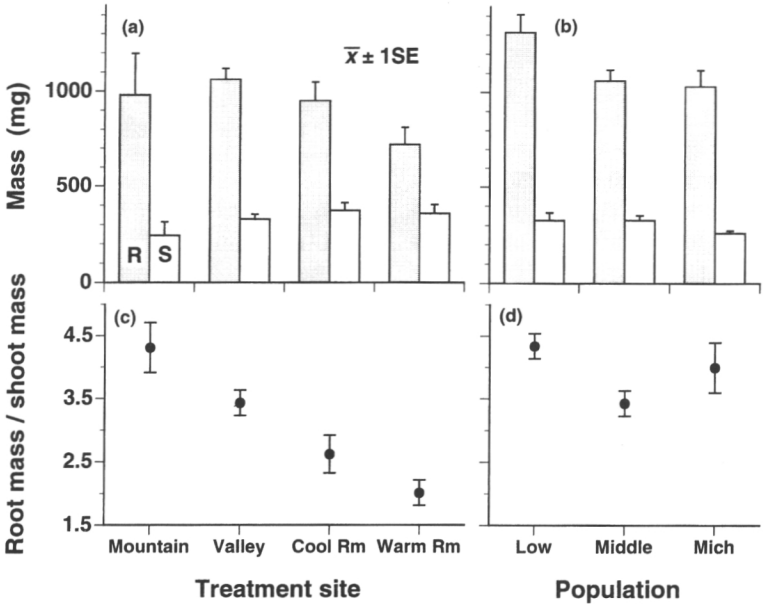


Fig. 6. Root masses (R), shoot masses (S), and root : shoot ratios of *B. papyrifera* (n = 3–15 seedlings per treatment combination). Figures on left (a and c) show data from the Middle elevation population grown at four sites. Figures on right (b and d) show data from three populations grown at the valley site.

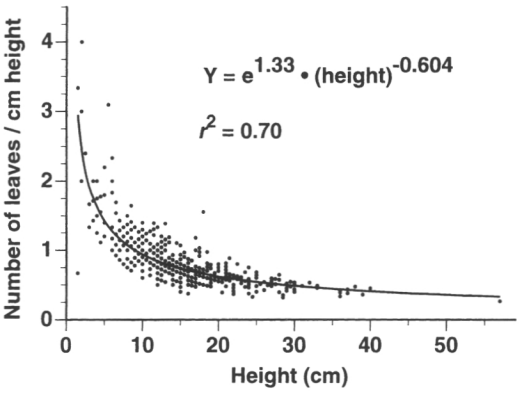


Fig. 7. The number of leaves per unit height as a function of height. Each point represents an individual seedling at the end of the growing season. All populations tended to fall on the same function.

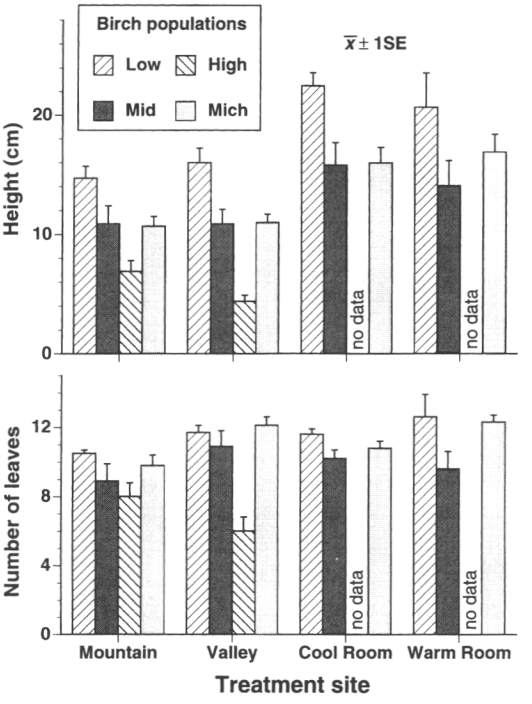


Fig. 8. Mean seedling height and total number of leaves at the end of the growing season for four *Betula* populations grown at four different sites (n = 1–10 seedlings per mother and 3–10 mothers per population).

0.08) or site × population interaction ($F_{2,117}$ = 0.56, p > 0.55) on leaf size.

Net photosynthetic rates of seedlings grown in the Warm Room were dramatically lower than those of seedlings grown at either the Mountain or Valley sites (mean ± SE = 5.8 ± 0.88 vs. 10.3 ± 0.50 and 12.0 ± 0.55 μmoles · m^{-2} · s^{-1}, respectively; $F_{2,103}$ = 7.21, p < 0.01). Seedlings grown in the Valley had higher photosynthetic rates than seedlings at the Mountain site (t = 2.35, p = 0.02, df = 80). There were no significant effects of population ($F_{2,103}$ = 1.51, p > 0.20) or measurement day ($F_{3,103}$ = 0.89, p > 0.44); nor were there any significant interactions (population × date $F_{3,103}$ = 0.02, p > 0.97; site × date $F_{1,103}$ = 0.20, p > 0.65; population × site $F_{2,103}$ = 0.96, p > 0.38). There were no significant effects on stomatal conductance (all F-statistics < 1.42, p > 0.24).

4 Discussion

Germination, relative growth rate and leaf area were strongly influenced by population of origin (Hypothesis 1 in introduction). This suggests genetic differences among paper birch populations. Given our experimental protocol, such differences could also have been due to maternal effects (e.g., due to differences in seed mass), but this seems unlikely because the populations with the most rapid seedling growth were those with the smallest seeds (Table 1, Fig. 5). Differences among treatment sites had strong effects on root : shoot ratio and net photosynthesis, which indicates that some parameters of growth and photosynthesis are highly dependent on environment (Hypothesis 2). Therefore, phenotypic variation among birch populations inhabiting different environments appears to have both genetic and environmental components. Variation in seedling growth across field sites (Figs. 5, 8) partially supported the hypothesis that populations differ in their temperature responses in ways that reflect evolutionary adaptation to environmental conditions (Hypothesis 3).

4.1 Germination

Low elevation seeds were much smaller than those from Middle and High elevations, but showed earlier germination and greater overall germination success (Table 1, Fig. 1). This runs counter to some data indicating that larger seeds germinate earlier and have greater germination success (Stanton 1984, Wang et al. 1994), although Wang et al. also showed that genetic differences often outweigh effects of seed mass. It is possible that the observed late germination in the High elevation population was a statistical artifact of the lower germination success, but this seems unlikely because we estimated germination time based on first germination within cells and the frequency distributions of germination time are strongly skewed to the right. Presumably, germination success in mountain populations is not so low every year, but years of low germination success could be more frequent because of overlap between frost-risk and seed maturation. Further studies are needed to fully characterize inter-annual and geographic variation in seed size and viability.

Relatively later germination in seeds from higher elevations (Fig. 1b) could represent an adaptation to minimize the risk of mortality from late spring frosts in the mountains. In the absence of freezing risk, we would have expected selection to favor early germination in the mountains because of the shorter growing season. In fact, greenhouse comparisons of birch from Alaska and Michigan (D.A. Herms, unpublished data), indicate that the more northerly populations germinate sooner (with fewer degree days) than their southern counterparts. The timing of germination may be an attribute where the analogy between altitudinal and latitudinal patterns in physiological adaptation breaks down. Nonetheless, all data are consistent in indicating high genetic variation in the thermal sum required for germination. Thus, observed differences in the timing of germination in the wild are due to a combination of environmental and genetic factors. In some scenarios of climate warming, low elevation seeds dispersed into the mountains would benefit from earlier germination.

4.2 Seedling Growth Rate

The relative growth rates of seedlings grown in the field suggest that natural selection has led to variation among populations in the responses of growth to temperature (Fig. 5). Differences in growth rate across the sites indicate relatively high phenotypic plasticity in high elevation populations. Reduced growth of the high elevation seedlings in the valley site could have resulted from an inability of high elevation seedlings to acclimatize to the warmer valley environment. Low and middle elevation seedlings did not show phenotypic plasticity in above-ground growth (i.e., they maintained similar relative growth rates across the sites; Fig. 5). Apparently, 1994 temperatures in the mountains were within the range suitable for growth of valley seedlings, while valley temperatures were too warm for optimal growth of mountain seedlings. Obviously, these results could be sensitive to year-to-year variation in climatic patterns. Temperatures during this field study happened to be rather typical of long-term patterns: at Concord, NH (65–90 km from our field sites) the mean August temperature in 1994 was only 0.5 °C different (cooler) than the long term average (NOAA 1994).

Emery et al. (1994) compared alpine and valley populations of *Stellaria longipes* (Caryophyllaceae) using a similar reciprocal transplant. Results were similar to those for *Betula* in that valley populations of *Stellaria* tended to grow faster than mountain populations at the valley site, while all *Stellaria* populations had similar growth rates at the mountain site. However, *Stellaria* differed from *Betula* in that the valley population showed higher phenotypic plasticity than the mountain population (i.e., valley populations grew slower in the mountains than the valley, while alpine populations showed no effect of site). Some interspecific comparisons have indicated that valley species (like valley populations of *Stellaria*) tend to be more affected by environmental variation than their alpine counterparts (Woodward 1975, 1979, Graves and Taylor 1988). Studies with *Stellaria* and *Betula* support the expectation that valley genotypes are the best competitors in their native environment, but pose a paradox by suggesting that mountain genotypes may not be superior competitors in

any environment.

It could still be that high elevation *Betula* trees are actually better adapted to the mountains than valley trees, but if so, it is because of parameters or time scales that were not included in this study. Long-term treatment effects (i.e., over many years) could differ from the short-term effects reported here. Inter-annual climatic variation could also be important. For example, mountain populations may be better able to survive unusually short, cool summers; increased allocation to storage (Sawada et al. 1994) instead of growth might benefit survival in cool summers but subtract from growth during favorable summers. It is also possible that mountain populations have adapted to herbivory and pathogen pressures present in their native environment with increased allocation towards chemical defenses (and therefore reduced growth; Herms and Mattson 1992). Our study was also unable to test for differences in winter cold-hardiness, which can be important for some tree species in the region (Marchand and Chabot 1978, Kincaid and Lyons 1981, Marchand et al. 1986, Doulis et al. 1993).

Relative growth of valley and mountain populations may differ with different soils. We were only able to use one soil type in this study (and it was drawn from the valley), so it is possible that our experimental soil favored the valley populations. We are planning factorial experiments that will compare mountain and valley populations grown in naturally occurring soils from the mountains and valley to test for local adaptation to soils.

4.3 Root : Shoot Allocation

The root : shoot ratios indicate high phenotypic plasticity in relative allocation to above-ground and below-ground organs. Cooler temperatures resulted in markedly increased allocation to roots relative to shoot tissue (Fig. 6c). Similar trends have been reported in an herbaceous perennial (*Scrophularia marilandica*, Cline 1966), a sedge (*Carex aquatilus*, Chapin and Chapin 1981), Douglas fir (*Pseudotsuga menziesii*, Sorensen 1983), and a number of other plant species (Graves and Taylor 1986, Clarkson et al. 1988, Patterson 1990, Winter and Königer 1991, Jones 1993, Clark et al. 1995). Increased relative allocation to roots at lower temperatures could be adaptive if nutrient uptake (per gram of root) is more limited by low temperature than photosynthetic rate (per gram of leaf). This seems likely because mineralization rates and root uptake kinetics are strongly temperature sensitive (Chapin 1974, Bravo-F and Uribe 1981, Clarkson et al. 1986, MacDuff et al. 1987), while photosynthetic rates can be relatively insensitive across a broad range of temperatures (Berry and Björkman 1980, Hällgren et al. 1982, Sveinbjörnsson 1983). If this is true for *Betula*, increased root : shoot ratios might be required to maintain a favorable carbon : nutrient balance in cool environments.

4.4 Photosynthesis

When compared in a common environment (the valley site), seedlings grown at the valley site showed higher rates of carbon assimilation per unit leaf area than seedlings grown at the mountain site or in the Warm Room. This pattern might reflect adaptive phenotypic plasticity (i.e., seedling response to the treatment sites altered optimal photosynthetic temperatures to match treatment temperature regimes), but the experiments would have been strengthened if we had measured photosynthetic rates under a range of temperatures spanning that of the mountain and greenhouse treatments. Seedlings grown in the warm greenhouse treatment, versus those grown in the field, may have had lower photosynthetic rates per unit leaf area due to differences in leaf structure. Although we were unable to obtain measurements, greenhouse trees appeared to have much larger leaves than trees grown in the field which suggests that photosynthetic rates on a per leaf basis might have been similar.

4.5 Conclusions

This study suggests that climatic warming could rapidly produce important phenotypic changes in birch trees (e.g., decreased root : shoot ratio, reduced growth in alpine populations). On a long-

er time scale, warming could also result in genetic changes (e.g., as natural selection favors valley genotypes in alpine sites where they are presently rare). In combination, such phenotypic and genetic changes could have broad implications for forest productivity, community interactions, and ecosystem processes in boreal forests.

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Testing of Frost Hardiness Models for *Pinus sylvestris* in Natural Conditions and in Elevated Temperature

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Two dynamic models predicting the development of frost hardiness of Finnish Scots pine (*Pinus sylvestris* L.) were tested with frost hardiness data obtained from trees growing in the natural conditions of Finland and from an experiment simulating the predicted climatic warming. The input variables were temperature in the first model, and temperature and night length in the second. The model parameters were fixed on the basis of previous independent studies. The results suggested that the model which included temperature and photoperiod as input variables was more accurate than the model using temperature as the only input variable to predict the development of frost hardiness in different environmental conditions. Further requirements for developing the frost hardiness models are discussed.

Keywords climatic warming, dynamic models, photoperiod, Scots pine, temperature
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1 Introduction

The annual development of frost hardiness in northern forest trees has been adapted to the climatic conditions of the growing site of each tree origin. This adaptation usually prevents heavy frost damage during all phases of the annual cycle of trees. When environmental conditions change, for example, as a result of provenance transfers and possible climatic warming, it is possible that changes in the regulation of frost hardiness increase the risk of frost damage (Cannell et al. 1985, Murray et al. 1989, Hänninen 1991, Kellomäki et al. 1995).

Models for the dependence of frost hardiness of trees on environmental factors are needed in order to estimate the survival of trees under changing climatic conditions. The model developed for Finnish Scots pine (*Pinus sylvestris* L.) (Repo et al. 1990) describes the development of frost har-

diness as a first order dynamic process. The model assumes that there is a discrete stationary level of frost hardiness which is dependent on the prevailing air temperature. This level of frost hardiness is attained if the temperature remains constant for a sufficient time. In the model, the relationship between the stationary level of frost hardiness and the daily minimum temperature is assumed to be linear. The rate of development of the prevailing frost hardiness, i.e. hardening or dehardening, is assumed to be dependent on the difference between the stationary level of frost hardiness and the prevailing frost hardiness (feedback control). In natural conditions, the stationary level is probably never reached, due to a delay in the changes of frost hardiness as a result of fluctuating environmental conditions.

Leinonen et al. (1995) developed the frost hardiness model of Repo et al. (1990) further by taking into consideration the effect of photoperiod. In their model the increasing effect of temperature and photoperiod on frost hardiness was assumed to be additive (Aronsson 1975, Christersson 1978, Chen and Li 1978, Jonsson et al. 1981, Greer and Warrington 1982). The response of the stationary level of frost hardiness to these environmental factors was assumed to be piecewise linear. Furthermore, when applied to the Douglas fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco), the dynamics of frost hardiness was modelled as a second order process.

Models for frost hardiness may be applied by linking them to larger ecosystem models to predict the survival and growth of trees (Kellomäki et al. 1992, 1995). Before possible applications, however, the validity of the models must be tested in field conditions. So far, there have only been a few tests of the prevailing models in the natural conditions of Finland, and these tests have been limited to the model predictions in the present climate (Repo et al. 1990).

The aim of this study was to test both the model of Repo et al. (1990) and the modification of the model of Leinonen et al. (1995) with Scots pine saplings growing in their natural environment and in semi-controlled field conditions where the temperature was raised to simulate the predicted climatic warming, and according to the results examine the requirements for further development of the models.

2 Materials and Methods

2.1 Experimental Set-up and Assessment of Frost Hardiness

The empirical data concerning frost hardiness used in this study is based on a natural Scots pine stand near the Suonenjoki Forest Research station, (62°40' N, 27°00' E, 130 m asl.) and on an experiment at the Mekrijärvi Research Station, (62°47' N, 30°58' E, 144 m asl.), University of Joensuu.

In Suonenjoki, the frost hardiness of 15- to 20-year-old Scots pine saplings was determined on stems of last-year shoots using the impedance method. The daily minimum air temperature used as input of the models in this study was recorded with a thermograph (Fig. 1 A). For details of the measurement of frost hardiness, see Repo (1992).

In Mekrijärvi, naturally regenerated 20–25 year old Scots pine saplings were surrounded by chambers (2.5 m × 2.5 m × 3.5 m) and the temperature inside the chambers was elevated during autumn, winter, and spring using two different levels depending on the treatment. For details of the experimental set-up, see Hänninen et al. (1993), Hänninen (1995a), Repo et al. (1996).

The frost hardiness of saplings in Mekrijärvi was determined on last-year needles of the lateral shoots. The needles were exposed to different frost temperatures and the index of injury was determined using the electrolyte leakage method (Flint et al. 1967, Burr et al. 1990). At the end of the study period, frost hardiness was also assessed by visual damage scoring of needles. For details, see Repo et al. (1996).

In the testing of the models, data from three treatments of the Mekrijärvi experiment were used: a) control treatment with natural temperature, b) moderately elevated temperature, and c) highly elevated temperature. Both treatments with elevated temperature were designed to correspond to exceptionally warm winters after climatic warming predicted to be caused by a doubling of the atmospheric carbon dioxide concentration (Hänninen 1995a). The frost hardiness data for each treatment were obtained from a period which began on 7 October 1992 and ended on 13 June 1994. The daily minimum temperatures for treat-

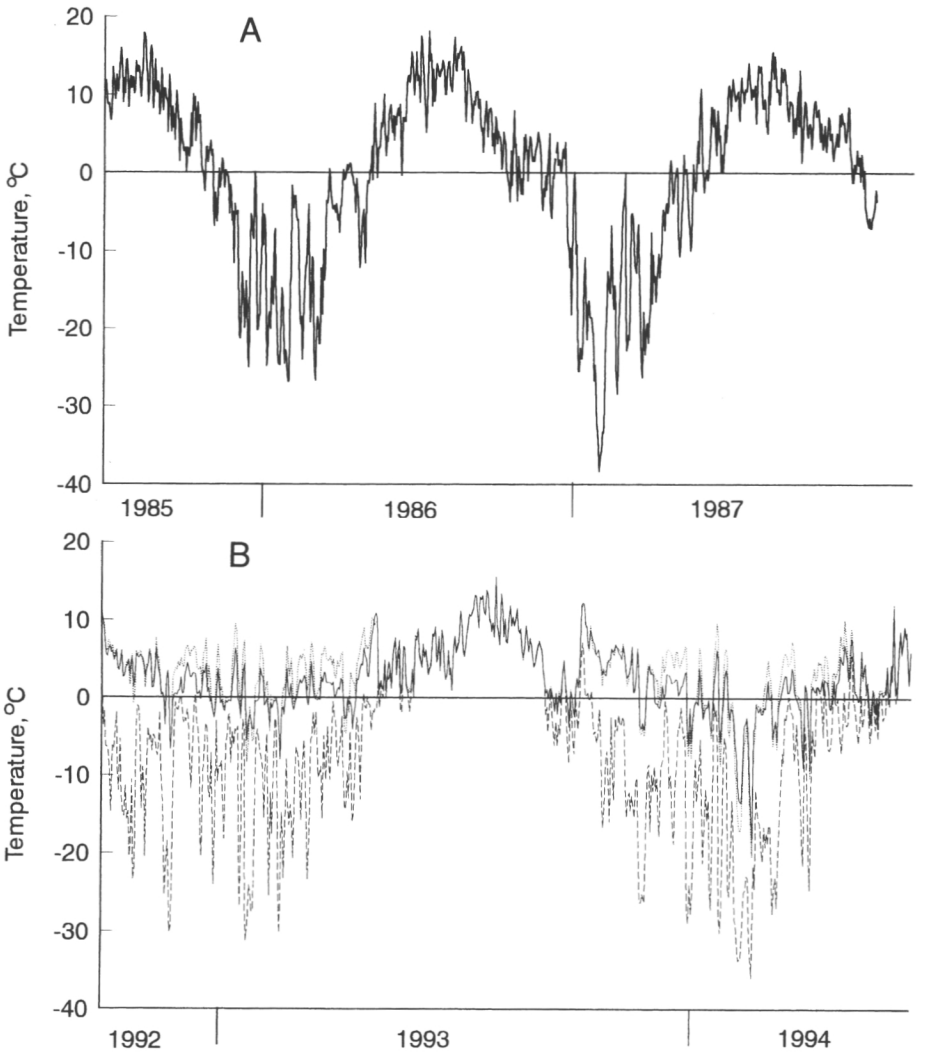


Fig. 1. (A) Daily minimum temperatures during the experiment in Suonenjoki. (B) Daily minimum temperatures during the experiment in Mekrijärvi, control treatment (– – –), moderately elevated temperature (——) and highly elevated temperature (·····).

ments from the same period were used as the input of the models (Fig. 1 B).

2.2 Structure of the Models

In the model of Repo et al. (1990) (temperature model) a dependence between daily minimum temperature and the stationary level of frost hardiness was determined according to the equation:

$$\hat{R}(t) = a \times T(t) + b \quad (1)$$

where $\hat{R}(t)$ is the daily stationary level of frost hardiness, T(t) the daily minimum temperature and a and b are constants. The rate of the change of frost hardiness was described as a first order dynamic process:

$$\frac{dR(t)}{dt} = \frac{1}{\tau}\left(\hat{R} - R(t)\right) \quad (2)$$

where R is the prevailing frost hardiness and τ the time constant.

In the model of Leinonen et al. (1995) (additive model) the stationary level of frost hardiness was assumed to be the result of the additive effect of temperature and photoperiod:

$$\hat{R}(t) = \hat{R}_{min} + \Delta\hat{R}_T + \Delta\hat{R}_P \quad (3)$$

where $\hat{R}_{min}$ is the minimum level of frost hardiness with no hardening induced by environmental factors, $\Delta\hat{R}_T$ the increase of frost hardiness induced by temperature and $\Delta\hat{R}_P$ the increase of frost hardiness induced by photoperiod. Furthermore, the dependence of the increase of frost hardiness on temperature is assumed to be piecewise linear:

$$\Delta\hat{R}_T = \begin{cases} a_T \times T(t) + b_T, & T_2 \le T \le T_1 \\ 0, & T > T_1 \\ \Delta\hat{R}_{T\,max}, & T < T_2 \end{cases} \quad (4)$$

where a_T and b_T are constants, T is the daily minimum temperature and T_1 and T_2 the upper and lower limits of the effective range of temperature needed to change the increase of frost hardiness.

Similarly, the dependence of the increase of frost hardiness on photoperiod is assumed to be piece-wise linear:

$$\Delta\hat{R}_P = \begin{cases} a_P \times NL(t) + b_P, & NL_1 \le NL \le NL_2 \\ 0, & NL < NL_1 \\ \Delta\hat{R}_{P\,max}, & NL > NL_2 \end{cases} \quad (5)$$

where a_P and b_P are constants, NL is the prevailing night length and NL_1 and NL_2 the lower and upper limits of the effective range of night length needed to change the increase of frost hardiness.

Conversely to the second order model used for Douglas fir (Leinonen et al. 1995), in this study the development of frost hardiness of Scots pine was modelled as a first order process according to equation (2).

2.3 Model Parameters

The parameters of the models were obtained from previous independent studies of Scots pine by using available literature. In the temperature model the original parameters of Repo et al. (1990) were used (obtained in a controlled experiment). The parameters used to describe the dependence of the stationary level of frost hardiness on temperature were a = 1.501 and b = –21.4 °C. The time constant τ was 12 days (see Fig. 5 in Repo et al. 1990).

In the additive model the minimum level of frost hardiness ($\hat{R}_{min}$) was determined to be –4.5 °C (Repo 1992). The lower limit of the effective range of night length needed to change the increase of frost hardiness (NL_1) was determined to be 8 hours, and the upper limit (NL_2) 16 hours, respectively (Aronsson 1975, Jonsson et al. 1981). Furthermore, according to the data of Christersson (1978) the stationary level of frost hardiness at a constant 16-hour night length (temperature = 20 °C) was assumed to be –23 °C. Thus, the maximum increase of frost hardiness induced by photoperiod ($\hat{R}_{min}$ subtracted) was determined to be –18.5 °C. According to these observations, the following values of the parameters for $\Delta\hat{R}_P$ were obtained: a_P = –2.31 and b_P = 18.5 °C (Fig. 2 A).

The upper level of the effective range of temperature (T_1) needed to change the increase of frost hardiness was determined to be 10 °C (Repo 1992). Furthermore, the stationary level of frost hardiness at a constant temperature of 2 °C (night length = 4 hours) was assumed to be –19 °C (according to the data of Christersson 1978). Thus, as in the case of photoperiod, when $\hat{R}_{min}$ was subtracted, the parameters for $\Delta\hat{R}_T$ were determined to be a_T = 1.81 and b_T = –18.1. In addition, the maximum frost hardiness during winter in natural conditions according to visual observations was found to be about –70 °C (Repo et al. 1996). Thus, when $\hat{R}_{min}$ and $\Delta\hat{R}_P$ were subtracted, the value for $\Delta\hat{R}_{T\,max}$ was determined to be –47 °C (Fig. 2 B). Finally, the value for the time constant τ was determined to be 12 days (Repo et al. 1990).

The model predicting frost hardiness was simulated by calculating the change of frost hardiness for each day as a result of environmental

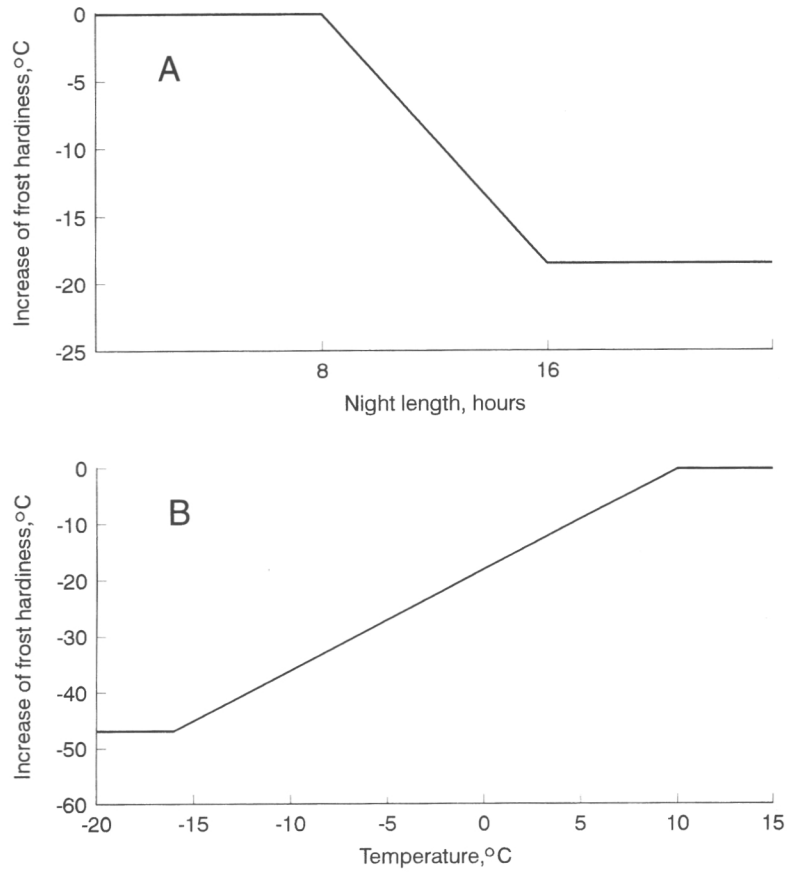


Fig. 2. (A) Dependence of the increase of the stationary level of frost hardiness on photoperiod as used in the additive model. (B) Dependence of the increase of the stationary level of frost hardiness on temperature as used in the additive model.

factors (temperature in the temperature model, temperature and photoperiod in the additive model). The first measured value in each data set was used as the starting value for frost hardiness development. The goodness of the fit of each model in each treatment was determined by calculating the mean square root error (MSRE) between the predicted and measured (impedance method in Suonenjoki, electrolyte leakage method in Mekrijärvi) values of frost hardiness.

3 Results and Discussion

According to the mean square root errors, the temperature model was slightly more accurate than the additive model, as compared to the data gathered from natural conditions in Suonenjoki (Table 1). In the case of the additive model, the most significant difference between measured frost hardiness and that predicted by the model occurred in winter (Fig. 3). This difference is probably partly caused by the different methods used to determine the frost hardiness in Suonenjoki and to estimate the parameters. The parameters for the environmental response of frost har-

Table 1. Mean square root errors (°C) between the measured frost hardiness and that predicted by the model in natural conditions in Suonenjoki and in three treatments of the experiment in Mekrijärvi.

	Mekrijärvi			Suonenjoki
	Control treatment	Moderately elevated temperature	Highly elevated temperature	Natural conditions
Temperature model	1.6	3.1	3.5	0.9
Additive model	3.3	1.8	2.0	1.5

diness in the additive model are mainly based on a classification of the survival of trees as a result of frost treatment (Christersson 1978) and on visual damage scoring of needles (Repo et al. 1996). When compared with these methods, the impedance method obviously underestimates frost hardiness during the hardiest stage in winter (Repo 1992). However, when the level of hardiness is low and the conditions are most critical for frost damage, the impedance method, as well as the electrolyte leakage method, gives a good estimate of frost hardiness, when compared to the visual damage scoring (Repo 1992, Repo et al. 1996). During the hardening phase in autumn, the additive model predicted the development of frost hardening more accurately than the temperature model. In spring, both models were relatively accurate in predicting the timing of dehardening (Fig. 3).

In the control treatment at Mekrijärvi, excluding the hardening phase, the additive model predicted a much higher frost hardiness than the measured data (Fig. 4 A). However, it is obvious that the electrolyte leakage method, used to determine the frost hardiness in this experiment, considerably underestimates hardiness in the hardiest stage of trees (Sutinen et al. 1992). According to the data used in this study, the results of electrolyte leakage method, when compared to visual damage scoring, were accurate only when frost hardiness was above –30 °C (Repo et al. 1996). Therefore, despite the seemingly good fit of the temperature model in this treatment, it is probable that the actual frost hardiness during winter is closer to the predictions of the additive model.

In treatments with moderately elevated and highly elevated temperatures in Mekrijärvi, the temperature model could predict the development of frost hardiness only at the beginning of the hardening phase. During all other phases of the annual development of frost hardiness, the model predicted estimates were highly inaccurate (Fig. 4 B,C). This indicates that a high preci-

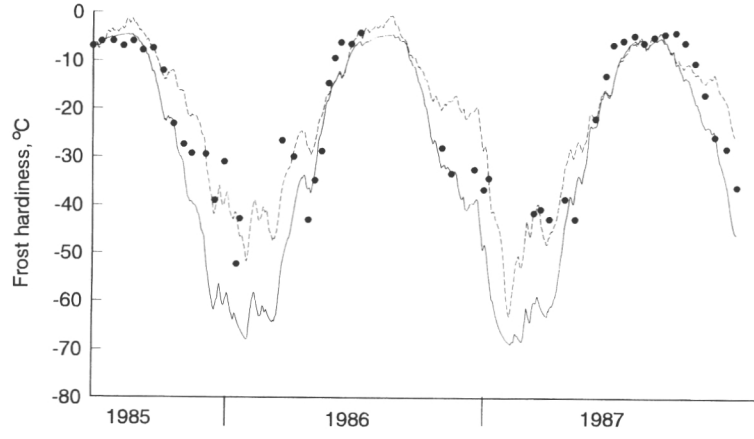


Fig. 3. Frost hardiness as estimated by the impedance method (●), predicted by the temperature model (– – –) and by the additive model (——) in the experiment in Suonenjoki.

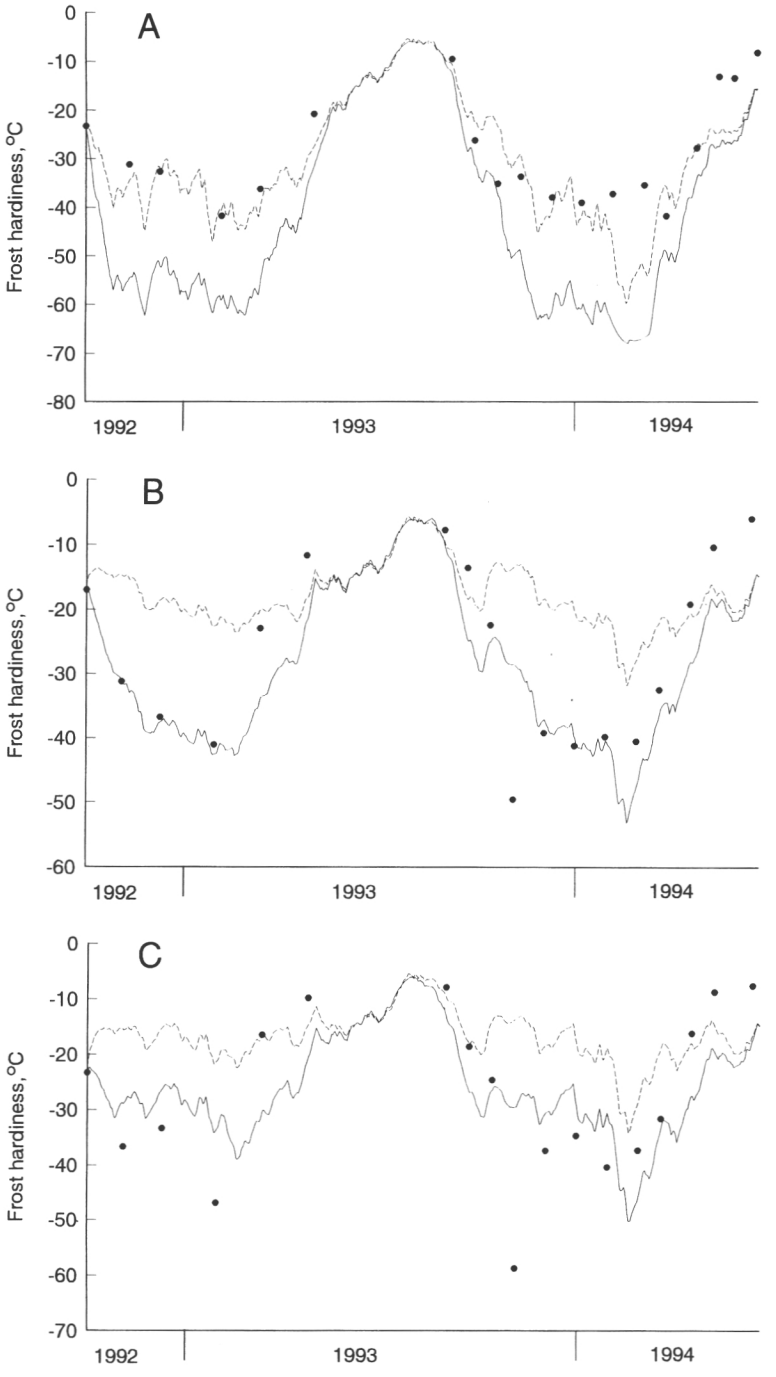


Fig. 4. Frost hardiness as estimated by the electrolyte leakage method (●), predicted by the temperature model (– – –) and by the additive model (——) in the experiment in Mekrijärvi. (A) control treatment, (B) moderately elevated temperature and (C) highly elevated temperature.

sion of any ecological model in present climatic conditions does not necessarily guarantee the reality of the model and its application potential in a changing climate (Hänninen 1995b).

In the case of the additive model, the predicted frost hardiness fitted the measured data during the entire hardening phase in autumn much better than the temperature model. During the hardy phase in winter as well, the additive model predicted the frost hardiness more accurately than the temperature model (Fig. 4 B,C). However, the predictions of the additive model may also be underestimates due to methodological problems in measuring the frost hardiness during this phase.

During the dehardening phase in spring, the additive model predicted the timing of dehardening to occur later than observed in measured frost hardiness data. Furthermore, at the end of the dehardening phase, the model predicted partial rehardening, which was not observed in the data. Therefore, it seems obvious that the model underestimates the risk of damage caused by spring frosts.

According to the results of this study, the additive model predicts frost hardiness considerably better during autumn and winter than the temperature model. This suggests that it is not sufficient to use temperature as the only input variable in models to predict the dynamics of frost hardiness. The effect of photoperiod has been found to be important in the development of frost hardiness in Scots pine in controlled experiments (e.g. Aronsson 1975, Christersson 1978, Jonsson et al. 1981), and including this aspect in the model increases its reality. The additive effect of temperature and photoperiod on frost hardiness has also previously been found in several tree species (e.g. Chen and Li 1978, Christersson 1978, Greer 1983).

In the natural conditions of Finland, the frost hardiness of trees is at its highest level during winter, and at that time frost damage is not usually common. Conversely, the most critical phases are hardening in autumn and dehardening in spring, when an abrupt drop in temperature may damage trees. The most important defect of the additive model is its inability to predict the timing of dehardening in spring. The parameter values describing the environmental response of frost hardiness were obtained from experiments concerning the hardening phase of trees. There is, however, evidence that the dependence of the stationary level of frost hardiness on environmental factors in Scots pine changes in relation to the release of dormancy (Aronsson 1975, Valkonen et al. 1990, Repo 1991). Thus, during the dehardening phase a certain temperature induces a different level of frost hardiness compared to the hardening phase. The loss of rehardening capacity during the dehardening phase (Repo 1991) is obviously also related to this phenomenon. Furthermore, the role of photoperiod during dehardening has been found to differ significantly from that observed during hardening phase (Aronsson 1975).

The values of most of the parameters used in the model simulation are based on experimental results using different pine origins than those in the testing of the model in this study. Furthermore, the estimates of the parameters are based only on a few data points. Despite this fact, the structure of the additive model seems to be useful in predicting changes of frost hardiness in Scots pine in different environmental conditions. To further develop the model, experiments are needed to estimate the model parameters for different pine origins and to examine the application potential of the model for other tree species.

In further experiments, strictly controlled environmental conditions are needed to determine the dependence of frost hardiness on separate environmental factors. In natural (and semicontrolled) conditions environmental factors (temperature and photoperiod) correlate highly with each other and therefore their independent effects are impossible to determine. Primary consideration in further experiments should be given to determining the environmental response of frost hardiness during the dehardening phase in late winter and spring. It is obvious that during this phase it is possible to predict the development of frost hardiness only if the status of dormancy of trees is taken into consideration. Therefore, more studies are also needed concerning the development of dormancy as a result of environmental factors.

The occurrence of exceptional weather conditions is critical for the frost damage both in the present climate and in the predicted conditions

with climatic warming. It would be valuable to test the models with long-term observations from natural conditions including years with different weather conditions. Unfortunately, the measured frost hardiness data is so far too limited for this purpose. In the experiment in Mekrijävi, the temperature elevation was 5–20 °C during winter, and this can be considered as an extreme case of the temperature scenarios (Repo et al. 1996). The conditions in the experiment can not be straightly compared to the natural conditions even in the changed climate. For example, the growing conditions of the saplings were changed very abruptly, and the possible shock effect on the development of frost hardiness can not be excluded (Deans and Harvey 1995).

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Climate Change and the Risks of *Neodiprion sertifer* Outbreaks on Scots Pine

Tarmo Virtanen, Seppo Neuvonen, Ari Nikula, Martti Varama and Pekka Niemelä

The European Pine Sawfly (*Neodiprion sertifer*) is one of the most serious defoliators of Scots pine in northern Europe. We studied the pattern in the regional occurrence of the outbreaks of *N. sertifer* in Finland in years 1961–90, and made predictions about the outbreak pattern to the year 2050 after predicted winter warming. We tested whether minimum winter temperatures and forest type and soil properties could explain the observed outbreak pattern. We analysed outbreak patterns at two different spatial levels: forest board- and municipal-level. The proportion of coniferous forests on damage susceptible soils (dry and infertile sites) explained a significant part of the variation in outbreak frequency at small spatial scale (municipalities) but not at large spatial scale (forest boards). At the forest board level the incidence of minimum temperatures below –36 °C (= the critical value for egg mortality) explains 33 % of the variation in the outbreak pattern, and at the municipal level the incidence of cold winters was also the most significant explaining variable in northern Finland. Egg mortality due to cold winters seems to be the most parsimonious factor explaining why there have been so few *N. sertifer* outbreaks in northern and northeastern Finland. We predict that climate change (increased winter temperatures) may increase the frequency of outbreaks in eastern and northern Finland in the future.

Keywords Scots pine, *Neodiprion sertifer*, insect outbreaks, climate change, cold tolerance, GIS

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1 Introduction

A predicted increase in temperature with accompanying changes in precipitation will have profound consequences for ecosystems (Graham and Grimm 1990, Oechel and Vourlitis 1994). Herbivorous insects will be subject to indirect effects of climate change on the trophic level above and below, as well as to direct effects (Martinat 1987, Solbreck 1990, Williams and Liebhold 1995). Climate change may alter the dynamics of outbreak species in time and space, changing the freqency of outbreaks and their spatial patterns, size, and geographical range (Williams and Liebhold 1995). Generally, populations are expected to extend their ranges to higher latitudes and elevations as climate warms (Solbreck 1990, Williams and Liebhold 1995).

The European Pine Sawfly, *Neodiprion sertifer* (Geoffroy) (Hymenoptera: Diprionidae) is one of the most serious defoliators of Scots pine (*Pinus sylvestris* L.) in northern Europe. Local, isolated mass-occurrences occur almost every year in Fennoscandia. Sometimes they spread into regional outbreaks (Juutinen 1967, Larsson and Tenow 1984, Juutinen and Varama 1986). This defoliating insect can be important on a regional scale in boreal forests as a controller of primary productivity, carbon budgets, and nutrient cycling. Thus, in addition to responding to climate change it also feeds back to global change.

Our aim is to analyse the regional occurrence of the outbreaks of *N. sertifer* in 1961–90 in Finland, and test whether winter minimum temperatures (Neuvonen 1992) and forest type and soil properties (Larsson and Tenow 1984, Juutinen and Varama 1986) can explain the observed pattern. Furthermore, we present a conjectural prediction how climate change (increased winter temperatures in the future) may affect the frequency and regional occurrence of these outbreaks.

In the analyses we concentrate on explanatory variables with close connection to some mechanistic processes known and/or suggested to be important for the population dynamics of *N. sertifer*: 1) *N. sertifer* overwinters in the egg stage. The critical temperature for the death of *N. sertifer* eggs is about –36 °C (Sullivan 1965, Juutinen 1967, Austarå 1971). 2) Outbreaks are known to occur mainly on dry or dryish infertile mineral soil sites (Larsson and Tenow 1984, Juutinen and Varama 1986); mechanisms may involve both host quality and natural enemies (Hanski 1987, Mattson and Haack 1987, Saikkonen and Neuvonen 1993).

2 Material and Methods

We analysed outbreak patterns at two different spatial levels: 1) Forest boards: Finland has been divided into 19 forest boards (459 municipalities in total). Mean yearly proportion of outbreak municipalities from all forest boards municipalities was used as the response variable. This was

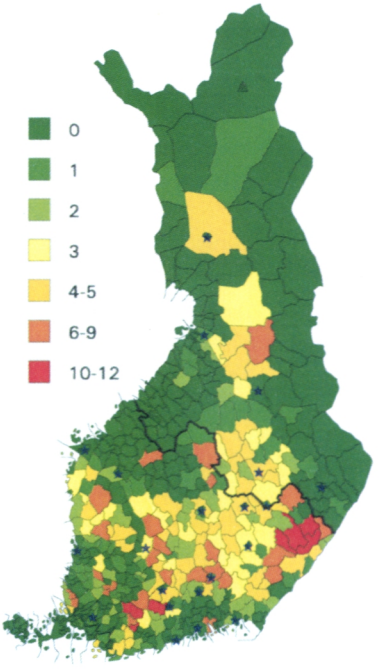


Fig. 1. Number of the years with *N. sertifer* outbreaks in 1961–90. Based on published and unpublished yearly collected information by the Finnish Forest Research Institute; municipalities as observation units. Stars = major cities, omitted from the analysis, triangle = Saariselkä, omitted from the analyses (see text), bold line = line between southern and northern part (see text).

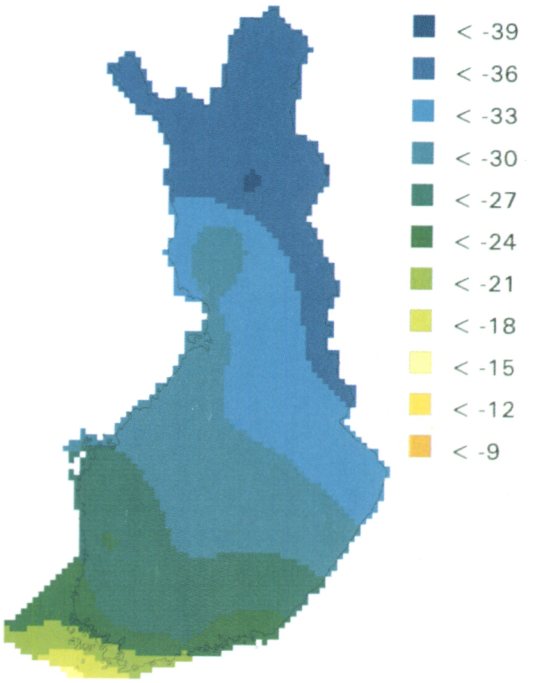


Fig. 2. Mean minimum winter temperatures 1960–90. Grid size 10 km. Source: The Finnish Meteorological Institute.

calculated over the whole study period (1961–90). 2) Municipalities: Number of years with *N. sertifer* outbreaks per municipality in years 1961–90 was the response variable. All the cases in which densities of larvae were clearly higher than in latent populations or *N. sertifer*-damaged pines were observed are classified as outbreaks. Latent populations are very sparse and larval groups can be observed only rarely (Hanski 1987). Consequently, there is no risk that a latent population would be classified as outbreak. The observations were made by forest owners and forest authorities as well as by the Finnish Forest Research Institute (more about outbreak-data and collecting method: Juutinen 1967, Juutinen and Varama 1986).

In the forest board-level analysis we used the following explanatory variables: 1) incidence of (absolute) minimum temperatures below –36 °C (= COLD), 2) percentages of damage-susceptible area (= SOIL; see below), 3) number of municipalities in forest board (= MUNICIPAL). In the municipality level analysis the explanatory variables were: 1) incidence of (absolute) minimum temperatures below –36 °C (= COLD), 2) percentage of damage susceptible area (= SOIL), 3) size of the municipality (values in km^2, = AREA). We used logarithmic transformation in the size of the municipality values to normalize their distribution. At the municipality level we analysed data in two ways: as a whole or divided into the southern and northern part (see Fig. 1). Stepwise regression analysis (SAS user's... 1985) was used at both spatial levels.

We used the databases in Arc/Info geographic information system. The explanatory variables are in grid-format. As outbreak data observation units are municipalities (or forest boards), we calculated and used municipality- and forest-board-means of explanatory variables in analyses.

The incidence of (absolute) minimum temperatures below –36 °C was calculated for every grid cell as a proportion of winters with minimum temperatures below the threshold during 1960–1990. The southern populations seem to be more susceptible to cold than the northern populations (Sullivan 1965, Juutinen 1967, Austarå 1971). We took value –36 °C as a representative for Finnish populations. Mean of the winter minimum temperatures during 1960–90 in different parts of the Finland is shown in Fig. 2.

Both Larsson and Tenow (1984) and Juutinen and Varama (1986) state that *N. sertifer* outbreaks occur mainly on dry or dryish infertile mineral soil sites. On the basis of land use and forest classification, and soil type data we classified coniferous forests growing on dry and dryish sites as potentially damage-susceptible areas and calculated the mean percentage of damage susceptible area (in relation to total land area; Fig. 3)). The soil type classification has the following categories (those in *italics* were considered as 'potentially damage-susceptible'): basal till; *bedrock terrain*; hummocky moraine; *eskers, deltas, ice marginal and interlobate formations; boulder fields; valley trains and other extramarginal deposits*; fluvial deposits; clay deposits; littoral deposits; peat deposits.

We omitted from the analyses major cities (Fig. 1), and observations from the Saariselkä-

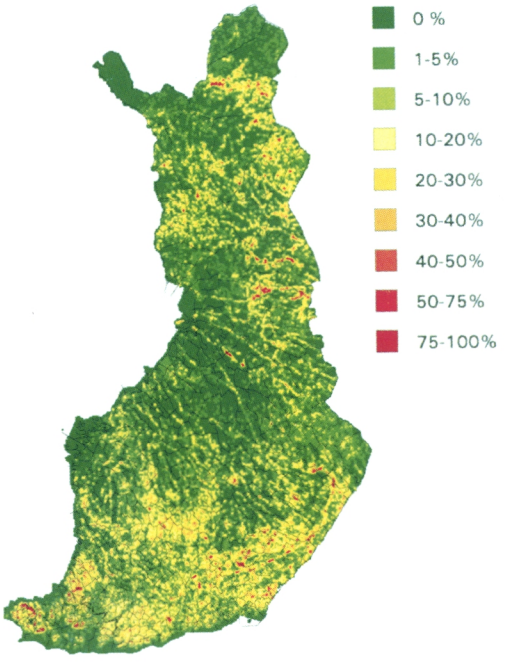


Fig. 3. Percentage of damage susceptible areas from the whole land area, based on forest classification (satellite image based land use and forest classification; grid size 200 m, source National Land Survey of Finland) and soil type (grid size 200 m, based on 1:1 000 000 map, source Geological Survey of Finland).

area (Fig. 1), because outbreaks there situated in mountainous area (Juutinen 1967, Niemelä et al. 1987) and the minimum temperature data is not representative for that site due to temperature inversion. Initial screening of the data showed also that *N. sertifer* outbreaks have been rare in coastal areas (Fig. 1). Since we do not have at present any mechanistic explanation for this pattern we excluded coastal areas (municipalities with seashore) from subsequent analyses.

We made our future predictions for the year 2050 with SILMUSCEN policy scenario (Central), which is recommended as the "best guess" scenario for the project SILMU (= The Finnish Research Programme on Climate Change; Carter et al. 1995). This scenario predicts that mean winter temperature increase is +3.6 °C over 1990–2050 (Carter et al. 1995). Predictions for outbreak pattern were made by regression model equation (Table 1), using minimum temperature incidencies in 2050 in the place of 1960–90 incidencies. Since the SILMU scenarios do not offer information about possible changes in climate variability (Carter et al. 1995) we have to make the most parsimonious assumption of no change in variability which automatically alters the probability of extreme events. We added +3.6 °C to the years 1960–90 minimum temperature data and calculated the incidencies of minimum temperatures below –36 °C at year 2050.

3 Results

The outbreaks of *N. sertifer* were most common in the inland areas of Southern and Central Finland with usually three to nine outbreak years during the period 1961–1990 (Fig. 1). The proportion of forest area dominated by Scots pine is highest in northern Finland and coastal areas (Yearbook... 1994) and so the abundance of Scots pine does not explain the distribution of damage at all.

At the forest board level the incidence for minimum temperatures below –36 °C explains 33 % of the variation in the proportion of municipalities with *N. sertifer* outbreaks (Table 1, Fig. 5a). Also the number of municipalities per forest board explains significant proportion (18 %) of variation (Table 1). This may be due to a mere technical reason: the number of municipalities is used as a divisor when calculating the response variable. At the forest board level the proportion of coniferous forests on damage-susceptible soils does not explain the occurrence of outbreaks (Table 1).

There have been only a few outbreaks in municipalities where the incidence for minimum temperatures below –36 °C has been higher than 0.35 (Fig. 4). At the municipal level, in the regression analysis of the whole country, the incidence of minimum temperatures below –36 °C is the best explanatory variable for variation in outbreak frequency in years 1961–90 (10 %, Table 2a), and the second best explanator is the percentage of damage-susceptible area (7 %, Table 2a). Also, the size of the municipality (more outbreaks in bigger municipalities) explains a significant part of the

Table 1. Regression model at forest board level.

Dependent variable: Mean proportion of outbreak municipalities/year/forestry board. N = 17.

Step	Variable entered	Partial R^2	Model R^2	F	Prob > F	Range of variable
1	COLD	0.3288	0.3288	7.3481	0.0161	0.022–0.668
2	MUNICIPAL	0.1782	0.5070	5.0602	0.0411	6–30
Variable not included in to the model:						
	SOIL	0.0085	0.5155	0.2283	0.6407	1.52–14.24

Equation: $0.1788 - (0.2257 \times \text{COLD}) - (0.00350 \times \text{MUNICIPAL})$

Table 2. Regression models at municipal level.

Dependent variable: Number of outbreak years/municipality 1961–90

a) Finland as a whole (N = 342):

Step	Variable entered	Partial R^2	Model R^2	F	Prob > F	Range of variable
1	SOIL	0.0682	0.0682	24.87	0.0001	0–29.34
2	Log(AREA)	0.0235	0.0916	8.75	0.0033	1.48–4.10
3	COLD	0.0991	0.1907	41.40	0.0001	0–0.90

Equation: $-4.284 - (6.936 \times \text{COLD}) + (0.0807 \times \text{SOIL}) + (2.455 \times \text{Log(AREA)})$

b) Southern Finland (N = 224):

Step	Variable entered	Partial R^2	Model R^2	F	Prob > F	Range of variable
1	Log(AREA)	0.1304	0.1304	33.30	0.0001	1.49–3.20
2	SOIL	0.0460	0.1764	12.34	0.0005	0.40–29.34
Variable not included in to the model:						
	COLD	0.0060	0.1824	1.60	0.2067	0–0.23

Equation: $-5.256 + (0.0949 \times \text{SOIL}) + (2.606 \times \text{Log(AREA)})$

c) Northern Finland (N = 118):

Step	Variable entered	Partial R^2	Model R^2	F	Prob > F	Range of variable
1	COLD	0.1174	0.1174	15.43	0.0001	0.07–0.90
2	SOIL	0.0586	0.1760	8.18	0.0050	0–19.9
3	Log(AREA)	0.0485	0.2245	7.13	0.0087	2.08–4.10

Equation: $-1.971 - (7.386 \times \text{COLD}) + (0.144 \times \text{SOIL}) + (1.678 \times \text{Log(AREA)})$

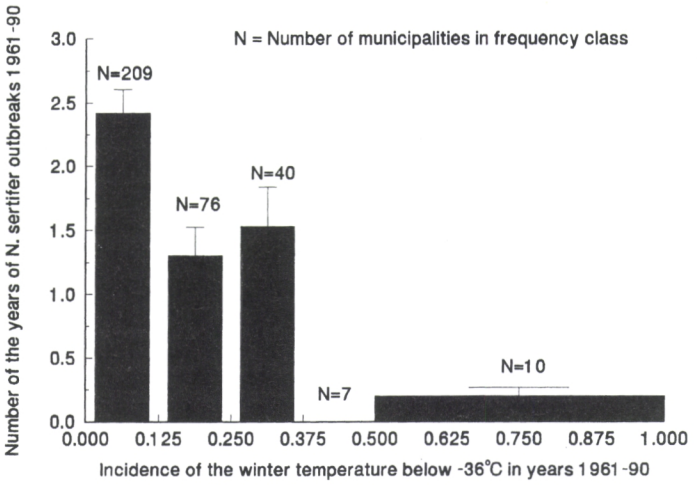


Fig. 4. Number of the years of *N. sertifer* outbreaks/municipality in years 1961–90 in relation to incidence of the winter temperatures below –36 °C.

variation. However, the explanatory power of this model is not very high, only 19 % (Table 2a).

When the analysis is made separately for southern and northern Finland, results are different. In the southern municipalities the best explanator is the size of the municipality (13 % of variation), and also the percentage of damage-susceptible area is significant (Table 2b). In southern Finland, the incidence of minimum temperatures below –36 °C does not explain the number of the outbreaks (Table 2b). However, in northern Finland the incidence of minimum temperatures below –36 °C is the most significant explanator (12 % of variation), and also the damage-susceptible forest area and the size of the municipality are significant explanators (Table 2c).

When the predicted changed winter minimum temperatures are applied to the regression model at forest board level (Table 1), the model predicts more outbreaks/year in the future in eastern and northern forest boards (cf. Figs. 5a and 5b). Due to the generally very low explanatory power of municipality level regression models (Table 2a,b,c) and the apparent non-linearity between the number of outbreak years and the incidence of cold winters (Fig. 4) we do not find it feasible to use the regression model(s) in Table 2 for predicting outbreaks in 2050.

4 Discussion

In 1961–90 *N. sertifer* outbreaks were common in southern Finland but almost lacking in northern and north-eastern parts of the country (with the exception of Saariselkä, see below). The incidence of minimum winter temperatures colder than –36 °C explains well this distribution pattern. There is good evidence that temperature is critical for the survival of eggs (Sullivan 1965, Juutinen 1967, Austarå 1971). There are also reports of collapse of *N. sertifer* outbreaks after cold winters (Juutinen 1967).

Obviously, some other climatic parameters show the same geographic pattern as minimum winter temperatures, e.g. temperature sums are low in northern and northeastern Finland. However, there is no well understood mechanism that might connect low temperature sums with the lack of *N. sertifer* outbreaks. In fact, in Saariselkä (northern Finland, see Fig. 1) the outbreaks occur mainly at the top of the fjells with lowest temperature sum but with mildest winters (Niemelä et al. 1987, Niemelä et al. unpublished). So, we consider egg mortality in cold winters the most parsimonious factor explaining why there have been so few outbreaks in northern and north-eastern Finland.

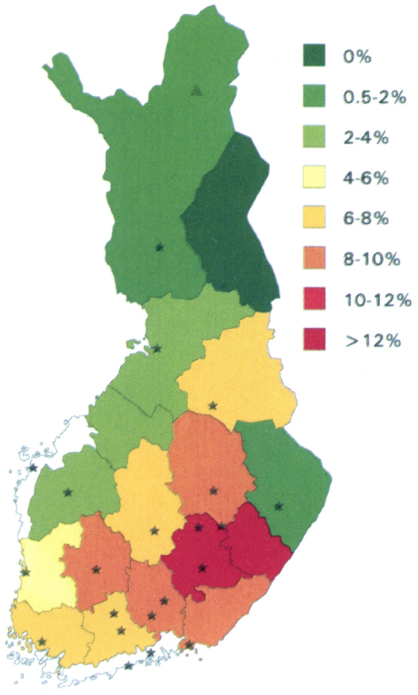


Fig. 5a. Mean percentage of outbreak municipalities per year in forestry boards in Finland in 1961–90. Legend values are upper limits.

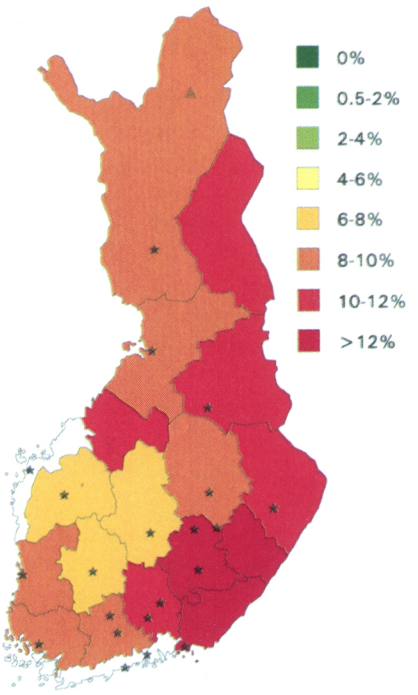


Fig. 5b. Predicted (see text) mean percentage of outbreak municipalities per year in forestry boards in Finland in year 2050. Legend values are upper limits.

Egg mortality is known to be of great significance determining the areal distribution of outbreaks in Autumnal moth, *Epirrita autumnata* (Bkh) (Tenow and Nilssen 1990). During temperature inversions in winter cold air accumulates to lower areas, and the temperature differences can be over 10 °C just within few square kilometres (Tammelin 1988, Tenow and Nilssen 1990). Modelling local, topographic variation in minimum winter temperatures is necessary when studying the population dynamics of *E. autumnata* (T. Virtanen, S. Neuvonen and A. Nikula, unpublished observations) and also when aiming at more accurate predictions of *N. sertifer* outbreaks in northern Finland in the future.

The climatic models predict areal differences in the increase of winter temperatures in Finland. Models GFDL and UKMO predict less increase into northern Finland than in southern Finland, and ECHAM1 the opposite (Carter et al. 1995). According to Räisänen (1994) the most realistic winter temperatures in northern Europe are given by the GFDL simulations. If climate warming will happen according to GFDL simulation, then SILMU policy scenario value which we used in our predictions (+3.6 °C increase) could be too high for northern Finland. However, the minimum winter temperatures occur during temperature inversions (clear calm periods). There are also predictions of increase in winter precipitation (Räisänen 1994, Carter et al. 1995), which possibly will result in rarer inversions. This, in turn, could lead to a larger increase in minimum temperatures than in mean temperatures (see also, Karl et al. 1995).

There are also connections between precipitation and population dynamics of *N. sertifer*. It has been hypothesized that drought periods can be the triggering factor which releases an outbreak, either through changes in needle chemistry (Larsson and Tenow 1984) or in cocoon predation (Hanski 1987). Predation of pine sawfly

cocoons by shrews can be one of the most important factors in keeping the population levels below the outbreak numbers (Hanski and Parviainen 1985, Hanski 1987), and it is known that high summer precipitation affects positively shrew densities (Pankakoski 1985). Precipitation and high moisture also enhance the dispersal and infection of the nuclear polyhedrosis virus of *N. sertifer* (Olofsson 1988).

Climate models predict a slight increase in precipitation for continental northern Europe, but seasonal cycle and geographical details vary from model to model (Räisänen 1994, Carter et al. 1995). Thus, changes in precipitation may counteract the effects of increased winter temperatures on *N. sertifer* population dynamics.

The proportion of coniferous forests on damage-susceptible soils explained significant part of the variation in outbreak frequency at the municipal level thus supporting the ideas of Larsson and Tenow (1984) and Juutinen and Varama (1986). The proportion of damage susceptible forest did not emerge as a significant explanatory variable in the forest board level analysis. This may be either because the range of variation in the explanatory variable was smaller with forest boards than with municipalities, or because other (here unstudied) explanatory variables masked its effects at the more robust spatial scale.

We see a need to further develop the damage susceptibility index by considering especially: 1) Age structure of forests (which is actually changing): young 20–40 year old stands seem to be most vulnerable (Juutinen 1967, Larsson and Tenow 1984); 2) Better quality soil type, land use, and forest classification data should be used, and also include as susceptible certain types of pine bogs where outbreaks have been reported (Juutinen and Varama 1986).

In the future, the following aspects should also be taken into account: 1) In Finland the nuclear polyhedrosis virus has been used to control *N. sertifer* outbreak's since year 1972 (Juutinen and Varama 1986). This has changed locally the severity, areal distribution, and duration of outbreaks during the later part of our analysis period. 2) For some of the outbreak periods all the pre- and postgradation years are not recorded, as an outbreak usually lasts at least 2 to 3 years (Juutinen 1967, Larsson and Tenow 1984, Juutinen and Varama 1986, Hanski 1987).

Our prediction that *N. sertifer* outbreaks will be more probable in the northern Finland in the future (year 2050; Fig. 5b) should be considered with some caution because the basic mechanism (winter mortality of eggs) used in the prediction is asymmetric in a causal sense. Very cold winters are sufficient to prevent the outbreaks of *N. sertifer* but the lack of eggs-killing temperatures are, on the other hand, a necessary but not sufficient condition for the occurrence of outbreaks. Thus, for predicting increased outbreak risks in northern Finland as a consequence of warming (winter) climate we have to make the additional assumption that the other factors controlling *N. sertifer* population dynamics behave essentially as they do in southern Finland at present.

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Performance of Pine Sawflies under Elevated Tropospheric Ozone

Päivi Lyytikäinen, Pirjo Kainulainen, Anne Nerg, Seppo Neuvonen, Tarmo Virtanen and Jarmo K. Holopainen

Concentration of the phytotoxic air pollutant, ozone (O_3) is continually increasing in the lower layer of the troposphere. The purpose of this study was to compare performance of pine sawflies on Scots pine seedlings in ambient and future levels of ozone. Scots pine seedlings were grown in field fumigation system where the ozone doses in fumigated plots were 1.5–1.6 times the ambient level. Larvae of the European pine sawfly (*Neodiprion sertifer*) and *Gilpinia pallida* were reared on the foliage of Scots pine. The levels of resin acids and monoterpenes in foliage were analysed. There were no significant effects of ozone fumigation on sawfly performance or levels of defence compounds in pine foliage. The results suggest that the elevated ozone concentrations do not strongly affect the needle quality of young Scots pine and the importance of these two diprionid sawfly species as forest pests.

Keywords air pollution, *Neodiprion sertifer*, *Gilpina pallida*, Scots pine, resin acids
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1 Introduction

Pine sawflies are forest pests of greatest economic significance in Fennosscandia. Occasionally outbreaks of the European pine sawfly (*Neodiprion sertifer* Geoffr.) can spread over tens of thousands of hectares in Scots pine (*Pinus sylvestris* L.) forests. Outbreaks may last several years. Large-scale outbreaks appear at 20 to 30 years' intervals, while local outbreaks occur more frequently (Juutinen and Varama 1986). *Gilpinia pallida* (Klug) causes defoliation to young pine stands. Environmental stresses may reduce the capacity of host trees to produce defensive substances leading to greater susceptibility of trees to sawfly damage (Larsson and Tenow 1984).

Ozone is a phytotoxic air pollutant that show an elevating trend in the lower layers of the troposphere (Runeckles and Krupa 1994). It is known to decrease plant carbon gain by reducing photosynthetic rate and leaf area and accelerating senescence of plants (Chappelka and Chevone 1992, Greitner at al 1994). Ozone-induced disturbances in metabolism of conifers are indicated e.g. by reduced levels of carbohydrates (Paynter et al 1990, Friend et al. 1992, Kainulainen et al 1994), increased levels of free amino acids (Dohmen et al 1990), and induced formation of pathogenesis-related proteins (Kärenlampi et al 1994).

Carbohydrates (e.g. soluble sugars) promote growth of insect larvae (Albert and Parisella 1985). Starch content has been generally considered a good indication of conifer vigor after stress (Webb 1981). Herbivorous insects exposed to air pollution stress have been shown to change in feeding or oviposition behaviour. The Mexican bean beetle preferred bean plants exposed to sulfur dioxide or ozone (Endress and Post 1985), the gypsy moth had a variable preference response to oak seedlings under elevated ozone concentrations (Jeffords and Endress 1984) and willow leaf beetle showed an increased feeding preference for ozone-fumigated eastern cottonwood (Jones and Coleman 1988). Ozone may cause a significant reduction in the rate of photosynthesis, which decreases leaf carbon concentrations. According to the theory of carbon/nutrient balance (Bryant et al. 1983, Herms and Mattson 1992) leaf carbon concentrations can directly affect the level of carbon-based defensive compounds, e.g. monoterpenes and resin acids. The mechanism of ozone as an environment stress factor is not clearly known, but raising ozone levels can be predicted to decrease foliage carbon/nitrogen ratio and promote the consumption of herbivores.

The aim of the present study is to unravel the possible effect of elevated tropospheric ozone concentration on the larval performance of two pine sawfly species on Scots pine in open field, and by means of these experiments to estimate the pest status of the sawfly species under future atmospheric conditions.

2 Materials and Methods

The effect of tropospheric ozone on needle quality of Scots pine was tested by rearing two species of diprionid sawflies (*N. sertifer* and *G. pallida*) (Hymenoptera: Diprionidae) on 3-year-old seedlings in an open-field fumigation system at the University of Kuopio. Bare-rooted pine seedlings (seed origin: Leppävirta) were planted in 7.5 l plastic pots in a mixture of sand and fertilized and limed peat (2:1, v/v) in 1992, and in quartz sand in 1994. Seedlings were sufficiently watered during growing season and fertilized with full-nutrient fertilizer (N 32 kg ha^{-1} in 1992 and N 45 kg ha^{-1} in 1994).

There were two replicate plots with a diameter of approx. 10 m in with ambient ozone levels and two similar plots with elevated ozone levels. Ozone was produced from pure oxygen with ozone generators (Model 500 and OZ 500, ozone generator, Fisher, Bonn Germany) and released to exposed area through perforated plastic tubes in upwind position. The target ozone concentration at the center of exposed plots was 2 times the ambient level, monitored near control plots. The ozone fumigation started in May in both years. The total ozone dose in fumigated plots was 1.5 and 1.6 times the ambient dose, in 1992 and 1994, respectively (Table 1). The ozone concentrations in the center of the plots were measured with an ozone analyzer (Model 1008-RS, Dasibi Environmental Corp., Glendale, Califor-

Table 1. Mean monthly ozone concentrations (ppb, 7 h mean) at the open-field experiments. Maximum daily 7h-means of ozone concentrations are presented in parentheses.

Month	Ozone concentration		
	Ambient	O_3 block 1	O_3 block 2
1992			
May	41 (58)	51 (84)	48 (74)
June	35 (53)	47 (68)	56 (103)
July	27 (47)	41 (75)	48 (77)
August	24 (43)	33 (65)	38 (58)
September	22 (39)	35 (58)	36 (64)
1994			
May	31 (40)	45 (64)	45 (61)
June	30 (41)	48 (64)	48 (66)
July	33 (52)	53 (73)	51 (79)
August	30 (44)	49 (71)	50 (73)
September	23 (35)	39 (62)	40 (65)

nia). More details of the fumigation system are given by Wulff et al. (1992).

Ten Scots pine seedlings per plot were used in bioassays with *N. sertifer* and 16 seedlings with *G. pallida*, in 1992 and 1994, respectively. In 1994, half of the seedlings per plot were treated with the fungicide propiconazole to control ectomycorrhizal infection. The interactions between larval performance and mycorrhizal status of pine roots will be reported later.

The sawfly species used in the bioassays are gregarious and univoltine (Schwenke 1982). The sawfly cultures were collected from field. *N. sertifer* originated from northern Finland and *G. pallida* from southern Finland, since either of these species has not appeared on outbreak level in the Kuopio area recently. In 1992, relative growth rate ($RGR = (\ln(w_2) - \ln(w_1)) / t$, w_2 = final mass, w_1 = initial mass, t = duration of the growth trial (days)) and survival of *N. sertifer* larvae was determined. The bioassay lasted for 17 days, starting in June 25. The larvae were reared in mesh bags in groups of 10 larvae on 10 pine seedlings per plot. Bioassay with third instar larvae of *G. pallida* larvae was accomplished with detached branches in plastic containers (Lyytikäinen 1993) during a seven-day period, starting in August 8, 1994. The effect of dead larvae was estimated by making an assumption, that they lived until the middle of a bioassay period. Relative growth rate (RGR), survival, total consumption (TC) were determined. Food utilization indices, relative consumption rate (RCR), efficiency of conversion of ingested material (ECI) and approximate digestibility (AD) were calculated according to Waldbauer (1968):

TC = dry weight of plant material eaten

RCR = dry weight of plant material eaten / (mean larval dry weight × time)

ECI = 100 × larval dry weight gain / dry weight of plant material eaten

AD = 100 × (dry weight of plant material eaten – dry weight of frass) / dry weight of plant material eaten

For TC measurement average needle weight of each seedlings was determinated by weighing. The weight of totally consumed needles was estimated by multiplying the average weight by the numbers of eaten needles. The weight of consumed biomass of partly eaten needles was estimated by measuring the over-left needle parts, and using the difference between an average needle and an uneaten needle part as an estimate.

To determine the chemical quality of needle material with gas chromatography-mass spectrometry (Kainulainen et al. 1994), current needles for resin acid analysis were sampled in mid-September 1992, and at the time of *G. pallida* larval feeding in 1994 in liquid nitrogen.

3 Results

Ozone did not have significant ($p > 0.05$) effect on the survival and the relative growth rate of *N. sertifer* -larvae (Fig. 1). The larval weights of *G. pallida* tended to be lower in elevated ozone concentration, but the relative growth rate (RGR) attained higher. However, there were no significantly ($p > 0.05$) different values under the same treatment (Fig. 2). The treatments had no effects

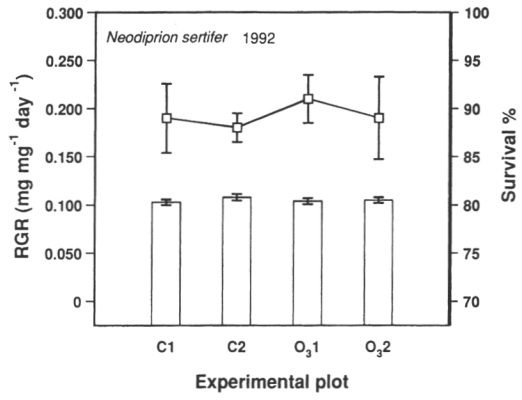


Fig. 1. Relative growth rate (± S.E.) (bar) and survival (± S.E.) (line) of *Neodiprion sertifer* larvae in 1992. Experimental plots: C1 = ambient air, plot 1, C2 = ambient air, plot 2, $O_3$1 = elevated ozone, plot 1, $O_3$2 = elevated ozone, plot 2. n = 10.

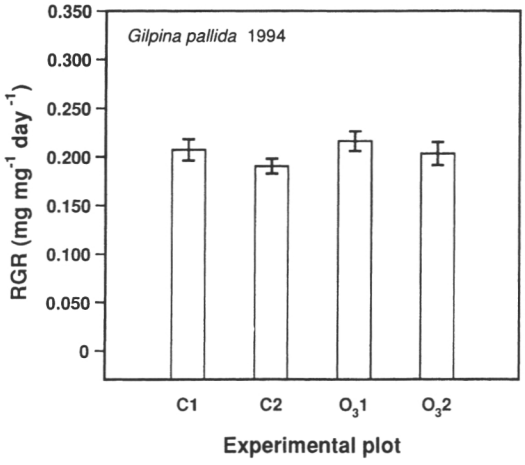


Fig. 2. Relative growth rate (± S.E.) *Gilpina pallida* larvae in 1994. Experimental plots are explained in Fig 1. n = 16.

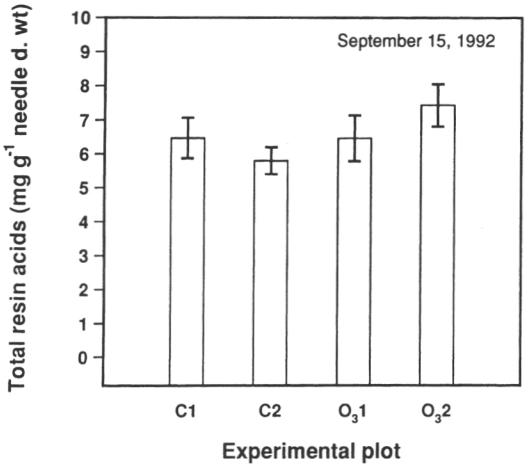


Fig. 3. Levels of total resin acids (± S.E.) in the current-year needles of Scots pine seedlings at the end of the growing season 1992. Experimental plots are explained in Fig 1. n = 6

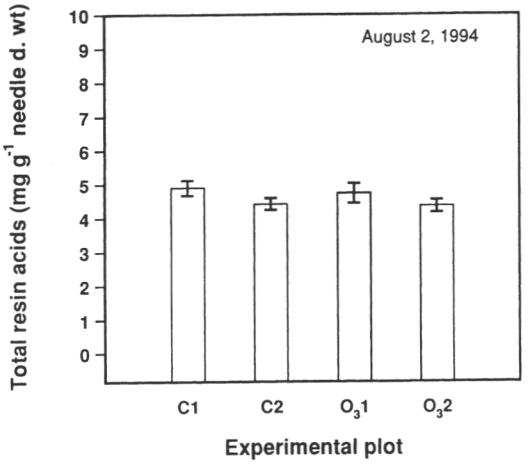


Fig. 4. Levels of total resin acids (± S.E.) in the current-year needles of Scots pine seedlings during feeding experiment in 1994. Experimental plots are explained in Fig 1. n = 16.

on larval survival, since only very few larvae were dead during a bioassay period. The values of relative consumption rate (RCR), total consumption (TC), approximate digestibility (AD) and growth efficiency (ECI) declined slightly in elevated ozone concentration, but did not reach a statistical significance.

There were no differences in total (Figs. 3 and 4) or individual resin acid concentrations between the treatments.

4 Discussion

The current results from the field experiments suggest that the elevated ozone concentrations in the field do not strongly affect the needle quality of young Scots pine and the performance of these two diprionid sawfly species. Spatial variation of microclimate between the plots in the experimental field may affect suitability of pine foliage to sawflies more than ozone dose.

One further explanation for the lack of responses in sawflies may be their chewing feeding behaviour. Insects belonging to different feeding guilds may have differences in stress response (Larsson 1989). Cambium feeders, represented by bark beetles and sucking insects like aphids have been more sensitive to stress-induced changes in host plants than chewing insects that do not separate chemical fractions in their food as efficiently. Studies of herbivorous insects on plants exposed to air pollutants, especially to SO_2 and NO_2 have supported this hypothesis (Whittaker 1994).

Scots pine seems to be relatively resistant against ozone, because ozone exposures in chamber experiments does not affect aphid growth (Brown et al. 1993) or reproduction (Kainulainen et al 1994). However, the effect of ozone fumigations on insect performance has been complex and it seems to depend on the exact pattern of fumigation (Whittaker 1994). Therefore, comparison of insects performance in current ozone levels to elevated levels may give more reliable estimates of the ecosystem effects of ozone than comparison of filtered air to constant ozone concentration in chamber experiments using short term fumigations. The seedlings in this study were exposed to elevated ozone concentrations several weeks and the levels followed the natural diurnal variation of ozone levels.

Outbreak species may be less affected by foliage quality than uncommon species (Hanski and Otronen 1985, Lyytikäinen 1994). Different types of stress with variability in time and dosage scale may result in different plant responses, e.g. variations in concentrations of phenolic compounds (Larsson et al. 1986). Such environmental stresses that alter plant carbon/nutrient balance would affect most strongly plant-herbivore interactions. It is obvious, that applied ozone fumigation or propiconazole treatment are not this kind of stresses. This conclusion is supported by the fact that we did not find any ozone-induced response in the levels of oleoresins in pine foliage.

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Change in Siberian Phytomass Predicted for Global Warming

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An equilibrium model driven by climatic parameters, the Siberian Vegetation Model, was used to estimate changes in the phytomass of Siberian vegetation under climate change scenarios (CO_2 doubling) from four general circulation models (GCM's) of the atmosphere. Ecosystems were classified using a three-dimensional climatic ordination of growing degree days (above a 5 °C threshold), Budyko's dryness index (based on radiation balance and annual precipitation), and Conrad's continentality index. Phytomass density was estimated using published data of Bazilevich covering all vegetation zones in Siberia. Under current climate, total phytomass of Siberia is estimated to be 74.1 ± 2.0 Pg (Petagram = 10^{15} g). Note that this estimate is based on the current forested percentage in each vegetation class compiled from forest inventory data. Moderate warming associated with the GISS (Goddard Institute for Space Studies) and OSU (Oregon State Univ.) projections resulted in a 23–26 % increase in phytomass (to 91.3 ± 2.1 Pg and 93.6 ± 2.4 Pg, respectively), primarily due to an increase in the productive Southern Taiga and Subtaiga classes. Greater warming associated with the GFDL (General Fluid Dynamics Laboratory) and UKMO (United Kingdom Meteorological Office) projections resulted in a small 3–7 % increase in phytomass (to 76.6 ± 1.3 Pg and 79.6 ± 1.2 Pg, respectively). A major component of predicted changes using GFDL and UKMO is the introduction of a vast Temperate Forest-Steppe class covering nearly 40 % of the area of Siberia, at the expense of Taiga; with current climate, this vegetation class is nearly non-existent in Siberia. In addition, Subboreal Forest-Steppe phytomass doubles with all GCM predictions. In all four climate change scenarios, the predicted phytomass stock of all colder, northern classes is reduced considerably (viz., Tundra, Forest-Tundra, Northern Taiga, and Middle Taiga). Phytomass in Subtaiga increases greatly with all scenarios, from a doubling with GFDL to quadrupling with OSU and GISS. Overall, phytomass of the Taiga biome (Northern, Middle, Southern, and Subtaiga) increased 15 % in the moderate OSU and GISS scenarios and decreased by a third in the warmer UKMO and GFDL projections. In addition, a sensitivity analysis found that the percentage of a vegetation class that is forested is a major factor determining phytomass distribution. From 25 to 50 % more phytomass is predicted under climate change if the forested proportion corresponding to potential rather than current vegetation is assumed.

Keywords phytomass, Siberia, climate change, global warming, carbon cycle, vegetation modeling, bioclimatology

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1 Introduction

We begin with the premise that significant global climate change induced by a buildup of greenhouse gases (e.g., carbon dioxide (CO_2), methane, chloroflourocarbons, nitrous oxide) in the atmosphere is an increasing possibility (Houghton et al. 1990). Currently the speed of the warming is high, 0.26 °C per decade during the past 15 years (Woodwell and Mackenzie 1995). The Intergovernmental Panel on Climate Change (IPCC) has concluded that a doubling of the atmospheric CO_2 concentration would likely change the mean global temperature by 1.5 to 4.5 °C after equilibrium conditions were reached (Houghton et al. 1990). Warming is projected to take only 50 to 100 years and would be concentrated more at high latitudes than low latitudes, more during winter than summer (Houghton et al. 1990). Woodwell and Mackenzie (1995) state that the earth's climate is not merely moving from one state of approximate equilibrium to another, but rather to a state of progressive instability.

Expected warming has been estimated to alter the distribution of vegetation over the globe, especially in the boreal and temperate zones (Emanuel et al. 1985, Leemans 1989, Smith et al. 1992, Monserud et al. 1993b). An increasing number of studies have used global vegetation models to analyze carbon (C) storage changes in the global biosphere under CO_2 doubling climate scenarios derived from general circulation models (GCM's) (Prentice and Fung 1990, Smith et al. 1992, Solomon et al. 1993, Smith and Shugart 1993, Cramer and Solomon 1993, Melillo et al. 1993, Dixon et al. 1994). More detailed process-based carbon dynamic models have been developed to assess both the influence of CO_2 concentration and climatic change on global and regional patterns of NPP (net primary productivity) (Janecek et al. 1989, Running and Nemani 1991, Smith et al. 1992, Mellilo et al. 1993).

Terrestrial vegetation may affect warming by means of feedbacks directly through the heat balance with changed albedo and indirectly through a mass transfer of carbon into the atmosphere (Janecek et al. 1989, Apps et al. 1993). Because boreal forests store a large amount of carbon (Kolchugina and Vinson 1993a) and are located in latitudes that are predicted to undergo the greatest warming, they may play a key role in future carbon fluxes (Dixon et al. 1994). Signs and magnitudes of resulting fluxes are still unclear, however. Neilson (1993) indicate that with warmer and drier climates boreal forests with high C stores will likely decrease in extent because of strong invasion by grasslands. Greater frequency and severity of forest fires predicted for boreal forests under global warming would release considerable carbon into the atmosphere (Perry et al. 1991). Smith et al. (1992) estimated enlarged C pools in boreal forests due to increased forest productivity and expansion into the current Tundra zone. A more accurate estimation of carbon gain or loss in vegetation under future warming could correct estimates of future CO_2 concentrations.

Our goal is to evaluate changes in phytomass of the vegetation of Siberia under projected CO_2-doubling climate change scenarios. Phytomass is total live plant mass (above- and belowground), including all forest stories and surface

layers. Phytomass density is phytomass per unit area. Because we use climate change projections from different GCM's, we can assess phytomass sensitivity to different climate change scenarios. We couple a Siberian vegetation model (Tchebakova et al. 1994) with four CO_2-doubling climate change scenarios varying in global warming predictions. As with Solomon (1986), our strategy is to study regional climate change effects by coupling climate change scenarios from GCM's with a regional vegetation model. Regional vegetation models afford much greater accuracy and resolution than global vegetation models for the same region. We derive phytomass density estimates from the authoritative and comprehensive compilation of Bazilevich (1986, 1993), supplemented by additional literature on Siberian forests (see Methods section 2.3). We assume that all changes in phytomass are a result of the redistribution of vegetation zones. Because the Siberian vegetation model is an equilibrium model, we do not consider dynamic aspects of the carbon cycle, such as transient changes in vegetation redistribution (e.g., migration rate). We assume that the future forested percentage of a given vegetation class will remain unchanged from the present, which implicitly assumes a continuation of current rates of land use, fires, insect outbreaks, and other disturbances. Furthermore, we focus on phytomass, and do not attempt to evaluate possible effects of climate change on soils and the enormous amount of carbon stored in peatlands.

2 Methods

2.1 Climatic Data

We used an improved version of the IIASA Climate Database (Leemans and Cramer 1991) containing a global network of temperature, precipitation, and cloudiness. Vapor pressure was taken primarily from climatic reference books for the former USSR (Gidrometeoizdat 1964–1970). Data from about 1200 weather stations in Siberia were used to interpolate precipitation on a 0.5° grid, and about 800 to 900 stations were used to interpolate temperature, vapor pressure, and cloudiness. Albedo (necessary to calculate Budyko's dryness index) was taken from Matthews' (1983) digitized albedo estimates for the continents. This climatic data became input to the Siberian vegetation model, which predicted a vegetation class for each half-degree latitude by half-degree longitude grid cell.

Climate change scenarios are expressed in terms of temperature and precipitation using the procedures listed by Monserud and Leemans (1992). The differences between the current climate computer control run and the doubled CO_2 run are determined for a given general circulation model (GCM) of the atmosphere. These differences are interpolated from the coarser GCM grid to the finer 0.5° by 0.5° vegetation model grid using the same smooth surface fitting procedure of Leemans and Cramer (1991). This interpolation was done for all monthly temperature and precipitation values. The absolute value of the temperature differences and the ratio of the precipitation estimates are calculated for each grid cell on the finer grid. The doubled CO_2 climate database is created by adding the temperature differences to the current climate database and by multiplying precipitation by the precipitation ratio. The climate change scenario is then created by using the doubled CO_2 climate database as input to the Siberian vegetation model.

We used climate change projections corresponding to a doubling of CO_2 from the following four GCM's: GFDL, Geophysical Fluid Dynamics Laboratory of NOAA at Princeton (Wetherald and Manabe 1986, Manabe and Wetherald 1987); GISS, Goddard Institute for Space Studies of NASA at Columbia University (Hansen et al. 1983); OSU, Oregon State University at Corvallis (Schlesinger and Zhao 1989); and UKMO, United Kingdom Meteorological Office (Mitchell 1983, Wilson and Mitchell 1987). Based on predictions of vegetation change from two global vegetation models and the Siberian vegetation model used here, the GISS and OSU scenarios indicated more moderate warming than did the GFDL or UKMO scenarios, which predicted the greatest change (Monserud and Leemans 1992, Monserud et al. 1993a, 1993b).

We used the following boundaries to delineate

Siberia: the area between 60°E (Ural Mountains) in the west, 140°E (Tchersky Mountains) in the east, 50°N (Mongolian border) in the south, and 76°N (Arctic Ocean) in the north. Because the model was not designed for maritime climates, we excluded the southeast corner of this region (the vicinity of the Sea of Okhotsk): south of 60°N and east of 130°E. Note that this simplified region includes a portion of Kazakhstan in the southwestern corner, as well as a small area of northern Mongolia (between the Tuva and Buryat regions) and northeastern China (near the Amur River); these regions outside Siberia total 9 % of our study area.

2.2 The Siberian Vegetation Model

The Siberian vegetation model (Tchebakova et al. 1994) is based on bioclimatological considerations. It simulates the major vegetation classes (biome subdivisions) of Siberia from three climatic indices: growing degree-days (base 5 °C), dryness index, and continentality index. Because these indices reflect requirements of plants for warmth, drought resistance, and cold tolerance, they define the main features of vegetation zones (biomes) and their subdivisions. Climatic inputs (monthly mean temperature, precipitation, vapor pressure, cloudiness, and albedo) are obtained from a global climatic database, supplemented by additional weather stations in Siberia; resolution is 0.5° longitude by 0.5° latitude. Because this model is a static equilibrium model, it can only predict the types of vegetation that are suited to the climate of a locality, not the vegetation that will actually be there. Note that the Siberian vegetation model is not sensitive to the distribution of permafrost.

Growing Degree-Days (Tuhkanen 1980) and the closely related concept of Temperature Sums used in Russian literature (Tchebakova et al. 1994) are widely recognized as useful parameters for characterizing the heat requirements for plants. We chose Growing Degree Days above a base temperature of 5 °C (GDD_5), the minimum temperature required for plant growth in cold climates (Prentice et al. 1992).

Dryness Index characterizes the dryness of climates (Budyko 1974). It is the ratio of annual potential evaporation to precipitation. Potential evaporation is approximated as radiation balance divided by the latent heat of vaporization of water. This converts energy flux (radiation balance) to an equivalent evaporation. Radiation balance is determined according to the methodology of Budyko (1974), with improvements by Zubenok (1976) and Efimova (1977) (see Tchebakova et al. 1993 or Monserud et al. 1993b for details). Dryness Index (DI) is strongly related to a ratio of actual and equilibrium evapotranspiration used by Prentice et al. (1991) to characterize drought stress in plants.

Continentality Index (Conrad 1947) attempts to characterize the severity of climates on large continents. We characterize severe continental climates in Siberia as having low winter temperatures, short frost-free periods, limited moisture in spring, and the maintenance of permafrost in eastern and northern Siberia. Moving west to east, there are gradients of increasing continentality and decreasing humidity as moisture is removed from air masses.

Conrad's Continentality Index (CI) is a function of latitude (distance from the equator) and the difference in summer maximum and winter minimum temperatures. Nazimova et al. (1990) found continentality index of great importance for classifying vegetation in the Siberian subcontinent. Tchebakova et al. (1994) found that CI was strongly correlated ($r = 0.94$ for 116 stations in Siberia) to mean temperature of the coldest month (January for Siberia), which was used effectively by Prentice et al. (1992) in their global biome model.

These three indices classify Siberian vegetation in three dimensions. Dryness index classifies vegetation into broad biomes such as *Taiga* ($DI < 2$), *Steppe* ($2 \leq DI < 3.3$), and *Desert* ($DI \geq 3.3$); these are zonobiomes according to Walter (1983). Growing degree-days classify vegetation into mostly latitudinal thermic bands representing vegetation zones as *Tundra*, *Forest-Tundra*, the subdivisions of the Taiga biome (*Northern, Middle*, and *Southern Taiga*, and *Subtaiga*), and *Forest-Steppe*. Forest-Steppe is additionally separated as a drier class than Southern Taiga and Subtaiga by dryness index. Continentality index classifies vegetation into three longitudinally distinct sectors: the continental western sec-

tor, the more continental central sector, and the extremely continental eastern sector. Note that the moderate continental climate of European Russia (west of the Ural Mountains) is less continental than all these sectors of Siberia. The intersection of a zone and a sector determines a vegetation class. These latitudinal and longitudinal divisions are only approximate and may be interrupted by mountains.

Three temperate classes (Forest-Steppe, Steppe, and Semidesert) have been incorporated into the model although they do not occur under modern climates in Siberia. These temperate classes are predicted to become significant under global warming.

Tchebakova et al. (1994) examined the performance of the model by comparing predictions with the detailed Landscape Map of the USSR (Isachenko 1988), which was not used for model development. Isachenko's map is based primarily on vegetation and geomorphology, using a vegetation classification similar to that used by Tchebakova et al. (1994). Predicted vegetation generally matches well with mapped vegetation. The general locations of all vegetation zones are predicted correctly. Kappa statistics, which objectively measure cell-by-cell agreement between maps (Monserud and Leemans 1992), show good agreement at all scales of comparison (Tchebakova et al. 1994).

2.3 Phytomass Estimation

We rely on the Russian literature to obtain estimates of phytomass density. Our main sources are the major compilations by Bazilevich (1986, 1993) and Bazilevich et al. (1986), which we refer to simply as Bazilevich. These papers summarize phytomass results for the former USSR compiled from over 500 publications describing more than 2500 research plots. For our Siberian study area we used data from approximately 500 of these plots. Bazilevich used a zonal vegetation classification system – including sectors of continentality – very similar to the classification system used by Tchebakova et al. (1994). Therefore, our vegetation classes were easily identified in terms of the Bazilevich classification, although auxiliary information on dominant tree species was also used. For each vegetation class we calculate mean phytomass density (and standard deviation) from the plot data presented by Bazilevich (1986, 1993) and Bazilevich et al. (1986), with additional data from Pozdnyakov et al. (1969), Wielgolaski (1972), Mitrofanov (1977), Protopopov and Zyubina (1977), Semechkina (1978), Semechkin and Tetenkin (1980), Kuzmina and Spitsyna (1984), Stakanov (1984), Zyubina (1984), Falaleev (1985), Ermolenko (1987), and Alimov et al. (1989) (Table 1).

To estimate total phytomass density, above-ground phytomass was summed with root phytomass per unit area (Bazilevich 1986, 1993, Bazilevich et al. 1986). If roots were not measured, root phytomass was estimated to be 20 % of above-ground phytomass, based on results from Atkin (1984), Onuchin and Borisov (1984), and Ermolenko and Ermolenko (1982). Bazilevich (1993, p. 8) lists root phytomass in productive stands to be 17–20 % of above-ground phytomass, increasing to 25 % in less productive stands.

The studies of Semechkin and Tetenkin (1980), Zyubina (1984), Falaleev (1985), and Alimov et al. (1989) were designed to measure stem volume rather than phytomass for the stand. We calculated total phytomass density by multiplying stem volume per hectare by species-specific conversion coefficients (Isaev et al. 1993) relating stem volume to phytomass of leaves, woody above-ground and below-ground parts of plants, and general stage of stand development. Because understory vegetation was not measured in these stem volume studies, we assumed understory vegetation accounted for an additional 10 % of total phytomass density. This figure is intermediate between the 3–5 % found for Middle and Southern Taiga and the 20 % reported in open Northern Taiga (Alexeev and Birdsey 1994).

We make one modification to Bazilevich's estimates; her phytomass density values are for the Forest component only in forest ecosystems. We calculate a weighted average for total phytomass density using the observed forested and non-forested proportion in each vegetation class compiled by Alexeev and Birdsey (1994) from 1988 forest inventory data (Table 2).

Bazilevich does not give a measure of variation or precision for her phytomass density esti-

Table 1. Mean and standard deviation of phytomass density for Siberian vegetation classes. Data sources are listed under References.

No.	Vegetation class (and sector)	Mean density (t ha^{-1})	Standard deviation (t ha^{-1})	Reference
1	Tundra	17.9	10.0	Bazilevich 1986, 1993, Bazilevich et al. 1986, Wielgolaski 1972
2	Spruce-larch Forest-Tundra (Western Sector)	51.7	22.4	Bazilevich 1986, 1993, Bazilevich et al. 1986
3	Larch Forest-Tundra (*Larix sibirica, L. gmelinii*) (Central Sector)	49.6	16.5	Bazilevich et al. 1986, Bazilevich 1993
4	Larch Forest-Tundra (*L. cajanderii*) (Eastern Sector)	47.0	8.9	Bazilevich 1993
5	Dark-needled Northern Taiga (Western Sector)	123.5	-	Bazilevich et al. 1986
6	Light-needled Northern Taiga (Central Sector)	107.6	24.0	Bazilevich 1993, Pozdnyakov et al. 1969
7	Larch Northern Taiga (Eastern Sector)	57.8	14.9	Bazilevich et al. 1986, Bazilevich 1993, Pozdnyakov et al. 1969, Alimov et al. 1989
8	Dark-needled Middle Taiga (Western Sector)	207.5	35.5	Bazilevich 1986, 1993, Bazilevich et al. 1986, Mitrofanov 1977, Falaleev 1985
9	Light-needled Middle Taiga (Central Sector)	153.3	97.3	Bazilevich 1993, Bazilevich et al. 1986, Pozdnyakov et al. 1969, Mitrofanov 1977
10	Larch Middle Taiga (Eastern Sector)	138.6	43.4	Bazilevich 1986, 1993, Bazilevich et al. 1986, Pozdnyakov et al. 1969, Mitrofanov 1977
11	Dark-needled Southern Taiga (Western Sector)	229.2	51.7	Bazilevich 1986, 1993, Bazilevich et al. 1986
12	Light-needled Southern Taiga (Central Sector)	224.3	79.3	Bazilevich 1993, Bazilevich et al. 1986, Semechkin and Tetenkin 1980, Ermolenko 1987
13	Birch Subtaiga (Western Sector)	213.3	-	Bazilevich 1993, Bazilevich et al. 1986
14	Light-needled Subtaiga (Central Sector)	181.6	57.9	Bazilevich 1986, Protopopov and Zyubina 1977, Zyubina 1984
15	Birch Forest-Steppe (Western Sector)	156.8	68.7	Bazilevich 1986, 1993, Bazilevich et al. 1986
16	Light-needled Forest-Steppe (Central Sector)	179.6	38.6	Bazilevich 1986, 1993, Kuzmina and Spitsyna 1984, Zyubina 1984, Stakanov 1984, Semechkina 1978
17	Larch Forest-Steppe (Eastern Sector)	131.5	-	Pozdnyakov et al. 1969
18	Semiarid Steppe (Western Sector)	17.8	3.3	Bazilevich 1986, 1993, Bazilevich et al. 1986
19	Arid Steppe (Central Sector)	15.3	4.9	Bazilevich 1986, 1993, Bazilevich et al. 1986
20	Cryoarid Steppe (Eastern Sector)	10.9	1.8	Bazilevich 1986, 1993, Bazilevich et al. 1986
21	Temperate Forest-Steppe	163.6	-	Bazilevich 1986
22	Temperate Steppe	14.4	5.3	Bazilevich 1986, 1993, Bazilevich et al. 1986
23	Semidesert	8.2	1.5	Bazilevich 1986

Table 2. Total phytomass densities (t ha^{-1}) calculated for Siberian vegetation classes, assuming each class contains a specified non-forest component as well. Component class densities are multiplied by the forested and non-forested proportion to produce a mean density for the forest and non-forest components, respectively. Their sum is the total density for the vegetation class. Note that the non-forest component for all Taiga classes is "Meadows of the Boreal Zone" with an mean phytomass density of 13.8 t ha^{-1} (Bazilevich 1986, 1993).

Vegetation class (and sector)	Phytomass density by component (t ha^{-1})		Proportion		Total phytomass density (t ha^{-1})		
	Forested	Non-forested	Forested	Non-forested	Forested	Non-forested	Total
Tundra	0.0	17.9	0.00	1.00	0.0	17.9	17.9
Spruce-larch Forest-Tundra (Western)	51.7	17.9	0.25	0.75	12.9	13.4	26.3
Larch Forest-Tundra (Central)	49.6	17.9	0.30	0.70	14.9	12.5	27.4
Larch Forest-Tundra (Eastern)	47.0	17.9	0.25	0.75	11.7	13.4	25.2
Dark-needled Northern Taiga (Western)	123.5	13.8	0.40	0.60	49.4	8.3	57.7
Light-needled Northern Taiga (Central)	107.6	13.8	0.85	0.15	91.5	2.1	93.5
Larch Northern Taiga (Eastern)	57.8	13.8	0.35	0.65	20.2	9.0	29.2
Dark-needled Middle Taiga (Western)	207.5	13.8	0.40	0.60	83.0	8.3	91.3
Light-needled Middle Taiga (Central)	153.3	13.8	0.85	0.15	130.3	2.1	132.4
Larch Middle Taiga (Eastern)	138.6	13.8	0.75	0.25	103.9	3.5	107.4
Dark-needled Southern Taiga (Western)	229.2	13.8	0.35	0.65	80.2	9.0	89.2
Light-needled Southern Taiga (Central)	224.3	13.8	0.85	0.15	190.7	2.1	192.7
Birch Subtaiga (Western)	213.3	13.8	0.35	0.65	74.7	9.0	83.6
Light-needled Subtaiga (Central)	181.6	13.8	0.85	0.15	154.4	2.1	156.4
Birch Forest-Steppe (Western)	156.8	17.8	0.20	0.80	31.4	14.2	45.6
Light-needled Forest-Steppe (Central)	179.6	15.3	0.40	0.60	71.8	9.2	81.0
Larch Forest-Steppe (Eastern)	131.5	10.9	0.40	0.60	52.6	6.5	59.1
Semiarid Steppe (Western)	119.1	17.8	0.05	0.95	6.0	16.9	22.9
Arid Steppe (Central)	221.9	15.3	0.05	0.95	11.1	14.5	25.6
Cryoarid Steppe (Eastern)	119.1	10.9	0.05	0.95	6.0	10.3	16.3
Temperate Forest-Steppe	163.6	15.3	0.30	0.70	49.1	10.7	59.8
Temperate Steppe	194.3	14.4	0.05	0.95	9.7	13.7	23.4
Semidesert	0.0	8.2	0.00	1.00	0.0	8.2	8.2

mates. By compiling all individual plot phytomass density values from Bazilevich (1986, 1993), Bazilevich et al. (1986), and the other phytomass publications, we were able to estimate the standard deviation of the distribution of phytomass density for each vegetation class (Table 1); note that this value is not the standard error of the mean. These estimates of variation allowed us to calculate the precision of our final phytomass estimates for Siberia. The 95 % confidence interval was calculated using the standard formula of $\bar{X} \pm z \times S / \sqrt{n}$, with mean $\bar{X}$, z the standard normal deviate corresponding to $\alpha = 5$ %, S the standard deviation, and n the sample size. The standard deviation S of total phytomass was estimated by first calculating total phytomass using $\bar{X}_i + S_i$ and $\bar{X}_i - S_i$ from Table 1 and dividing the difference by 2, where $\bar{X}_i$ is mean phytomass density and S_i the standard deviation for vegetation class i.

Table 3 lists area estimates for each vegetation class based on the current climate and climate change projections. Simple multiplication of area by mean phytomass density gives total phytomass per vegetation class.

Table 3. Areas and predicted total phytomass of vegetation classes under present and climate warming.

Vegetation class (and sector)	Area (units = 10 000 km^2)					Phytomass (Pg)				
	Current climate	Climate change				Current climate	Climate change			
		GISS	OSU	GFDL	UKMO		GISS	OSU	GFDL	UKMO
Tundra	140.0	22.0	40.1	14.9	19.4	2.5	0.4	0.7	0.3	0.3
Spruce-larch Forest-Tundra (Western)	31.0	42.8	35.2	19.4	22.2	0.8	1.1	0.9	0.5	0.6
Larch Forest-Tundra (Central)	93.3	17.3	23.6	6.9	1.1	2.6	0.5	0.6	0.2	0.1
Larch Forest-Tundra (Eastern)	10.9	0.9	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0
Dark-needled Northern Taiga (Western)	64.6	77.8	45.1	41.9	54.3	3.7	4.5	2.6	2.4	3.1
Light-needled Northern Taiga (Central)	186.5	99.0	88.0	43.1	12.5	17.4	9.3	8.2	4.0	1.2
Larch Northern Taiga (Eastern)	19.8	4.3	7.8	1.1	0.0	0.6	0.1	0.2	0.0	0.0
Dark-needled Middle Taiga (Western)	53.5	50.2	35.0	26.4	41.2	4.9	4.6	3.2	2.4	3.8
Light-needled Middle Taiga (Central)	105.9	85.0	101.6	48.6	24.5	14.0	11.3	13.4	6.4	3.2
Larch Middle Taiga (Eastern)	29.8	1.3	7.2	0.1	1.2	3.2	0.1	0.8	0.0	0.1
Dark-needled Southern Taiga (Western)	52.2	36.7	25.0	16.6	21.1	4.7	3.3	2.2	1.5	1.9
Light-needled Southern Taiga (Central)	37.7	65.4	85.4	43.8	41.1	7.3	12.6	16.5	8.4	7.9
Birch Subtaiga (Western)	53.2	99.4	61.2	39.7	70.4	4.4	8.3	5.1	3.3	5.9
Light-needled Subtaiga (Central)	15.2	122.7	134.9	73.2	110.6	2.4	19.2	21.1	11.5	17.3
Birch Forest-Steppe (Western)	50.0	41.2	31.6	30.7	15.2	2.3	1.9	1.4	1.4	0.7
Light-needled Forest-Steppe (Central)	13.7	34.2	53.9	79.3	54.8	1.1	2.8	4.4	6.4	4.4
Larch Forest-Steppe (Eastern)	5.5	21.6	47.5	30.1	1.3	0.3	1.3	2.8	1.8	0.1
Semiarid Steppe (Western)	28.1	0.5	0.2	2.6	0.2	0.6	0.0	0.0	0.1	0.0
Arid Steppe (Central)	7.2	2.0	3.9	3.2	0.0	0.2	0.1	0.1	0.1	0.0
Cryoarid Steppe (Eastern)	7.5	0.8	2.0	6.4	0.4	0.1	0.0	0.0	0.1	0.0
Temperate Forest-Steppe	0.2	138.7	119.0	379.3	444.4	0.0	8.3	7.1	22.7	26.6
Temperate Steppe	23.2	76.3	83.1	132.7	101.3	0.5	1.8	1.9	3.1	2.4
Semidesert	12.3	1.0	9.9	1.2	4.1	0.1	0.0	0.1	0.0	0.0
Total	1041.1	1041.1	1041.1	1041.1	1041.1	74.1	91.3	93.6	76.6	79.6

3 Results

3.1 Phytomass

Under current climate, we estimate the total phytomass of Siberia to be 74.1 ± 2.0 Pg (Petagram = 10^{15} g). Note that this estimate is based on the observed forested proportion in each vegetation class compiled by Alexeev and Birdsey (1994) from current forest inventory data (Table 2). Phytomass estimates for climate change (CO_2-doubling) scenarios fell into two groups (Table 3). Moderate warming associated with the GISS and OSU projections resulted in a 23–26 % increase in phytomass (to 91.3 ± 2.1 Pg and 93.6 ± 2.4 Pg, respectively). Extreme warming associated with the GFDL and UKMO projections resulted in a small 3–7 % increase in phytomass (to 76.6 ± 1.3 Pg and 79.6 ± 1.2 Pg, respectively). In all four climate change scenarios, the phytomass stock of all colder, northern classes is predicted to be reduced considerably (viz., Tundra, Forest-Tundra, Northern Taiga, and Middle Taiga). In the moderate OSU-GISS warming this reduction was 40 %, from 50 Pg to 30 Pg. The reduction with the extreme UKMO-GFDL scenarios was 70–75 %, down to approximately 15 Pg. Phytomass increases 30–50 % in Southern Taiga with the OSU-GISS scenarios, and decreases 15 % with the UKMO-GFDL scenarios. Phytomass in Subtaiga increases greatly with all scenarios, from a doubling with GFDL to quadrupling with OSU and GISS. Overall, phytomass of the Taiga biome (Northern, Middle, Southern, and Subtaiga) increased 15 % in the moderate OSU and GISS scenarios and decreased by a third in the UKMO and GFDL projections. The phytomass of Forest-Steppe doubles with all GCM's.

The most important change found in all scenarios is the introduction of a vast Temperate Forest-Steppe zone, predicted to cover up to 40 % of the area of Siberia (UKMO-GFDL); with current climate, this vegetation class is nearly non-existent. Temperate Forest-Steppe phytomass is three times larger in the warmer UKMO-GFDL scenarios (23–27 Pg) than in the moderate OSU-GISS scenarios (7–8 Pg). The area of the Temperate Steppe zone also increases greatly (3–5 times in all scenarios), but the low mean phytomass values of Steppe means that this expansion will not be accompanied by an important increase in phytomass.

In Figs. 1–3, we calculate the geographic distribution of phytomass density by 40 t/ha classes for current climate as well as both moderate (GISS) and extreme (GFDL) warming. Under current climate (Fig. 1), the most productive ecosystems with density > 120 t/ha are found in the southeast quarter of Siberia, mostly below 60°N latitude and east of 90°E longitude. Under the moderate warming in the GISS scenario (Fig. 2), the area of high phytomass density significantly expands and spreads northeast, as far as 70°N latitude. Under the extreme warming of the GFDL scenario (Fig. 3), these high density areas would noticeably shift northwards and somewhat increase in size. The highest density class (light-needled Southern Taiga) shifts so far north that it is centered at 67°N latitude, in the heart of Yakutia. In the GFDL scenario, smaller high density regions also remain in southern Siberia in the Sayan Mountains and the tablelands northeast of Lake Baikal. Medium density (80–120 t/ha) vegetation classes both shrink in size and shift to the north as simulated warming increases from current climate to moderate (GISS) and extreme (GFDL) warming (Figs. 1–3).

Under both the GISS and GFDL warming scenarios, the area of low density ecosystems (Tundra and Forest-Tundra, all less than 40 t/ha) in the north shrinks dramatically. In the south, the location and area of the low phytomass density ecosystems (primarily Steppe) do not change much.

The most striking features of the phytomass predictions from an increasingly warm climate in Figs. 1–3 are both the dramatic northeastern shift in the high phytomass density classes (light-needled Middle Taiga, Southern Taiga, and Subtaiga), and the enormous expansion of the intermediate density class (40–80 t/ha) dominated by Temperate Forest-Steppe.

We also estimated phytomass assuming potential vegetation is possible. We replaced the observed forested percentages from Alexeev and Birdsey (1994) with potential values by Permiakov (1974). Potential forested percentage increased to 55 % for Forest-Tundra, 85 % for all Taiga classes, and 60 % for Forest-Steppe. As a result, current potential phytomass increased to 98.1 ± 2.4 Pg, a substantial increase (24 Pg) over

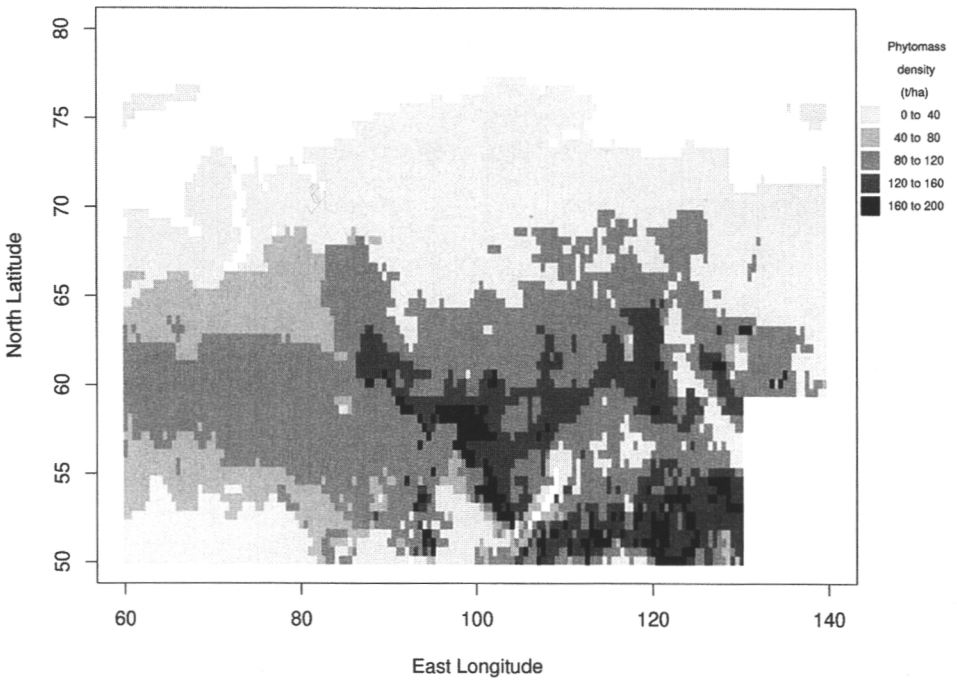


Fig. 1. Predicted Siberian phytomass distribution under current climate.

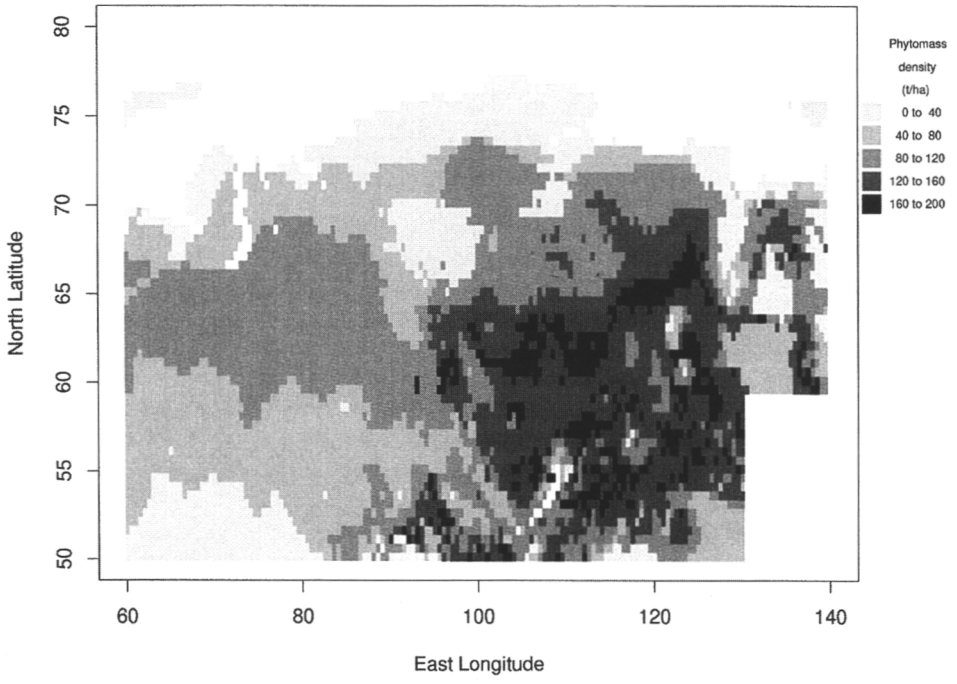


Fig. 2. Predicted Siberian phytomass distribution under the moderate warming of the GISS climate change scenario.

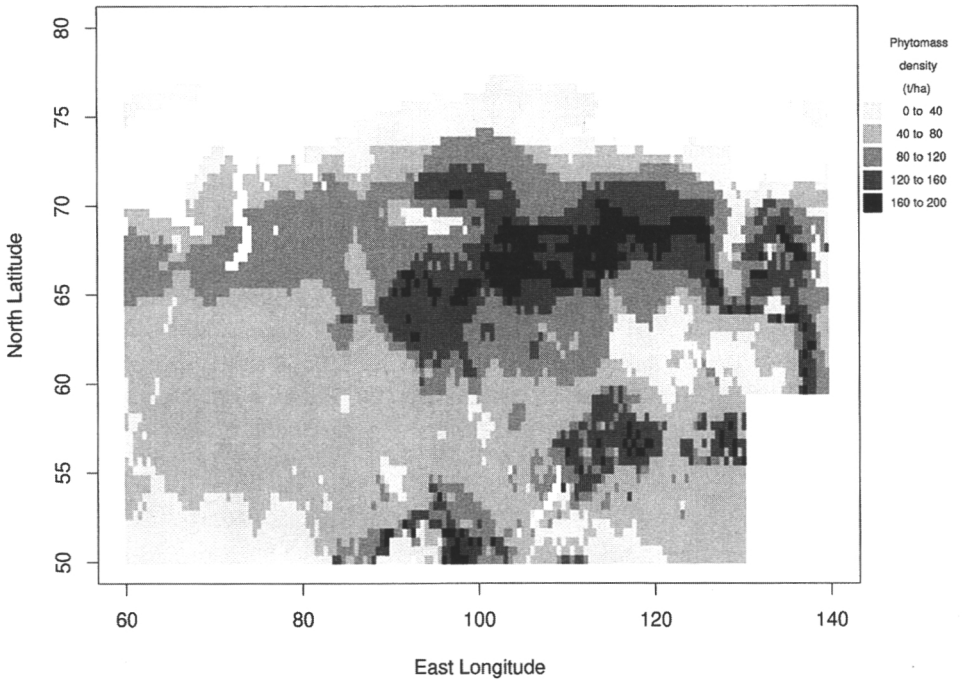


Fig. 3. Predicted Siberian phytomass distribution under the extreme warming of the GFDL climate change scenario.

actual current phytomass. Most of this difference results from an increase in the forested percentage in the Taiga biome. Estimates of potential phytomass from climate change scenarios increased 25–38 Pg (25–50 %) over estimates using the observed forested percentage. The major difference was in the Temperate Forest-Steppe class, and was a result of increasing the forested percentage from 30 % to 60 %.

4 Discussion

Results indicate enormous potential change in the spatial distribution of vegetation in Siberia due to climate change (CO_2-doubling). Although the GFDL and UKMO scenarios predict more extreme warming than the GISS and OSU scenarios, all four GCM's predict large reductions in the area of Tundra and Forest-Tundra, reductions and northern shifts in the various classes of Taiga, and reductions in Steppe. Large increases in area are predicted for the Temperate Forest-Steppe and Temperate Steppe vegetation zones, and for Forest-Steppe and Subtaiga in the Boreal zone. Generally, vegetation bands are predicted to shift northward and somewhat east, with extensive areas of temperate vegetation introduced in the south. Steppe and Tundra will shift eastward. Tundra and Northern Taiga are predicted to move 600–1000 km north, while Middle and Southern Taiga are predicted to move 1000–1500 km north (Monserud et al. 1993a). Subboreal Steppe and Temperate Forest-Steppe will invade north as far as 2500 km. Under the somewhat more moderate changes predicted by the GISS and OSU scenarios, distances that vegetation classes shift will be about 1.5 times less than with the GFDL and UKMO scenarios, although the direction of shift (northeasterly) is about the same. Temperate Forest-Steppe is predicted to penetrate into the current boreal zone as much as 3000 km. Kappa statistics (Monserud and Leemans 1992) for judging agreement between the current climate vegetation map and the climate

change predictions indicate essentially no agreement between maps, thus confirming the visual impression of wholesale change in the predicted vegetation of Siberia (Monserud et al. 1993a).

The resulting effect on total phytomass depends on the degree of warming. With moderate warming (OSU and GISS), phytomass is predicted to increase by 25 %. With greater warming (UKMO and GFDL), the predicted increase in phytomass is small, 3–7 %. These conflicting results can largely be explained by the effect of warming on the future distribution of Taiga. Southern Taiga and especially Subtaiga will flourish under the moderate warming scenarios. In contrast, Taiga will shrink while Forest-Steppe and Steppe expand with the more extreme warming scenarios. Because Forest-Steppe and Steppe have considerably less mean phytomass than Taiga, a decrease in total phytomass then occurs. Thus, for phytomass estimation, it matters greatly which GCM is being used to predict climate change.

The question of precision is difficult, for the accuracy of the maps is not stated, and no measure of precision or variation is listed in Bazilevich (1986,1993) or the other phytomass publications. We overcame this latter shortcoming by estimating the variance (by vegetation class) of all the individual plot phytomass density values that we could find in the available literature, primarily Bazilevich (1993). This allowed us to estimate the precision of the final phytomass estimate for current climate as 74.1 ± 2.0 Pg, the 95 % confidence interval based on S = 23 Pg and sample size n = 520. Note that these estimates assume equilibrium conditions with the same rate of mortality due to forest fires, insects, and diseases. Although all three rates could increase under global warming, we have not attempted to adjust for such changes.

Permafrost is an important component of the Siberian landscape. Essentially all of eastern Siberia is in the permafrost zone, and most of that is continuous permafrost (Kolchugina and Vinson 1993b). Based on paleoanalogues from warm epochs like the mid-Holocene and the Last Interglacial climatic optima, the permafrost zone is predicted to retreat far north in Siberia under global warming (Velichko et al. 1995). Because eastern Siberia is already quite dry, it has the greatest potential for vegetation change with global warming. If eastern Siberia remains relatively dry under global warming, two divergent outcomes are possible. If drainage is poor, the buildup of extensive mire formations could begin. If drainage is good, current permafrost forest sites could become considerably drier, so dry that in such locations in Yakutia the *Larix* forests could be replaced by xerophytic shrubs and grasses (Tchebakova et al. 1995). In either case, above-ground phytomass storage would decrease. However, if precipitation is sufficient under warming, Siberian spruce (*Picea obovata* Ledeb.) could replace Siberian larch (*Larix sibirica* Ledeb.) in Northern Taiga; Siberian cedar (*Pinus sibirica* Du Tour) and Siberian fir (*Abies sibirica* Ledeb.) could replace Siberian larch in Middle Taiga, and Scots pine (*Pinus sylvestris* L.) and birch (*Betula pendula* Roth) could replace *Larix gmelinii* (Rupr.) Litv. and *L. dahurica* Turcz. in the extremely continental climatic zone in Yakutia (Velichko et al. 1995). Replacing *Larix* species with the more productive Taiga species from the west will increase phytomass production in eastern Siberia.

We wish to compare our Siberian phytomass estimate to available estimates for Russia (Isaev et al. 1993, Alexeev and Birdsey 1994) or the former USSR (Kolchugina and Vinson 1993a); we proportionally adjust their estimates by area for Siberia. All three studies calculated phytomass of forest land by broad age classes; in addition, all three excluded the Tundra biome. By relying primarily on the phytomass density data of Bazilevich (1986, 1993), we implicitly assume that all forests are mature rather than young growth. Of course, this is not true, for harvesting and fires result in new stand formation. Both Isaev et al. (1993) and Kolchugina and Vinson (1993a) present data on the areal distribution of young growth vs. mature stands in Russia and the former USSR, respectively, with the result that approximately 10 % of the area is young growth. This 10 % is surely too high for Siberia, where forest access for harvesting is considerably reduced over European Russia (Alexeev and Birdsey 1994), especially in the north and on permafrost. Thus, we estimate very conservatively that 10 % of the forested area in Siberia is in young growth stands. We estimate the phytomass of these young stands to be 4.5 % of mature stand phytomass, based on

volume data by age class for administrative units in Siberia presented by Alexeev and Birdsey (1994). Reducing our phytomass estimate of 71.6 Pg (Tundra excluded) by 10 % for the area of young growth stands, and adding in the small contribution of phytomass from these young stands yields an estimate of 64.8 Pg for Siberia.

The studies of Isaev et al. (1993), Kolchugina and Vinson (1993a), Alexeev and Birdsey (1994), and Olson et al. (1983) are based on carbon, whereas ours is based on phytomass. For comparison purposes, we multiplied their estimates of total plant carbon by the constant 2, a conversion factor assuming phytomass is 50 % carbon (Isaev et al. 1993, Alexeev and Birdsey 1994).

We compared our estimates of current Siberian phytomass to those of Isaev et al. (1993), who examined Russia's forest ecosystems using the 1988 USSR Forest Inventory. Isaev et al. (1993) used phytomass density data from Bazilevich to calibrate the relationship between stand volume and phytomass. Because Isaev excluded the Tundra biome, we calculated the non-Tundra proportion of our Siberian study area to that of Isaev's to be 0.76. Multiplying by their total phytomass of 82.4 Pg yields 62.6 Pg. This is very close to our estimate of 64.8 Pg.

Kolchugina and Vinson (1993a) examined carbon pools in forest biomes in the former USSR, relying heavily on the work of Bazilevich (1986). Additional information on the proportion of young to mature stands was obtained from the USSR Forest Inventory. Kolchugina and Vinson (1993a) then reduced Bazilevich's mean phytomass densities for the proportion in young growth. Excluding both the Tundra and Steppe biomes, they estimated that the Taiga biome contained 100.8 Pg of phytomass over an area of 1306.2×10^4 km^2. The proportion of the area of the Taiga biome in our Siberian study area (822.7×10^4 km^2) is 0.63, which reduces their estimate to 63.5 Pg of phytomass for Siberia. This compares almost exactly to our estimate of 63.6 Pg, after excluding both Tundra and Steppe.

Alexeev and Birdsey (1994) give the lowest estimates of phytomass for Russia. They base their phytomass estimates of forest ecosystems on the same 1988 USSR Forest Inventory used by Isaev et al. (1993). Excluding the Tundra biome, Alexeev and Birdsey (1994) estimate phytomass for 723.9×10^4 km^2 of administrative units within our Siberian study area to be 32.9 Pg. This area is 80 % of our study area, which results in an estimate of 51.8 Pg of phytomass from our predictions. Thus, their estimate is 36 % less than ours for the same area. Because we use the same forested proportion (Table 2) as Alexeev and Birdsey (1994), one cause for such a large difference must be different estimates of phytomass density for the individual vegetation classes. For example, Alexeev and Birdsey (1994, Table 6.4) list the phytomass density of Middle Taiga in central and eastern Siberia as 90 and 58 t/ha, respectively, while we estimate the same densities from Bazilevich's data as 132 and 107 t/ha, respectively (Table 2).

Olson et al. (1983) provide plant carbon estimates for potential vegetation for the major biomes of the world. Under current climate, we compared our potential estimates for Siberia (using Permiakov's (1974) forested percentages) to Olson's global estimates for the Tundra, Taiga, and Steppe biomes as follows. First, we combined Northern, Middle, and Southern Taiga and Subtaiga into one Taiga class. Next, we calculated the proportion of the area in Siberia to Olson's global area for each of the three biomes. The resulting values compared to ours show very reasonable phytomass estimates: for Tundra our estimate is 2.5 Pg versus 2.3 Pg for Olson; for Taiga we estimate 93.9 Pg versus 90.7 Pg for Olson, and for Steppe we estimate 1.5 Pg versus 1.3 Pg for Olson. We conclude that our phytomass estimates are quite consistent with those of Olson et al. (1983), as well as those of Isaev et al. (1993), and Kolchugina and Vinson (1993a).

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Total of 67 references

Forest Zones of Siberia as Determined by Climatic Zones and Their Possible Transformation Trends under Global Change

Dina I. Nazimova and N.P. Polikarpov

A system of zonality in Siberia has been formed under the control of continentality, which provides the heat and humidity regimes of the forest provinces. Three sectors of continentality and four to six boreal subzones form a framework for the systematisation of the different features of land cover in Siberia. Their climatic ordination provides the fundamental basis for the principal potential forest types (composition, productivity) forecasting the current climate. These are useful in predicting the future transformations and successions under global changes.

Keywords Siberia, climatic ordinations, zonal forest types, modelling
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1 Introduction

The global change in climate and its impact on the vegetation, primarily on the forests, is discussed at different levels – from the global to the regional. The priority of climatic factors – warmth and water supply – is illustrated at the global level by advanced global biome models (Prentice et al. 1992, Solomon and Cramer 1993, Cramer and Solomon 1993, Tchebakova et al. 1992, 1994).

With the purpose of anticipating the effects of potential global warming, we applied experimental data on the climate-soil-vegetation links in different landscape zones and provinces of Siberia.

It is known that these links are not global but regional. Nevertheless, the first attempts to predict modern forest zones and subzones of Siberia on the basis of climatic indices were successful. All the models created have proved remarkably adequate in reproducing broad subcontinental-scaled patterns of biomes and zones (Pren-

tice et al. 1992, Tchebakova et al. 1994). The authors note that their approaches differ from that of Holdridge and Box and that they have some advantages for future biome modelling. All the models are static (equilibrium) and there are some limitations when they are applied to study land cover and forest ecosystems.

The purpose of this paper is (i) to present the forest zones and formations of Siberia on climatic ordination schemes and (ii) to discuss the ways these graphic portraits could be made use of in modelling. Formations and zones are traditional for Russian scientific literature (Vegetation 1990).

2 Materials and Methods

The study is based on voluminous empirical material and on long-standing observations of the climate (meteorological station data) and calculated climate indices for the belt boundaries in the mountains (Polikarpov 1966, 1970, Nazimova et al. 1981, 1990). Precipitation, warmth, and moisture indices were calculated with regional relationships with absolute height as well as the aspect and steepness of slopes (Sadovnichaya 1985, Tchebakova 1981,1983). For plains, we have calculated continentality indices for all weather stations involved in multi-dimensional analysis.

This work makes use of a few climatic indices and climatic ordination diagrams analysed from among a great number. The sum of active temperature (SAT) specifies the heat resources of climates in terms of plant requirements for active growth. It is defined as the sum of the mean daily temperatures above the threshold value of 10°C. It is preferable for comparative landscape-ecological analysis (Isachenko 1988). We used published data recorded at meteorological stations (Reference work ... 1966–1970). The SAT value does not coincide with the growing degree days (threshold value 5°C) (GDD) index. However, graphically they do correlate (Tchebakova et al. 1994). Dryness index (DI) (Budyko 1971) is the ratio of annual potential evaporation to annual precipitation (P). It was calculated by Tchebakova (see Tchebakova et al. 1994 for details). The continentality index (Cc) (Conrad 1947) is a function of the differences in July and January mean temperatures and latitude.

Among diverse indices, reflecting continentality, we took this parameter because it makes it possible to compare it with published data. This parameter reflects the annual replicability of oceanic and continental air masses and is important for the regions of Siberia and for Eurasia as a whole (Shumilova 1962, Sochava 1986, Tuhkanen 1984, Nazimova 1994).

3 Results and Discussion

A great number of altitudinal subzones were classified as follows (Fig. 1): subgolets-taiga woodland ecotone (1), subalpine dark-foliaged taiga (2), mountain taiga (3) dominated by fir (*Abies sibirica*) under a superhumid climate, by pine (*Pinus sibirica*) under a humid climate and perhumid climate, and by larch (*Larix sibirica*) mostly under a semi-humid climate. Mixed light-foliaged taiga with birch, or subtaiga (4) are zonal in low hills under a moderate humid climate. Three variants differ in composition, structure and productivity. Some of them are very similar to forest-steppe. The most humid subtaiga variant consists of aspen. Dark-foliaged "chern" taiga (5), mostly of fir, covers the windward macroslopes under perhumid climate. The forest-steppe ecotone (6) is typical under semi-humid and cool climates and dwindles under in cold climates. Mountain steppe and tundra also take their position and replace the oroboreal forest according to factors of humidity and heat supply, which limit the spread of the boreal forest . Sectors A, B, C, D appear as sectors of humidity, with their specific bioclimatic variants of mountain forests and soils. These belt spectra of forests have been described in the literature (Smagin et al. 1980, Polikarpov et al. 1986). We refer to them as the superhumid fir zone, humid dark-foliaged, semi-humid larch, and semiarid larch-and-steppe.

This subdivision is not entirely the same as the life zone classification (Holdridge 1967), but it is close to it. Our subdivision is based on empirical data. The values of the boundary between

the forest and the steppe are minimal in Yakutia, where permafrost is the factor favourable for the growth of larch forests (Budyko 1971, Buks 1977). Sector A shows only one situation, rather typical for zonal and mountain vegetation in the most continental (ultra-continental) part on eastern Eurasia. The steppes of Mongolia rise up to the mountain tundra, into close contact with mountain taiga. Superhumid (rain) forest is represented only on the windward slopes in several regions of southern Siberia, but it is fairly specific and not typical for Siberia as a whole. One can see some features of similarity with the dark-foliaged forest ecosystems of the Far East.

In 1987–1994, the authors of different versions of bio-climatic ordinations for Siberian zones used the same approach. They allow one to conclude that the climatic regimes of the zones (as well as the altitudinal belt complexes) express a certain degree of warmth and relative humidity, and the continentality indices are the main system-forming factors of zonality. They determine the most typical features of the structure and composition of the forest cover and landscape as a whole: the seasonal rhythms of natural processes, potential productivity, some soil processes. The climate-soil-vegetation links were formed during the last part of the Holocene when forest zones emerged first of all as a result of biotic adaptation to the continental boreal climate and to soil conditions.

We were often assured that the supply of warmth and water, together with the regional biotic composition, were the major inputs in bioclimatic systems called "zones", subzones, and their variants. The sectors of continentality and zones, which are multi-dimensional within the climatic context, but two-dimensional in the advanced graphic portraits, form the matrix systematising all information on forests, their structure, stability, and successions. This cannot be regarded as an underestimate of soil factors.

The composition and diversity of regional biota and vegetation pattern are of great importance for predictive modelling. Hence, regional bioclimatic models are preferable for many purposes of mountain and plain forestry in Siberia. It should be noted that the range of tree species in the

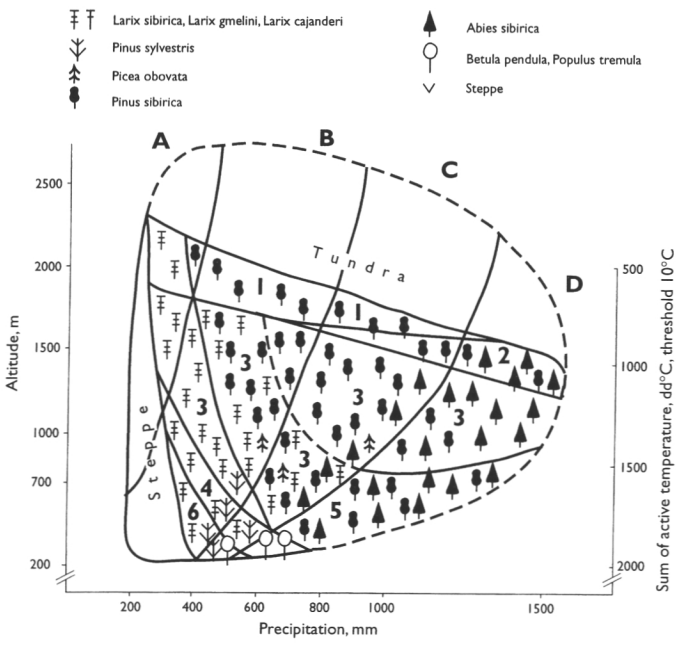


Fig. 1. The first conceptual model of the oroboreal forest. Altitudinal zones, biomes, and forest formations of South Siberian mountains in the climatic context: annual precipitation (Pmm) and active temperatures sum (T > 10) (Polikarpov & Nazimova 1976). 1 – Subgolets taiga (dark-foliaged) and larch woodlands; 2 – Subalpine woodlands (dark-foliaged); 3 – Mountain taiga (larch, dark-foliaged, mixed); 4 – Subtaiga (light-foliaged and mixed birch light-foliaged); 5 – Chern taiga (dark-foliaged) and "chern" mixed forest; 6 – Forest-steppe (larch and mixed pine-birch). H, m – absolute height on 52°N–54°N. A, B, C, D – climatic facia of the oroboreal forest (spectra of altitudinal zones): semi-arid larch-steppe, semi-humid larch, humid, and perhumid dark-foliaged, super-humid fir.

mountains of southern Siberia, as well as in Siberia as a whole, is narrow. This makes the models less informative as regards composition and productivity in both zonal and inter-zonal formations and forest types.

In addition to Fig. 1, presenting the climax formations and quasi-climax pyrogenic (postfire) formations, we have developed versions demonstrating the derivative anthropogenic stands, as well as zonal series and major forest types (Polikarpov et al. 1986).

Fig. 2 demonstrates the majority of plain and tableland Siberian zones in two-dimensional climatic context of the supply of warmth and humidity. Three zono-biomes - steppe, taiga, and tundra – take their places within the climatic context of Active Temperature Sums and Dryness Index. All meteorological stations representing dark-foliaged zonal forest types took their places only within the small, more humid part of the climatic context with DI equalling 0.5–0.8. *Pinus sibirica*, *Picea obovata*, and *Abies sibirica* within the southern subzone form mixed stands of dark-foliaged forest types. Birch and pine, and sometimes aspen, are common following forest fires and clear-felling of forest. They are not shown as secondary forests in Fig. 2, but these tree species should studied as potential constituents of future forests as they are most resistant to high levels of radiation, to drought, and other stress factors.

Pinus sylvestris dominates light-foliaged southern taiga and forms quasi-climax forest types in central Siberia. Larch taiga on permafrost occupies the remainder of the climatic context. Geographically, this is northern and eastern Siberia. Pine and birch sub-taiga with an admixture of aspen occurs under warm but sufficiently moist climates (GDD 1400–1700 and DI 1.2–0.9) while the forest-steppe forms the transition zone from sub-taiga to steppe under a semi-humid climate (DI 1.0–1.8).

Generally speaking, the distribution of zonal formations has confirmed the principal scheme of zonality in Siberia developed by Siberian botanists (Shumilova 1962). Besides, it should be mentioned that in the 1970s Finnish botanists emphasised zonal features within the boreal zone of Eurasia. They demonstrated the great potential of comparative analysis of vegetation zones abundant all over their range (Hämet-Ahti 1974, 1980, and others). According to field investigations, Hämet-Ahti suggested four subzones within the boreal zone (northern, middle, southern boreal, and hemiboreal) – these differing distinctly not only in terms of their flora but also in terms of their productivity, agricultural potential, seasonality, and other functional phenomena. This approach is rather close to the approach taken by Russian geobotanists. Besides this, the authors supported the concept of sectoral or longitudinal subdivision, as well as predicting the boreal (oroboreal) steppe lands within the continental sectors of Eurasia (Yakutia, Northern Mongolia, Trans-Baikal region). Sector C in Fig. 2 is probably the same for the climatic regions, and the most interesting for predictive modelling. It has the steppe stations, though there is no steppe zone on the geographical maps of Yakutia. The model has predicted all the locations of steppe in eastern Siberia (see Nazimova et al. 1990 for details).

A comparative analysis of mountain and plain zones (Figs. 1 and 2) leads to the conclusion that it is preferable to present the zonal forest formations of Siberia separately from the montane zones. In this way it is possible to get an informative and rather simple bioclimatic model fit to match the forest inventory data base and the meteorological station data base (Reference work ... 1966–1970).

In the bioclimatic graphic models (Figs. 1 and 2), each point of geographical space (meteorological station, for the sake of simplicity) is characterised by two major parameters of climate and, accordingly, by many features of the zonal ecosystem. The boundaries of the vegetation classes are empirical and static in ecological space. In short-term, and even long-term, successions they form a stable framework (constant). Vice versa, the points of geographical space could change their climatic co-ordinates.

The climate change modelled predicts new co-ordinates for each point in this parametric space. The point moves from one position to another and may even find itself within a climatic area where all the forest formations and many of the tree species are at risk. These transition zones may be revealed and predicted by computerised map modelling. It should be mentioned that each

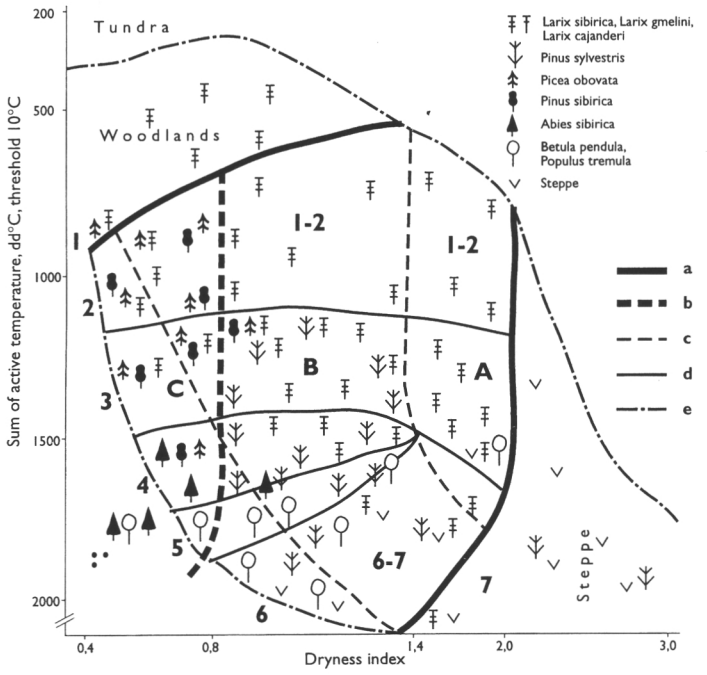


Fig. 2. Graphic model of zonobiomes and their subdivisions in Siberia along axes: Active temperature sum (t > 10°C and Dryness index DI). Zonobiomes: tundra, boreal forest (2–5), boreal and subboreal steppe (7). Zonoecotones: forest-tundra (1), forest-steppe (6). Boreal forest, sectors of humidity: A – light-foliaged cryo - semi-arid (*Larix gmelinii*, *L. cajanderi*); B – light-foliaged moderate humid and semi-humid (*L. sibirica*, *L. gmelinii*, *L. cajanderi*, *Pinus sylvestris*); C – dark-foliaged humid (*Pinus sibirica*, *Abies sibirica*, *Picea obovata*) and birch-pine semi-humid (*Pinus sylvestris*, *Betula pendula*). Forest zones and subzones: 2 – Northern taiga, 3 – Middle taiga, 4 – Southern taiga, 5 – Mixed birch – conifer subtaiga and "chern" forest with *Populus tremula*, *Abies sibirica* (denoted by dots in the left corner). Boundaries of: a) closed boreal forest, b) dark-foliaged subzones, c) sectors, d) termic subzones, e) real climatic space.

zone is likely to be transformed according to landscape structure and biotic composition, and its track will be represented by tracks of all structural elements combining to form the zonal class. Fig. 3 demonstrates the Siberian plain meteorological stations in a parametric space of continentality-warmth supply. One can see the less continental left part of this graphic portrait as being composed of dark-foliaged and pine forest types, the central part as being composed mostly of pine, and the rest as a continental part composed of larch. *Larix sibirica* replaces dark-foliaged forest types when Conrad's Cc is equal to 60–65, *Larix gmelinii* replaces *L. sibirica* formation when Cc is close to 72, and *Larix cajanderi* becomes the absolute dominant forest species under the most continental climate (Cc = 85–100).

It is reasonable to dwell upon the continentality index Cc as one of few climatic indices predicted with more confidence. Continentality is an integrated expression of many critical weather conditions during the year; cloudiness regime, spring insolation, winter severity, hydrothermic regime of soils, etc. Thus, it could be regarded as a multidimensional sign. In continental Siberia with a broad range of Cc (50–100) it is not less important than relative moisture. We suppose that for such a vast area as Siberia continentality is preferable as the first step of modelling, while relative moisture is the best for the next step.

The axis Cc makes it possible to distinguish

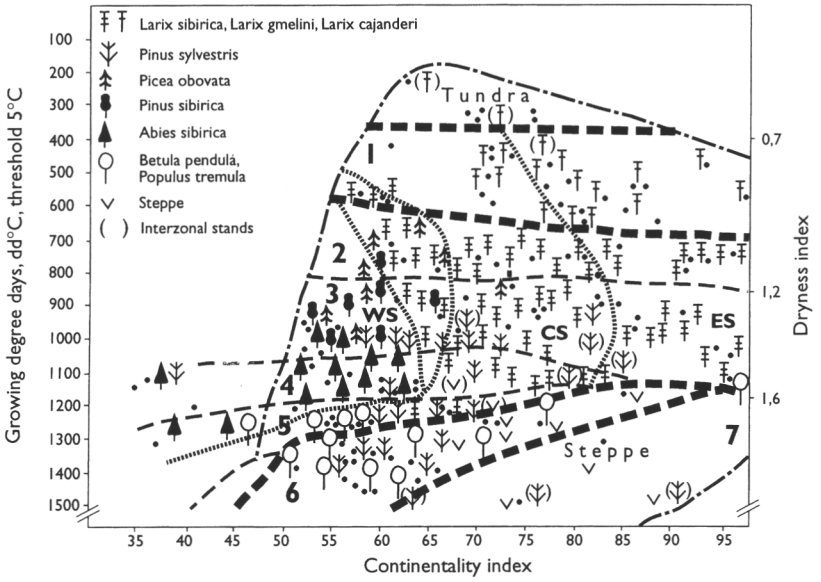


Fig. 3. Climatic ordination of meteorological stations (dots) and zonal forest types (signs) in Siberia. For conditional signs see Fig. 1, 2. GDD 5° – axes of heat supply, C. cont.– axes of continentality. 1,6 – zonoecotones forest-tundra and forest-steppe are cleared by bold dotted lines. Forest formations : i) *L. sib.*, *L. gm.*, *L. cj.* – larch forests with *Larix sibirica*, *L. gmelinii*, *L. cajanderi*. Sectors (groups of ecoregions): West Siberian continental humid and moderate-humid, CS – Central Siberian extremely continental humid and semi-humid, ES – East Siberian extremely and ultra-continental mostly semi-humid and semi-arid. ii) *P. slv.* – Scots pine forests (*Pinus sylvestris*), interzonal – in (), *P. ob.*– spruce forests (with *P. obovata*), *P. sib.* – *Pinus sibirica* forests, *A. sib.*, mixed – *Abies sib.* forests, and mixed, *B. p.*, *Pp. t.* – deciduous small-leaved forests with *Betula pendula*, *Populus tremula* (with no *Quercus* spp). St – steppe meteorological stations.

sectors of climatic space close to West Siberian (WS continental humid), Central Siberian (CS extremely continental), and East Siberian (ES ultra and extremely continental). The sector CS varies from semi-humid (DI 1.4–1.0) to perhumid (DI 0.6–0.4) on some high watersheds. Also, the sector ES is not limited by one class of humidity and it was evaluated as being in the humid and semi-humid sector; in some cases even as being semiarid (DI close to 1.5–2.5).

Changes in tree species domination are marked from one sector to another and even within the same sector. The dependence on continentality of dark-foliaged forest has been mentioned earlier (Shumilova 1962, Sochava 1986). Extremely continental (Cc 70–85) and even ultra-continental (Cc 85–100) sector ES determines the dominance of the vast larch biome (cold-conifer-deciduous in the biome model of Prentice et al. 1992).

Tables of tree species ecological parameters are helpful in any study concerned with land cover prediction and forest management planning. Such tables have been made in 1985–1990 for thirty tree species. They have been partly published (Shugart et al. 1992), but the majority have not yet been published. The tables have special interest for the evaluation of resistance of natural forest stands to critical factors of climate as well as to some soil factors.

The approach suggested above is not map modelling, although our graphic models formed the basis for computerised maps and for a new version of the Siberian vegetation model (Tchebakova et al. 1994). The Siberian vegetation model in its computerised map version has been successfully tested (Tchebakova et al. 1994) except for some discrepancies that appeared when the computerised maps were compared with conventional maps.

One of the reasons is the generalisation of the GDD 5 values for the northern border of the taiga in the Siberian computerised map model. As is mentioned above, the limits of the forest species differ sufficiently. *Larix cajanderi* (Abaimov and Koropachinskyi 1977), for example, is much more resistant to dry climate and frosty soils than is *L. sibirica* or *Picea obovata*, which form the northern forest boundary in western Siberia. The same discrepancies appear concerning the absolute values of the dryness index (DI) for the boundary between dark-foliaged and light-foliaged zonal formations in different sectors of continentality. It varies from 0.65 to 0.8 in West and Central Siberia, and tends to rise under extremely continental climate (Buks et al. 1977). This is an additional argument for improving the Siberian vegetation model to take into account the sectoral differences in bio-climatic relations.

4 Conclusion

Our long-termed study of the bioclimatic relations in Siberia has convinced us that the bioclimatic approach is valid not only for zones (subzones, altitudinal belts) but for Siberian tree species dominance, too. Many features of forest and non-forest ecosystems, including forest successions, productivity, possible insect invasions, pyrological characteristics, are reflected in multi-dimensional and two-dimensional climatic space. The continentality of the Siberian climate is one of the most important factors influencing land cover structure and its functioning. This parameter is preferable for zonal ecosystem modelling for the first step when broad-scale zonal classes are analysed.

The relative humidity of the climate is the main factor in zonal differentiation along with the supply of warmth at the next level of hierarchy. The landscape-ecological concept is preferable when studying forest lands. For a number of regions under investigation, the information content of graphic models could be markedly improved. Not only forest composition and productivity, but many other features of the vegetation and natural processes could be objects of prediction under the current climate. Among these features are landscape-forming forest types, pyrogenic and other successions, seasonal phenomena and processes, parameters of forest fire danger, biodiversity, etc. The zones do not look like uniform cells, but they may be presented as systems of fine-scaled units.

A new consideration concerning forest wildfires in Siberia is necessary in order to take into account the continental taiga. Fire is not only a factor disturbing forest ecosystems. Fires control to a large extent the forest ecosystem's dynamics, natural species selection, biodiversity, and species competition. Many features of taiga structure and functioning are directly dependent on periodical fire events, which correlate with the main climatic characteristics of the soils.

Acknowledgements

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Postfire Recovery of Forest Litter in Scots Pine Forests in Two Different Regions of Boreal Zone

Vadim V. Gorshkov, Irene J. Bakkal and Natalie I. Stavrova

Investigations carried out in the Kola peninsula (northern taiga) and in the South-western part of Western Siberia (southern taiga and forest-steppe) revealed identical course of the postfire restoration process of forest litter thickness in Scots pine forests. Despite the differences in mean annual temperature (2°C) and other climatic characteristics the recovery time for thickness of forest litter in both regions amounts to 90–100 years after fire in pine forests of lichen site type and 120–140 years – in green moss type; the thickness of forest litter therewith corresponds 3–4 cm and 7–8 cm respectively. That means that within the natural borders of pine forests, communities of a specific type possess uniform characteristics of restoration. On the basis of empirical data it appears that the predicted increase of mean annual temperature of earth surface by (2°C) will not bring changes into the character of postfire recovery of forest litter thickness. It was shown that during the period of the recovery, which spans about 90 years after fire in pine forests of lichen and green moss–lichen site types and 140 years in ones of green moss site types, the rate of increasing of carbon store in the forest litter averaged 0.6 t ha^{-1} $year^{-1}$, 0.1 t ha^{-1} $year^{-1}$ and 0.2 t ha^{-1} $year^{-1}$, respectively.

Keywords Scots pine forests, postfire recovery, forest litter
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1 Introduction

One of the probable impacts of the observed global increase of CO_2 concentration in the atmosphere is changes in climate. The question of what such a change will be like, and whether or not it will even occur, is much discussed nowadays (Clark 1982, Houphton et al. 1990, Anklin et al. 1993, Kondratjev 1993, Lorius and Oeschger 1994, Gorshkov 1995).

According to model-based calculations a twofold increase of the atmospheric carbon dioxide concentration will make the mean annual temperature of earth surface and mean annual temperature of earth surface in high latitudes rise up to 2–3°C and 7–9°C respectively (Clark et al. 1982, Klein 1982, Hoffton et al. 1990, Manabe et al. 1994).

Most modern papers concerning modelling and forecasting of possible changes in vegetation and soil due to predicted global warming (Peters 1990, Nazimova and Polykarpov 1995, Velichko and Morozova 1996) assume that there exists a direct relationship between average climate characteristics (average annual temperature, continental index) and biota.

The given research makes it possible to estimate the range of climate characteristics within which a forest community of a specific type would be stable. One of the main indicators of a community stability is their recovery after having been exposed to an external force. Recovery time of characteristics of various community components and their values in undisturbed communities are of fundamental nature.

Forest litter (forest floor, the upper part of the organic soil horizon excluding humus layer) – is one of the main components of boreal forest ecosystem. In the northern pine forests it contains 25–30 % of the total organic matter (alive and dead) and 10–20 % of organic carbon store in podzolic soils (Nikonov 1987, Alexeyev and Birdsey 1994).

This paper aims at investigation of the processes of forest litter postfire recovery in pine forests (*Pinus sylvestris* L.)* of two climatically different geographical regions.

2 Material and Methods

2.1 The Sites

The communities compared are situated in the north and the south of the natural area of pine (*Pinus sylvestris*) forests (Lavrenko and Sochava 1956) in the Kola peninsula (67–68°N, 30–34°E, northern taiga) and in the south-west of Western Siberia (55–59°N, 62–66°W, southern taiga and forest-steppe). Data on the Kola peninsula were obtained in this study, data on Western

* Vascular plant nomenclature follows Cherepanov (1995); lichens follow Santesson (1993); mosses follow Ignatov, Afonina (1992)

Table 1. Geographical and climatic characteristics of regions compared[(1)].

Characteristics		Region	
		Kola peninsula	SW of W.Siberia
Site location	latitude, N	67°–68°	56°–59°
	longitude, E	31°–35°	62°–66°
Altitude, m		130–200	100–150
Temperature, °C	mean annual	–0.5..–1.0	1.0..1.5
	mean January	–12..–14	–16..–18
	mean July	13..14	18..19
Duration of frost-free period, days		75–104	105–121
Quantity of	with $t \geq 5$°C	120–122	164–168
days	with $t \geq 10$°C	58–60	120–132
Precipitation, mm	450	550	
Potential evaporation, mm		250	600

(1) on data derived from Scientific and applied reference book on the climate of the USSR (1987, 1988, 1989, 1990).

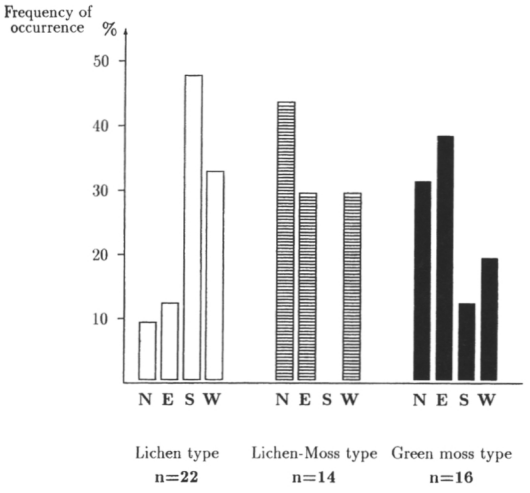


Fig. 1. Occurrence of Scots pine forests on slopes of differing aspects in the Kola peninsula. 1.Lichen site type (share of lichens in moss–lichen cover exeedes 70 %). 2.Green moss–lichen site type (share of lichens in moss–lichen cover 30–70 %). 3.Green moss site type (share of lichens in moss–lichen cover is under 30 %).

Siberia were taken from the work of S.N Sannikov and N.S Sannikova (1985). Climate characteristics of the regions of investigation are given in Table 1.

In the Kola peninsula Scots pine forests of three types were studied: lichen (a) – lichen share in moss–lichen cover exceeds 70 %, moss–lichen (b) – lichen share ranges from 30 % to 70 %, and green moss (c) – lichen share in moss–lichen cover is less than 30 %. The postfire period in the selected sites spans from 5 to 210 years.

In the south-western part of Western Siberia lichen (d) and green moss (e) site types of Scots pine forests with fire ages from 3 to 175 years were studied. Lichen site type was represented by communities "where lichens dominated in the ground cover", green moss site type was represented by ones "dominated by green moss" (Sannikov and Sannikova 1985).

The communities analyzed are situated on plains and hills formed by sandy and loam sandy deposits (glacial and glaciofluvial) in the Kola peninsula and alluvio-deluvial in the south-west of Western Siberia).

Table 2. Soil properties of regions compared (on data derived from Menshikova 1990, Nikonov 1987; Nadezhdin 1960; Sannikov 1992).

Region	Soil layer	Density, g/cm^3	Clay, % (1)	pH (KCl) (2)	C, % (3)	N, % (4)	Ca mequiv./100 g (5)	Mg mequiv./100 g (5)
Lichen site type of forest								
Kola	A0	0.12	–	3.0–3.2	25–40	0.5–0.6	3.3–16.0	3.6–14.8
penin-	A2	1.4–1.5	3–4	3.2–3.4	0.2–1.2	<0.1–0.1	0.1–0.8	0.2–0.7
sula	B_1	1.5–1.7	4–5	4.0–5.2	0.5–2.9	<0.1–0.1	0.4–0.5	0.1–0.4
SW of	A0	nd	–	4.6–5.3	nd	nd	nd	nd
Western	A_1A_2	nd	3–7	4.5–4.6	1.3	<0.1–0.1	2–3#	
Siberia	B_1	nd	3–7	4.5–5.3	0.5	<0.1–0.1	2–3#	
Green moss site type of forest								
Kola	A_0	0.08	–	3.0–3.2	34–52	0.5–1.1	3.3–18.4	4.0–19.7
penin-	A_2	1.4–1.5	5–6	3.2–3.5	0.3–2.0	<0.1–0.1	0.4–0.8	0.8–0.9
sula	B_1	1.5–1.7	8–9	4.7–4.9	1.1–3.6	<0.1–0.1	0.2–0.8	0.2–0.6
SW of	A0	0.08	–	4.6–4.7	nd	1.0–1.5	11.5–17.5	1.2–3.8
Western	A_1A_2	1.0–1.5	6–15	4.0–5.5	0.1–3.5	<0.1–0.1	3.4–3.8	0.4–0.6
Siberia	B_1	1.5–1.7	6–10	4.5–5.5	0.1–0.6	<0.1–0.1	2.0–2.6	0.2–0.4

(1) Particle size fraction < 0.01 mm
(2) 1N KCl extraction
(3) Determined by the Tjurin method
(4) Determined by the Kjelldahl method
(5) Determined by the trilonometric method in 0.01 N NaCl extraction
\# Ca + Mg
nd no data

Pine forests of lichen site type preferably cover summits and upper parts of southern and western slopes (Fig. 1) of hills and high plains, where ground water level is under 3 m. These sites are marked by well-drained podzolic soils (Table 2).

Pine forests of green moss site type are typical to the northern and eastern slopes of hills (Fig. 1) and plains (the ground water level is on the depth of 1.5–2 m). Soils at this study sites are moderately drained podzolic ones (Table 2).

Tree stand characteristics of the main studied site types (lichen and green moss) are given in Table 3.

The undergrowth in lichen Scots pine forests in both regions is usually absent, or remains within 1 %, if found; in green moss pine forests the protective coverage of the undergrowth is about 1–5 % (*Sorbus aucuparia* L. or *Sorbus sibirica* Hedl., *Salix caprea* L., *Juniperus communis* L.).

Regardless of the forest type, the principal dominants of the dwarf shrub and herb stratum in the Kola peninsula are species of two families: *Ericaceae* Juss. and *Empetraceae* S.F.Gray: *Empetrum hermaphroditum* Hagerup, *Vaccinium vitis-idaea* (L.); *V. myrtillus* (L.), *Arctostaphylos uva-ursi* (L.) Spreng., *Calluna vulgaris* (L.) Hull. The total projective coverage of the stratum amounts to 13 % in lichen type and 28 % – in green moss type.

In the south-western part of Western Siberia the principal dominant of the dwarf shrub and herb layer in Scots pine forests of lichen site type is *Vaccinium vitis-idaea*. The dwarf shrub and herb layer of green moss Scots pine forests dominates by *Vaccinium vitis-idaea* and *Vaccinium myrtillus*; *Lycopodium annotinum* L., *Calamagrostis arundinaceae* (L.) Roth are characteristic but considerably less abundant species. The total projective coverage of the stratum amounts to 10–15 % in lichen site type and 30–40 % in green moss site type (Zubareva 1960, Sannikov and Sannikova 1985). At the initial stage of recovery process in green moss forests of this regions the share of herbaceous plants in the total cover of the layer may be up to 50 %.

Species composition of the moss-lichen layer of pine forests in both regions studied are similar. The principal dominants of the moss-lichen layer in forests of lichen sites are the following species: *Cladonia deformis* Hoffm., *C. cornuta* (L.) Hoffm., *C. crispata* (Ach.) Flotov, *C. gracilis* (L.) Willd. at fire age of less than 40 years, *C. mitis* (Sarndst.) Hale et W. Culb., *C. rangiferina* (L.) Nyl., *C. uncialis* (L.) Wigg. at fire age of 60–90 years, *Cladina stellaris* (Opiz.) Brodo at fire age of more than 120 years. The moss-lichen layer in green moss pine forests is dominated by *Pohlia nutans* (Hedw.) Lindb., *Polytrichum juniperinum* Hedw. and *P. piliferum* Hedw. at fire

Table 3. Selected data on tree layer of Scots pine forests in the Kola peninsula and South-western part of Western Siberia (from data of authors and data reported by Zubareva 1960; Sannikov, Sannikova 1985) (from data of authors and data reported by Bakkal et al. 1990; Sannikov and Sannikova 1985).

Region	Stand characteristics				
	Average age, years	Share of pine, % (1)	Average height, m (2)	Average dbh, cm (2)	Average basal area, m^2ha^{-1} (2)
Lichen site type of pine forest					
Kola peninsula	30–300	90–100	12–14	20–23	20–22
SW of W. Siberia	50–180	90–100	19–21	25–28	25–27
Green moss site type of pine forest					
Kola peninsula	40–300	80–90	16–20	27–30	27–32
SW of W. Siberia	50–180	80–90	23–34	28–36	30–33

(1) Woodstands of Scots pine forests in the Kola peninsula have an admixture of spruce (*Picea abies* (L) Karst., *Picea obovata* Ledeb.) and (or) birch (*Betula subarctica* Orlova), in south-west of Western Siberia – of spruce (*Picea obovata*) and (or) birch (*Betula pendula* Roth).
(2) The data for woodstands of 50–200 years old.

age of less than 40 years and *Pleurozium schreberi* (Brid.) Mitt., *Dicranum* spp. at fire age of more than 60 years. The total projected coverage of the moss-lichen layer in Scots pine forests reaches 70–90 %.

2.2 Sampling Methods

Forest litter thickness was defined as the interval between the soil surface and mineral horizon (humus layer is absent in soils of this type) (Nadezjdin 1960, Nikonov 1987), lichen-moss cover and layer of newly fallen needles, leaves, cores and branches having been deleted. Litter thickness was measured in 20–100 regularly positioned points at each sampling site.

Sannikov and Sannikova (1985) measured litter thickness using a special electric probing rod*. In this study litter thickness was measured with a ruler in specially made small soil cuts of 20 cm wide and 20 cm depth; the frontier between the organic and mineral horizons was determined visually. In both cases the accuracy of measurements was about ±0.3 cm, number of observations being 2500.

Fire dating was based on the tree ring chronology, using living trees with fire scars at the radial distance of 50–100 m from sampling site. The age of the last fire was taken to be equal to the difference between the current age of a tree and that at the moment of injuring. In each case being analyzed the age of the last fire, determined in at least 5 of the trees, was one and the same.

2.3 Statistical Analysis

To process the data collecting principles of the single factor gradient analysis was used (Whittaker 1973 a, b). Correlation and regression analyses (Zachs 1976) were performed to examine relationships between the thickness of forests litter and the fire age. Coefficients of the regression equations were compared by the Student's t-test. To indicate the postfire time span where no statistically significant changes in the forest litter thickness (the stabilization of litter thickness) were found the one-way analysis of variance was used (Fisher 1955, Afifi and Azen 1982).

3 Results

3.1 Kola Peninsula

In forest types being studied initial stages of postfire recovery were characterized by linear increasing of litter thickness (Fig.2a,b,c; Table 4). The average thickness of forest litter and postfire age in lichen, green moss–lichen and green moss site types of Scots pine forests had positive correlation ($r = 0.68$, $\alpha = 0.01$; $r = 0.8$, $\alpha = 0.01$; and $r = 0.91$, $\alpha = 0.001$, respectively).

Thickness of forest litter, averaged 2.6 cm and 4 cm in lichen and green moss–lichen sites respectively at fire age of 90 years and did not change further on. Samples of averages for litter thickness during the period from 90 to 210 years after fire did not differ significantly (Table 5). In green moss site forests litter thickness stabilized more than 140 years after fire, approximating 8 cm. Samples of averages for litter thickness from 150 to 210 years after fire did not differ significantly (Table 5).

Making allowance for uncertainty inherent in small-volume samples and data deficiency for forests of lichen and green moss–lichen site types burned 70–85 years ago and that for green moss site type with fire ages of 100–140 years, the time of stabilization of forest litter thickness should be detected to be equal to 80–90 years after fire for forests of lichen and green moss–lichen site types and 120–140 years for green moss site type.

* The frontier between organic and mineral horizons was determined by measuring the voltage drop caused by different moisture content in the two layers (Sannikov and Sannikova 1985).

3.2 South-Western Part of Western Siberia*

In Scots pine forests of lichen site type within the whole studied period (from 5 to 85 years after fire), forest litter thickness increased linearly from 0.5–0.7 cm to 4.5 cm (Fig. 2d; Table 4). The average litter thickness positively correlated with fire age ($r = 0.96$, $\alpha = 0.001$).

In pine forests of green moss site litter thickness increased 100–140 years after fire from 1–2 to 8 cm (Fig. 2e). Within the period from 5 to 140 years after fire the form of the relationship was approximated with a high degree of accuracy by linear equation (Table 4). Correlation coefficient $r = 0.88$ at $\alpha = 0.001$. Samples of averages for litter thickness in green moss site pine forests during the period from 100 to 175 years after fire did not differ significantly (Table 5).

Considering the uncertainty inherent in small-volume samples and data deficiency for forests burned more than 100 years ago the time of stabi-

Table 5. Summary tables of one-way analysis of variance (ANOVA) for forest litter thickness.

Region	Forest type [2]	Postfire time span	Statistics [1] V_1	V_2	F-ratio	Significance [3]
Kola peninsula	L	90–210	1	9	1.06	–
Kola peninsula	ML	90–210	1	5	0.29	–
Kola peninsula	M	150–210	1	4	3.01	–
SW of W. Siberia	M	100–175	1	5	0.60	–

[1] L – Scots pine forest of lichen site type (lichen share in moss–lichen cover exceeds 70 %); ML – Scots pine forest of green moss–lichen site type (lichen share in moss–lichen layer ranges between 30 % and 70 %; M – Scots pine forest of green moss type (lichen share in moss–lichen cover is under 30 %).
[2] Statistics: V_1 – degrees of freedom between groups; V_2 – degrees of freedom within group.
[3] the value does not differ from 0 at $\alpha = 0.05$

* The analysis performed on the data derived from S.N. Sannikov and N.S. Sannikova (1995, p.46–48 Tables 3, 4).

Table 4. Summary of linear regression analysis for forest litter by fire age.

Region	Forest type [1]	Postfire time span	Parameter [2]	Statistics [3] *M*	*S*	*t*	Significance [4]
Kola peninsula	L	5–90	a	0.81	0.28	2.79	*
			b	0.02	0.005	3.26	**
Kola peninsula	ML	5–90	a	0.7	0.6	1.22	–
			b	0.03	0.01	3.44	**
Kola peninsula	L,ML	5–90	a	0.6	0.4	1.64	–
			b	0.03	0.006	4.31	***
Kola peninsula	M	40–150	a	0.7	0.8	0.89	–
			b	0.05	0.008	6.9	***
SW of W. Siberia	L,ML	3–85	a	0.3	0.2	1.88	–
			b	0.04	0.004	10.28	***
SW of W. Siberia	M	6–140	a	1.27	0.31	4.02	***
			b	0.06	0.006	9.20	***

[1] L – Scots pine forest of lichen site type (lichen share in moss–lichen cover exceeds 70 %); ML – Scots pine forest of green moss–lichen site type (lichen share in moss–lichen layer ranges between 30 % and 70 %; M – Scots pine forest of green moss site type (lichen share in moss–lichen cover is under 30 %).
[2] a – intercept; b – slope;
[3] M – mean; S – standard deviation; *t* – Student's t-test
[4] * significant at $\alpha = 0.05$; ** significant at $\alpha = 0.01$; *** significant at $\alpha = 0.001$, – the value does not differ from 0 at $\alpha = 0.05$

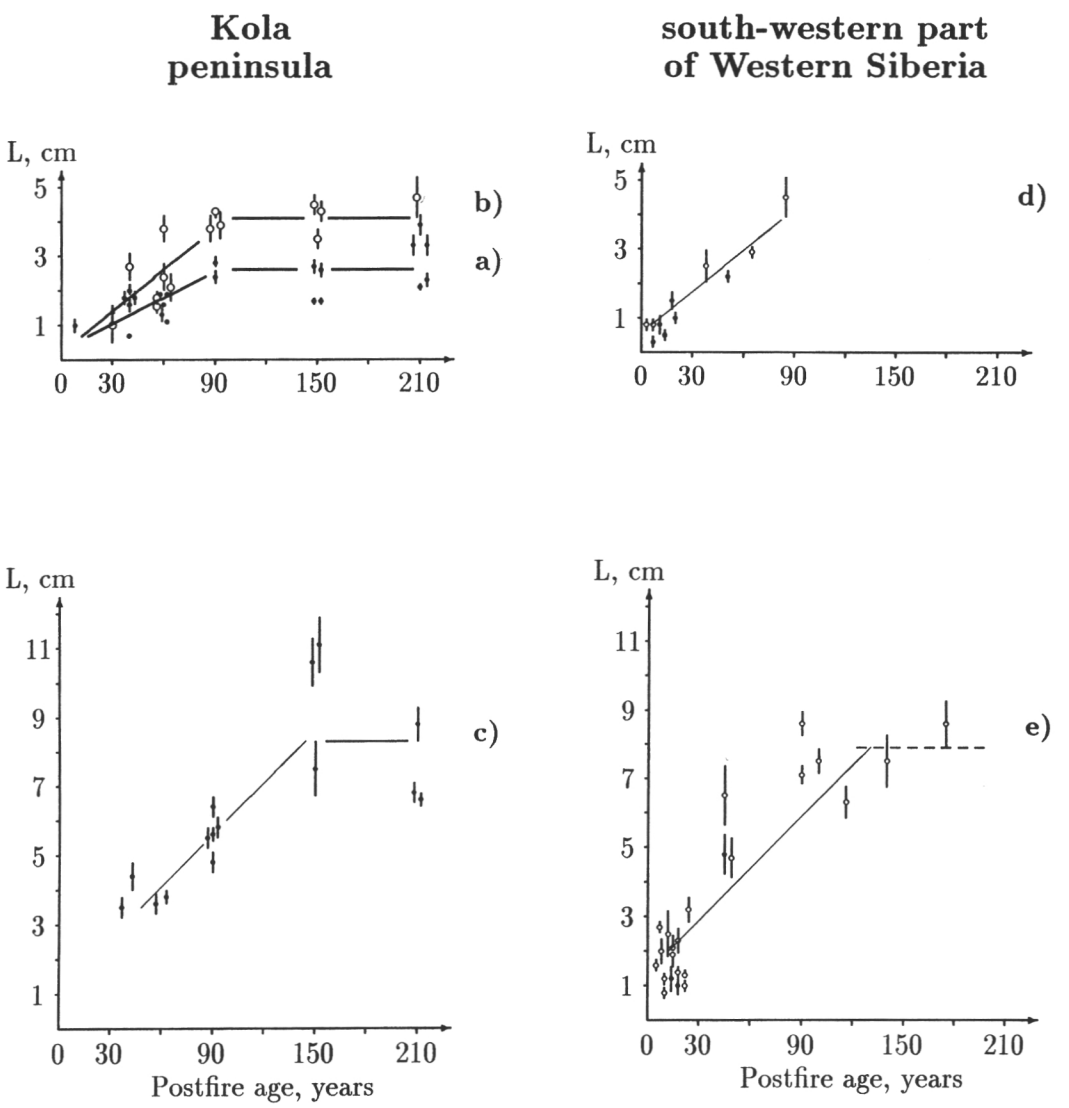


Fig. 2. Thickness of forest litter in Scots pine forests with differing postfire age. Kola peninsula: (a) – lichen site type (share of lichens in moss–lichen cover exeedes 70 %), (b) – green moss–lichen site type (share of lichens in moss–lichen cover range between 30–70 %), (c) – green moss site type (share of lichens in moss–lichen cover is under 30 %). South-western part os Western Siberia: (d) – lichen site type, (e) – green-moss site type (prepared on data derived from Sannikov and Sannikova (1985, Tables 3, 4, p. 46–48).

lization of litter thickness in green moss site type of Scots pine forests in south-western part of Western Siberia can be estimated as amounting to 120–140 years. In lichen site type of pine forests, due to the small time span being investigated, only the lower limit of recovery period was detected: it amounted to 80–90 years after fire.

4 Discussion

Results from these studies show identical course of the postfire recovery process of forest litter thickness in Scots pine forests of two comparable regions despite the differences in mean an-

Table 6. Properties of litter and its store in Scots pine forests of differing types and fire ages in separate geographical regions of Russia.

Region location	Forest type [1]	Fire age [2] years	Characteristics for forest litter					Source [5]
			Thick-ness,cm	Density g/cm^3 [3]	Store t/ha	C, %	Store C, t/ha cm [4]	
Kola peninsula 33–34°E 68°N	L	50#	1.5	0.12*	17.4	25	2.9	1
Karelia 34°E 62–63°N	L	60–90#	2.0	0.08	16.8	38	3.2	2
Yakutia 122–123°E 60–62°N	L	nd	2.0	0.09*	17.3	nd	nd	3
The same	L	4	0.6	0.09*	5.9	nd	nd	3
The same	L	27	1.2	0.09*	10.7	nd	nd	3
Yaroslavl' region 37–38°E 58–59°N	L	60#	1.4	0.09**	12.9	nd	nd	4
Belorussia 26–28°E 52–53°N	L	38#	2.0	0.10**	20.1	36	3.6	5
The same	L	40#	2.2	0.08**	18.9	nd	nd	5
Kola peninsula 33–34°E 68°N	M	50#	4.0	0.08*	30.9	44	3.4	1
Karelia 34°E 62–63°N	M	60–90#	4.5	0.05**	21.8	40	1.9	2
Yaroslavl' region 37–38°E 58–59°N	M	>40#	4.2	0.09**	38.2	38	3.4	4
Belorussia 26–28°E 52–53°N	M	60#	5.0	0.07*	33.6	45	3.1	5
The same	M	38#	4.0	0.07*	28.3	nd	nd	5
Ukraine 26–28°E 54–55°N	M	>70#	8.0	0.06*	44.3	nd	nd	6
The same	M	30–40#	3.0	0.05*	13.5	nd	nd	6
Krasnojarsk region 96–98°E 58°N	M	50	4.9	0.07	32.3	40	2.6	7,8
The same	M	<5	2.0	0.06*	12.9	nd	nd	8
The same	M	50	3.5	0.07*	25.5	nd	nd	8

(1) L – forests of lichen site type; moss–lichen site type; M – forests of moss site type.
(2) # – fire age was estimated on the basis of analysis of stand age and structure of species composition, and characteristics of moss–lichen cover (Gorshkov 1993)
(3) * – estimated by authors using the data on thickness and store from the source
** – calculated average meaning (from source's data)
(4) The store of carbon in 1 cm of litter stratum per hectare
(5) 1 – Nikonov 1987; 2 – Morozova 1978; 3 – Pozdnjakov 1953; 4 – Koshelkov 1961; 5 – Yurkevich, Yaroshevich 1974; 6 – Miakushko 1978; 7 – Gorbachev, 1967 8 – Gorbachev et al. 1982
nd – No data

nual temperatures (2°C) and other climatic characteristics (Table 1).

Coefficients in the regression equations between the thickness of forest litter and fire age in pine forests of lichen and green moss–lichen types as well as in green moss type of two regions compared (Table 4) did not differ significantly ($|t|$ is equal to 1.58 and 0.23, respectively, $\alpha = 0.05$).

It is significant that not only the limits of recovery time coincide in both northern and southern regions of the boreal zone (90–100 years after disturbance in lichen site type of Scots pine forests and 120–140 years – in green moss site type), but the values themselves (3–4 cm and 7–8 cm respectively).

Indicated values for forest litter thickness agree with the corresponding values for other parts of Boreal Pine Forest. Coefficients of the regression equations ($b_1 = 0.03$ – for lichen site forests and $b_2 = 0.05$ – for green moss site forests) calculated from pooled sample of the data obtained for Karelia, Yaroslavl' region, Belorussia, Ukraine, Krasnojarsk region and Yakutia (Table 6) did not differ significantly ($|t|$ is equal to 1.63 and 1.00, respectively, $\alpha = 0.05$) from the coefficients of corresponding equations (Table 4) derived from the data of authors (the Kola peninsula) and from one of S.N. Sannikov and N.S. Sannikova (south-west of Western Siberia).

An exact coincidence of process of postfire recovery of forest litter thickness in the geographically isolated communities indicates that characteristics of the recovery process are of fundamental nature and do not depend on the location of the community.

The border of both lichen and green moss types of Scots pine forests in the Eastern Europe and the Asia runs in latitude 66–69°N – in the north and 50–52°N – in the south (Lavrenko and Sochava 1956).

The range of the average annual temperature at the extremes of the Scots pine forests (from –8..10°C in the Yakutia to +6..7°C in the Ukraine) exceeds 10°C (Scientific and applied reference book ... 1987, 1988, 1989, 1990). It is evident from the data cited that the predicted increase of the average earth surface temperature in high latitudes will not produce changes in the character of postfire restoration of thickness of the forest litter.

Stabilization of thickness of forest litter is the result of establishment of the equilibrium between synthesis and decomposition of organic matter in forest ecosystem and thus indicates the recovery of its main characteristics.

This suggests that within the natural borders of Scots pine forests, communities of a specific type possess uniform characteristics of recovery.

Variations in the thickness of forest litter during the recovery process in pine forests have made possible to estimate the carbon loss (or store) in natural communities (on the basis of the data on carbon contents in forest litter (Table 6) and data represented in Fig. 2).

According to the data collected, the average density of forest litter in pine forests of Russia averaged 0.08 g cm^{-3}, the store of carbon in 1 cm of litter stratum per hectare averaged 3 tonnes (Table 6). During the period of the recovery, which spans about 90 years after fire in pine forests of lichen and green moss–lichen site type and 140 years in ones of green moss site types, the rate of increasing of carbon store in the forest litter averaged 0.6 t ha^{-1} $year^{-1}$, 0.1 t ha^{-1} $year^{-1}$ and 0.2 t ha^{-1} $year^{-1}$, respectively.

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Total of 37 references

Effects of CO_2 Concentration on the Nutrition of Willows (*Salix phylicifolia*) Grown at Different Nutrient Levels in Organic-Rich Soil

Jouko Silvola and Urpo Ahlholm

Willows (*Salix phylicifolia*) were grown for four months in organic rich soil at four nutrient levels (fertilization with a micronutrient-macronutrient mixture of 0, 100, 500 and 1000 kg ha^{-1} per month) and four CO_2 concentrations (300, 500, 700 and 1000 ppm). Nitrogen and phosphorus concentrations of the willows were reduced at CO_2 enhancement, the decrease being larger in the leaves and roots than in the stems. Nitrogen content of the willows plus extractable nitrate-N in the soil coincided well with the doses of nitrogen supplied, but the corresponding sums of phosphorus in the plants and soil were smaller. The total nitrogen content of willows grown in unfertilized soil was nearly two times higher than the sum of the extractable nitrate-N in soil and N content of the cuttings at the beginning of the experiment. The contents of nitrogen and phosphorus of the unfertilized willows were independent of CO_2 concentration, suggesting that CO_2 concentration did not affect through increased mineralization the availability of those nutrients to the willows.

Keywords CO_2 enrichment, nutrient status, nutrition, mineralization, *Salix*
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1 Introduction

As shown in numerous earlier experiments, CO_2 enhancement increases the photosynthetic rate and biomass production of plants (see review by Eamus and Jarvis 1989). There are many factors, however, that can limit or even hinder this production increase (Sionit and Patterson 1984, Smolander and Lappi 1984, Tolley and Strain 1985, Silvola and Ahlholm 1992). Furthermore, the increase in growth has often been found to be smaller than could be expected from short-term photosynthesis measurements (Tissue and Oechel 1987).

One important factor modulating the effect of CO_2 enhancement is nutrient status (Goudriaan and de Ruiter 1983, Tissue and Oechel 1987, Eamus and Jarvis 1989). Although the effect of a nutrient shortage in reducing the response to CO_2 has been demonstrated in many cases (e.g. Pettersson et al. 1993), an increase in the growth has been found in *Quercus alba* under conditions of severe nutrient deficiency at a doubled CO_2 concentration (Norby et al. 1986a,b). CO_2 enhancement has been shown to reduce the N concentration of plants, which means that less nitrogen is used to achieve a given amount of biomass at an elevated CO_2 concentration (Wong 1979, Overdieck et al. 1988, Curtis et al. 1989, Johnson and Lincoln 1991, Coleman and Bazzaz 1992). The reason for this reduced nitrogen concentration has been thought to lie in the lower nitrogen requirements of the plants (Hocking and Meyer 1985), in the poorer availability of nitrogen in the soil (Vessey et al. 1990) or in the accelerated ageing of plants caused by an enhanced CO_2 concentration (Coleman et al. 1993). The increase in C/N ratio at elevated CO_2 concentration is also partly caused by the accumulation of non-structural carbohydrates in plants (cf. Pettersson et al. 1993).

The increase in photosynthesis under conditions of elevated CO_2 has been found to increase carbon allocation to roots (Norby et al. 1986a, Zak et al. 1993), even if the real reason to increase in the root/shoot ratio may be the poorer availability of nutrients in soil at elevated CO_2 concentration (Pettersson et al. 1993). There is some evidence that the allocation of new carbon (root exudation and litter) to the soil increases the mineralization of older organic matter in it (Cheng and Coleman 1990), although some reports do not confirm this (Reid and Goss 1982). It has been proposed that a shortage of nutrients probably hampers increase in production to a great extent in natural ecosystems at elevated CO_2 concentrations (Kramer 1981). If increased mineralization as a result of CO_2 enhancement does occur, however, a long-term production increase could be possible in organic-rich soils.

The willows studied here were grown for four months in organic-rich soil in a greenhouse at different rates of nutrient supply and at four CO_2 concentrations. The aim was to test the effect of growth conditions on the uptake of nutrients (nitrogen and phosphorus). The extractable nitrate-N and P in soil were also measured in order to estimate the possible effect of CO_2 concentration in releasing nutrients from organic matter. The growth rhythm, biomass production and its partitioning of the same plant material have been described in a companion paper by Silvola and Ahlholm (1993).

2 Material and Methods

2.1 Material

Salix phylicifolia L. is common in Finland, growing mostly in habitats with moist soil. The shoots used here were taken from natural shrubs growing on the edge of an arable field at Iiksenvaara, near Joensuu, in eastern Finland.

The shoots were collected in winter and kept moist in a cold room (+5 °C). Cuttings 25 cm long and about 1 cm thick were prepared from them and kept in water for two days before establishing the experiments. At the beginning of May they were planted individually in pots of height 20 cm and diameter 15 cm containing a sand-peat mixture in a ratio of 3:7 by volume. The earth in the pots was limed with dolomite, 5 kg m^{-3}, and fertilized with a macronutrient-micronutrient mixture (Superex 9, Kekkilä; Table 1) at four nutrient levels corresponding to the following amounts of fertilizer calculated on the basis of the surface area of the pot (kg ha^{-1}) and its volume (kg m^{-3}, in parenthesis): 0 (0), 100

Table 1. Nutrient concentrations in the fertilizer used in the growth experiment (Superex 9, Kekkilä).

Nutrient concentration %					
N	P	K	Mg	S	
19.4	5.3	20.0	0.2	0.3	
Nutrient concentration mg kg^{-1}					
Fe	Mn	B	Zn	Cu	Mo	Co
1800	970	270	230	140	20	10

(0.052), 500 (0.26), 1000 (0.52). These amounts of fertilizer were mixed as powder into the earth of the pots at first, and later on 1/4 of each amount was added weekly when watering the plants, so that the basic dose was given once a month. The zero fertilization level was used to represent the conditions under which the only source of nutrients for the plants was the mineralization of organic matter and weathering from the mineral soil. No dynamic nutrient supply was employed (cf. Ingestad 1982), but on the basis of previous growth experiments with willows, 1000 kg fertilizer ha^{-1} was thought to maintain abundant nutrient conditions (free nutrient access) throughout the whole growing season. The pots were placed in plastic baths, from which the plants received their water and fertilizer through the pores in the pots.

The willows were grown under natural light in four plastic chambers situated in a greenhouse, the temperature being on average 3–6 °C higher than out of doors. The CO_2 concentrations of the chambers were kept at levels of 300, 500, 700 and 1000 ppm. Four cuttings were grown in each combination of CO_2 and nutrient conditions, except that only two samples were grown at CO_2 concentrations of 500 and 1000 ppm. Thus the material comprised a total of 48 individual willows. The growth conditions and the regulation of CO_2 concentration are described in more detail by Silvola and Ahlholm (1993).

2.2 Measurements

The roots, cuttings, stems and leaves of the willows were harvested, dried and weighed separately at the beginning of September for the biomass calculations. The roots were carefully separated from the peat by hand. The biomass increment in the cuttings was determined by subtracting the initial dry weight from the weights of the cuttings harvested.

Total nitrogen in the willows and soil was analyzed by the standard Kjeldahl method (e.g. Allen 1974). NO_3-N in the soil was extracted with potassium chloride and analyzed with the Automatic Chemical Analysis System (AKEA, Instrumentarium Ltd, Helsinki), in which nitrate is reduced to nitrite, converted to a reddish-purple azo dye and analyzed by a colorimetric procedure.

Total phosphorus in the willows and soil was measured by ashing the samples and dissolving the ash in HCl. The phosphates in the soil were extracted with ammonium acetate. The analyzing of P took place spectrophotometrically (phosphomolybdate).

3 Results

3.1 Nitrogen and Phosphorus Concentrations in the Plants and Soil

The fertilization treatments greatly affected the nutrient content of the willows (Fig. 1). Average nitrogen concentrations in the leaves increased from about 1.5 to about 3 % and those in the roots from 0.8 to about 2 % as the fertilization rate increased from 0 to 1000 kg ha^{-1}. The N concentration in the stems and cuttings was lower, from about 0.5 to about 1.2 %. The phosphorus concentration in the leaves and roots increased from 0.7–1.5 to 3.5–5 mg g^{-1} and that in the stems and cuttings from 0.4–0.8 to 1–2 mg g^{-1}. The increase in CO_2 concentration mostly led to a decrease in N and P concentrations in all parts of the willows, although the effect was not allways statistically significant (Fig. 1B).

Extractable N and P concentrations in the soil were very low at the fertilization rates of 0 and

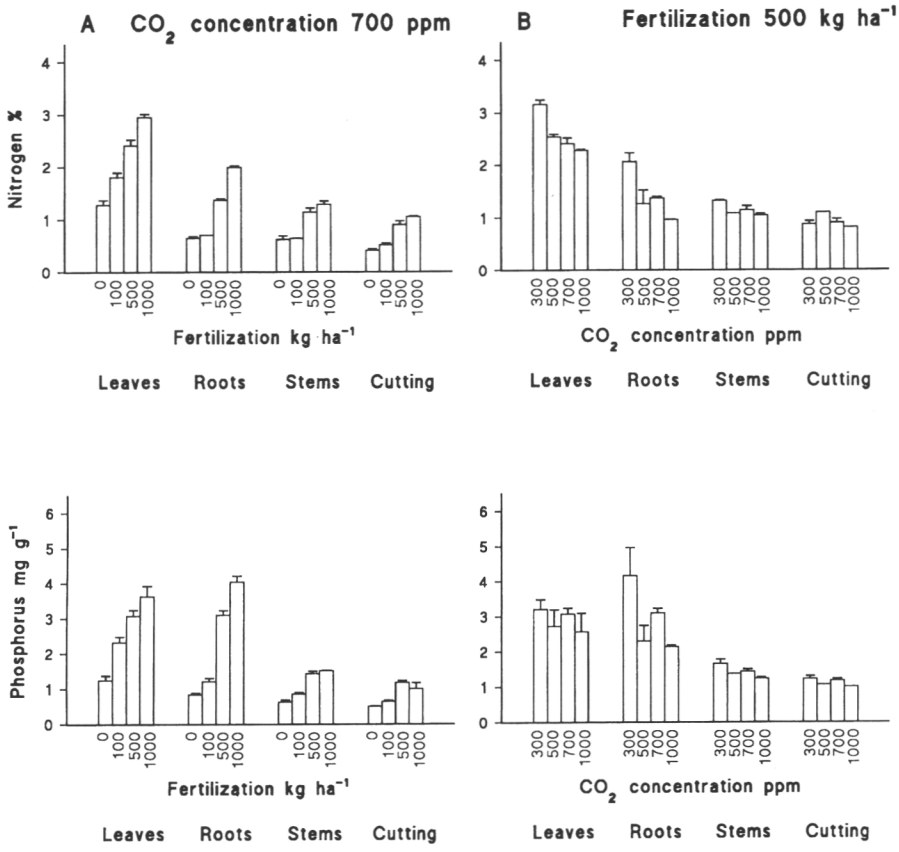


Fig. 1. Examples of the effects of fertilization (A) and CO_2 concentration (B) on nitrogen and phosphorus concentrations (mean ± S.E.) in different components of *Salix phylicifolia*.

100 kg ha^{-1} (NO_3-N mostly < 0.2 mg dm^{-3}, P < 3 mg dm^{-3}, Fig. 2), but the effect of the nutrient supply could be seen at higher fertilization levels, the maximal NO_3-N concentration being approx. 170 mg dm^{-3} and that of phosphorus approx. 40 mg dm^{-3} at the rate of 1000 kg ha^{-1}. The effect of CO_2 concentration on extractable nutrient concentrations in the soil could not be seen at the 0 and 100 kg ha^{-1}, but at higher fertilization rates the elevated CO_2 concentration led to lower nutrient concentrations in the soil. Soil nutrient concentrations were considerably higher at 300 ppm CO_2 in particular than at the higher CO_2 concentrations. Extractable nutrient concentrations in the soil were many times lower than the total nutrient concentrations, which were 429–754 mg dm^{-3} in the case of nitrogen and 80–171 mg dm^{-3} in the case of phosphorus (data not shown).

3.2 Nitrogen and Phosphorus Contents in the Willows and Soil

The nutrient uptake of the willow specimens was calculated by multiplying the dry weights (the biomass increment of the cuttings) of the various components of the willows by the corresponding nutrient concentrations. These amounts and the amounts of nutrients given during the growing season and the amounts of extractable P and NO_3-N available in the soil at the end of the growth experiments are presented in Fig. 3. The willows growing in unfertilized soil contained

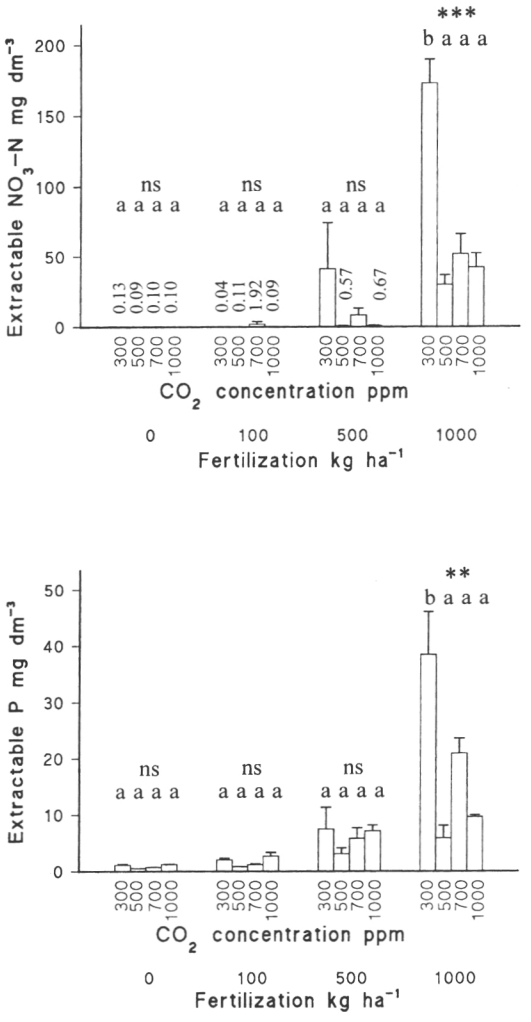


Fig. 2. Concentrations of extractable nitrate-N and phosphorus (mean ± S.E.) in the soil in which willows had been grown for four months at various fertilization rates and CO_2 concentrations.

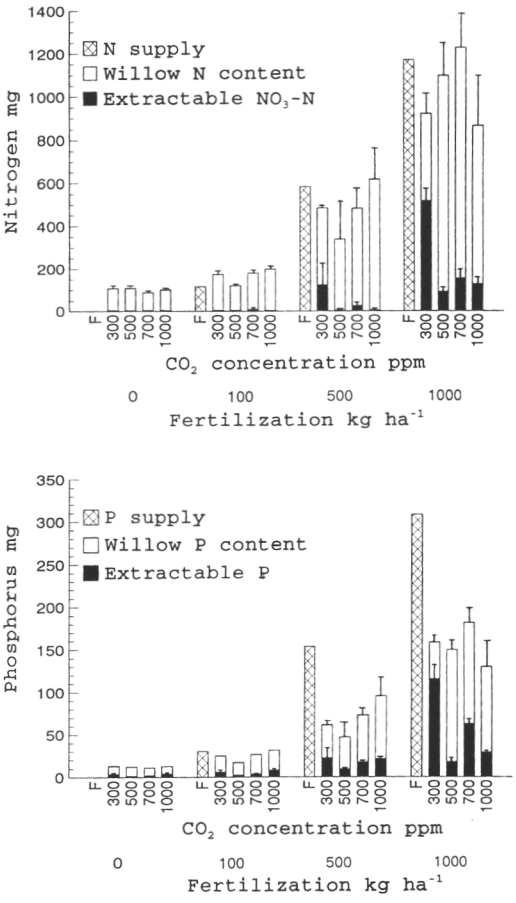


Fig. 3. Nitrogen and phosphorus budgets of willows (*Salix phylicifolia*) grown for four months at various CO_2 and nutrient levels. The groups of columns show the nutrient supply (F) to the willow specimens and the sum of extractable nutrients in the soil at the end of the experiment plus the nutrient content of the willows (mean ± S.E.). The nutrient content was obtained by multiplying the biomass production of the different components of the willows by the corresponding nutrient concentrations.

about 110 mg nitrogen, and there was less than 0.5 mg nitrate-N in the pot soil. At the fertilization rate of 100 kg ha^{-1} the average nitrogen content of the willows was about 200 mg, which is slightly less than the N content of those in the unfertilized soil plus the nitrogen given in the fertilizer. At the fertilization rates of 500 and 1000 kg ha^{-1}, the sums of the N content of the willows plus the nitrate-N available in the soil were on average slightly smaller than the amounts of N given in the fertilizer. 10–40 % of the nitrogen given was still left in the soil as NO_3-N at 1000 kg ha^{-1}, and there was also a small amount of unused NO_3-N in the soil of the 500

kg ha^{-1} experiment. At higher nutrient levels CO_2 enhancement increased nitrogen accumulation in the willows, but at lower nutrient levels no clear effects of CO_2 could be seen in either the nitrogen content of the willows or the nitrate-N in the soil.

The amounts of extractable phosphorus in the soil were higher than those of nitrogen at low fertilization rates (Fig. 3). At 100 kg ha^{-1} the phosphorus contents of the plants approximately corresponded to the amounts of phosphorus given, but at higher fertilization rates the phosphorus content of the willows was markedly lower than the phosphorus supplied to the soil. The effect of CO_2 concentration on phosphorus uptake was not very clear, even though CO_2 enhancement tended to increase the phosphorus content of the willows at higher nutrient levels and to reduce the extractable phosphorus in the soil.

4 Discussion

CO_2 enhancement reduced N and P concentrations in the willows, the decrease being less marked in the stems than in the leaves and roots. Similar concentration decreases in plants have been found to take place under various nutrient conditions by Wong (1979), Hocking and Meyer (1985) and Larigauderie (1988), for instance. The reason may lie in an increased amount of soluble carbohydrates in plants, in the reduced availability of nutrients in the soil or in a lower physiological demand for nutrients at enhanced CO_2 concentrations. Since the decrease has also been found to take place in the presence of substantial amounts of nutrients, one could assume that the reason must be the reduced nutrient requirement. The experiment of Vessey et al. (1990) does not support this conclusion, however, for when the plants were growing in flowing-solution culture, where nitrate was uniformly distributed and constantly re-supplied to the roots, the N concentration in the plants was independent of the CO_2 concentration. The authors thus conclude that in fact the lowered nutrient availability in the root system in porous media and not a reduced nutrient demand has been the reason for the decreased nutrient concentration in plants often found at elevated CO_2 concentrations.

The effect of CO_2 concentration on growth was here small at fertilization rates of 0 and 100 kg ha^{-1} but amounted to over a 100 % increase at higher fertilization rates (Silvola and Ahlholm 1993). The results are in accordance with those of Pettersson et al. (1993). In their experiment, at a suboptimal N supply the growth was controlled by N supply (not CO_2) but at free acces nutrient conditions the growth was depending on CO_2 concentration. These results differ from those by Norby et al. (1986a,b), who have found a remarkable growth increase in *Quercus alba* despite severe nitrogen deficiency. Since the nutrient concentrations in the plants are reduced at elevated CO_2 concentration, this will gradually lead to a decrease in soil fertility due to the lower nutrient content of the detritus. In organic-rich soil, however, there are large amounts of nutrients bound in the organic matter. Contradictory results exist regarding the effect of "new carbon" on the decomposition of "old carbon" in soil. Some experiments have indicated that the plant roots reduce the decomposition of organic matter in soil (Reid and Goss 1982, 1983, Sparling et al. 1982), but in many other experiments living roots have been seen to stimulate soil organic matter decomposition (Helal and Sauerbeck 1984, 1986, Cheng and Coleman 1990). The proportion of the biomass accounted for by the roots has been found to increase with increasing CO_2 concentration, especially under nutrient-poor conditions (Norby et al. 1986a), and CO_2 enhancement increases photosynthesis more than it does biomass increment, especially in cases of nutrient deficiency leading to an accumulation of soluble carbohydrates (Silvola and Ahlholm 1992, Pettersson et al 1993). Potential sinks for the "extra" carbon assimilated could be the root exudates and the accelerated growth and turnover of fine roots (cf. Norby et al. 1987, Zak et al. 1993). If stimulated mineralization of nutrients in the soil takes place due to elevated CO_2 (cf. Zak et al. 1993), this could compensate for the nutrient shortage in organic-rich soils due to the reduction in nutrients in the detritus.

If CO_2 enhancement accelerates mineralization in soil, an increase in microbial activity and

biomass could be expected. In the experiment of Norby et al. (1986a), CO_2 enhancement did not increase the density of rhizosphere bacteria, but the total bacterial biomass in the soil had probably increased because of the increased root biomass. Also Zak et al. (1993) found an increase in the microbial biomass and nitrogen mineralization at elevated CO_2. It remained open, however, whether the question was about an acceleration of N cycling or also that of N release from "native" soil organic matter. Here the uptake of nutrients by the willows at the fertilization rates of 0 and 100 kg ha^{-1} did not depend significantly on CO_2 concentration. It thus seems that here at low nutrient levels the small increase in biomass production was compensated for by a reduced nutrient concentration, and that CO_2 enhancement did not increase the availability of nutrients for the willows.

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Overwintering and Productivity of Scots Pine in a Changing Climate

Heikki Hänninen, Ilkka Leinonen, Tapani Repo and Seppo Kellomäki

The productivity of Scots pine (*Pinus sylvestris* L.) under changing climatic conditions in the southern part of Finland was studied by scenario analysis with a gap-type forest ecosystem model. Standard simulations with the model predicted an increased rate of growth and hence increased productivity as a result of climatic warming. The gap-type model was refined by introducing an overwintering submodel describing the annual growth cycle, frost hardiness, and frost damage of the trees. Simulations with the refined gap-type model produced results conflicting with those of the standard simulations, i.e., drastically decreased productivity caused by mortality and growth-reducing damage due to premature dehardening in the changing climate. The overwintering submodel was tested with frost hardiness data from Scots pine saplings growing at their natural site 1) under natural conditions and 2) under elevated temperature conditions, both in open-top chambers. The model predicted the frost hardiness dynamics quite accurately for the natural conditions while underestimating the frost hardiness of the saplings for the elevated temperature conditions. These findings show that 1) the overwintering submodel requires further development, and 2) the possible reduction of productivity caused by frost damage in a changing climate is less drastic than predicted in the scenario analysis. The results as a whole demonstrated the need to consider the overwintering of trees in scenario analysis carried out with ecosystem models for boreal conditions. More generally, the results revealed a problem that exists in scenario analysis with ecological models: the accuracy of a model in predicting the ecosystem functioning under present climatic conditions does not guarantee the realism of the model, nor for this reason the accuracy for predicting the ecosystem functioning under changing climatic conditions. This finding calls for the continuous rigorous experimental testing of ecological models used for assessing the ecological implications of climatic change.

Keywords climatic change, frost damage, gap-type model, model accuracy, model realism, overwintering, phenology

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1 Introduction

The climate in the boreal zone is expected to warm considerably in coming decades as a result of increased concentrations of CO_2 and other greenhouse gases in the atmosphere (Bach 1977, Kettunen et al. 1977, Houghton et al. 1992). Scenario analyses carried out with forest ecosystem models generally predict increased forest productivity as a result of the climatic warming in the boreal zone (Solomon 1986, Kellomäki et al. 1988, Pastor and Post 1988, Kellomäki and Kolström 1993,1994). These predictions appear plausible, as low air temperature is a major environmental factor restricting regeneration and growth of boreal forest trees (Hustisch 1948, Mikola 1952, Siren 1955, Henttonen et al. 1986). However, the scenario analyses using the ecosystem models often fail to address other ecological aspects which may complicate the predictions. Hänninen (1991), for instance, suggested that climatic warming may cause premature growth onset of trees during mild spells in winter and early spring, and heavy damage to the trees during subsequent periods of frost.

Kellomäki et al. (1992a,b) developed a holistic model for the whole annual cycle of the boreal forest trees by synthesizing ecophysiological models for the annual growth cycle, frost hardiness, and frost damage of the trees. Furthermore, they introduced the holistic model as a submodel into a gap-type forest ecosystem model. The submodel facilitates the explicit consideration of the hypothesis of increased frost damage as a result of climatic warming (Hänninen 1991) in forest ecosystem modelling; this submodel will later be referred to as the *overwintering submodel*. Scenario analysis using the gap-type model refined with the overwintering submodel suggested the increased mortality of trees, and hence decreased forest productivity in the boreal zone as a result of climatic change (Kellomäki et al. 1995); this result drastically conflicts with earlier predictions of increased forest productivity (Solomon 1986, Kellomäki et al. 1988, Pastor and Post 1988, Kellomäki and Kolström 1993,1994).

The general purpose of the present study is to examine the role of overwintering of Scots pine (*Pinus sylvestris* L.) trees in the regulation of stand development under changing climatic conditions in the southern part of Finland. For this purpose, 1) two scenario analyses of stand development in changing climate are carried out with a gap-type model, one with and the other without the overwintering submodel, 2) differences between the results of the two scenario analyses are examined with reference to the outcome of the overwintering submodel, and 3) the overwintering submodel is tested by previously published frost hardiness data from an open-top chamber experiment.

2 Material and Methods

2.1 Forest Ecosystem Model

The gap-type model of Kellomäki et al. (1992a,b) was used. The model was designed for Finnish conditions on the basis of the model of Pastor and Post (1985,1986). The model simulates the birth, growth, and death of individual trees, as well as the decomposition of organic matter in the soil, with a time step of one year. Available nitrogen in the soil, the amount of light, temperature sum of the growing season, and amount of water in the soil regulate the growth of the trees in the model. The Monte Carlo method is used to account for the stochasticity of stand development.

The overwintering submodel simulates the annual development of the individual trees with a time step of one day (Kellomäki et al. 1992a,b). The submodel involves three steps. *First*, the annual growth cycle of the trees is divided into four successive phases, i.e. active growth, lignification, rest, and quiescence. The dates of the phase changes are calculated on the basis of air temperature and night length. *Second*, the daily frost hardiness is calculated. The frost hardiness remains at its minimum during the active growth phase, increases with increasing night length during the lignification phase, and fluctuates according to air temperature during the rest and quiescent phases. *Third*, the extent of potential frost damage is assessed by comparing the daily frost hardiness with the daily minimum temperature. In the case of lethal frost damage the tree is

Table 1. Assumed increase in air temperature under conditions of a doubled level of atmospheric CO_2 (Bach 1977, Kettunen et al. 1977).

Month	Increase, °C
January	6.2
February	5.7
March	5.1
April	4.4
May	3.3
June	2.1
July	1.6
August	2.1
September	3.2
October	4.3
November	5.2
December	5.9

removed from the population and its biomass is transferred to the decomposition system in the soil. Sub-lethal daily frost damages are summarized in the ecosystem model with an additional annual growth multiplier: any daily frost damage decreases the value of the multiplier, hence decreasing growth and increasing the probability of tree death in the future. For details of the forest ecosystem model and its overwintering submodel, see Kellomäki et al. (1992a,b).

2.2 Calculations

Calculations with the forest ecosystem model were carried out for a site of medium fertility in Tampere (61°28'N, 23°44'E, 92 m asl). The calculations covered the time from stand establishment until the age of 120 years. Two types of simulations were applied, i.e., with and without the overwintering submodel. Parameter values similar to those used by Kellomäki et al. (1995) were applied in the overwintering submodel, with the exception of chilling requirement of rest completion, where the value of 20 chilling units was applied in the present study. The calculations were carried out separately for the present climate and for a scenario climate, in both cases using simulated weather data. In the case of the scenario climate, an increase of 4.1 °C in the annual mean temperature during the first 50 years was assumed, i.e., the mean elevation rate of temperature was 0.08 °C a^{-1}. The temperature elevation was allocated more to winter than to summer (Table 1). Eight iterations were used in all calculations. For details of the stand description and climatic conditions, see Kellomäki et al. (1995).

Additional calculations were carried out merely with the overwintering submodel, using temperature data measured by the Finnish Meteorological Institute during 1970–1972 in Jyväskylä, central Finland (62°14'N, 25°44', 86 m asl). The temperature records were collected in standard meteorological screens two meters above ground level. Daily mean temperatures were used in the calculations, and daily minimum temperatures were used in the analysis of the results. For the scenario climate, the observed daily mean and minimum temperatures were increased according to the same scenario which was used in the calculations with the ecosystem model after the age of 50 years (Table 1).

2.3 Testing the Overwintering Submodel

The overwintering submodel was tested during two winters in a field experiment located in eastern Finland near the Mekrijärvi Research Station (62°47'N, 30°58'E, 144 m asl). The frost hardiness dynamics predicted by the model was compared with independent observations of needle frost hardiness of 20–25 year old Scots pine saplings growing at their natural site of low fertility (Repo et al. 1996). The frost hardiness was assessed with the electrolyte leugage method after artificial freezing of the needles. Four replicate saplings in each of two treatments were considered: 1) saplings growing under natural conditions, and 2) saplings growing under elevated temperature conditions, both in open-top chambers. In the latter case the air temperature fluctuated for the most part during winter above 0 °C. Air temperature was monitored for each sapling at hourly intervals with two sensors, the mean of the records was used for model testing. For details of the experimental set-up and assessment of frost hardiness, see Repo et al. (1996).

3 Results

3.1 Simulated Stand Development

Only neglible differences were obtained in the development of stemwood volume in the present climate between the simulations with and without the overwintering submodel (Fig. 1, results given only for simulations without the overwintering submodel). In the case of the scenario climate, however, the results of the two simulations were drastically different. In the simulations without the overwintering submodel the climatic warming caused a slight increase in the growth rate before reaching the carrying capacity (Fig. 1). This was also the case in the simulation with the overwintering submodel until the age of 50 years, i.e., until the climatic warming attained its assumed final level of 4.1 °C. At that time the stemwood volume started to decrease as a result of increased mortality, thus resulting in a reduction of approximately 50 per cent in the stemwood volume at the age of 120 years, as compared with the present climate (Fig. 1).

3.2 Simulated Frost Hardiness Development

In the simulation for the present climate the annual development of frost hardiness was well-synchronized with the annual climatic cycle, i.e., the minimum temperature was constantly higher than the simulated frost hardiness of the trees (Fig. 2a). In the scenario climate, however, this synchronization was lost during year 2, and to a lesser extent during year 3, when the trees dehardened too early (Fig. 2b). The resulting frost damage was the reason for the tree mortality and growth reduction observed in the ecosystem simulation for the scenario climate (Fig. 1).

3.3 Testing the Overwintering Submodel

The overwintering submodel predicted quite accurately the needle frost hardiness of the Scots pine saplings growing under natural conditions (Fig. 3a). The model, however, failed to predict the needle frost hardiness for the saplings grow-

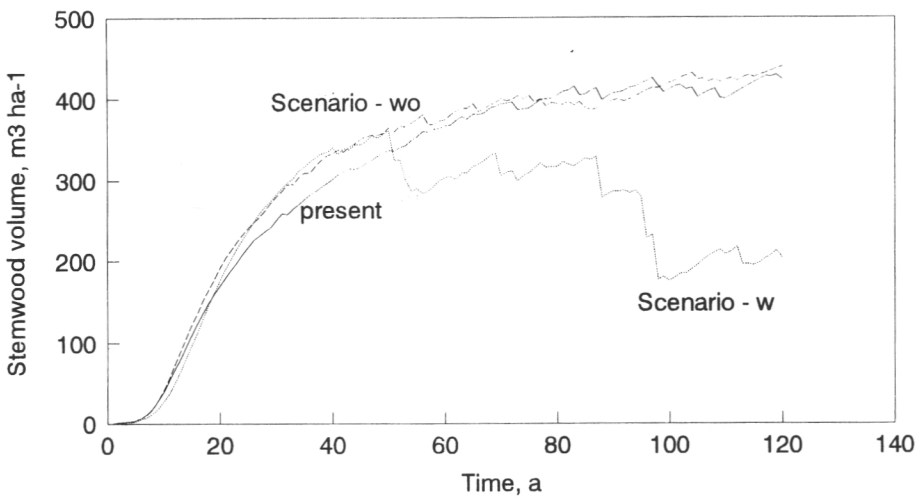


Fig. 1. Simulated development of stemwood volume in a Scots pine stand in southern Finland, in the present climate and in a scenario climate assuming an increase of 4.1 °C in the annual mean temperature during the first 50 years. Simulations for scenario climate with (Scenario-w) and without (Scenario-wo) the overwintering submodel.

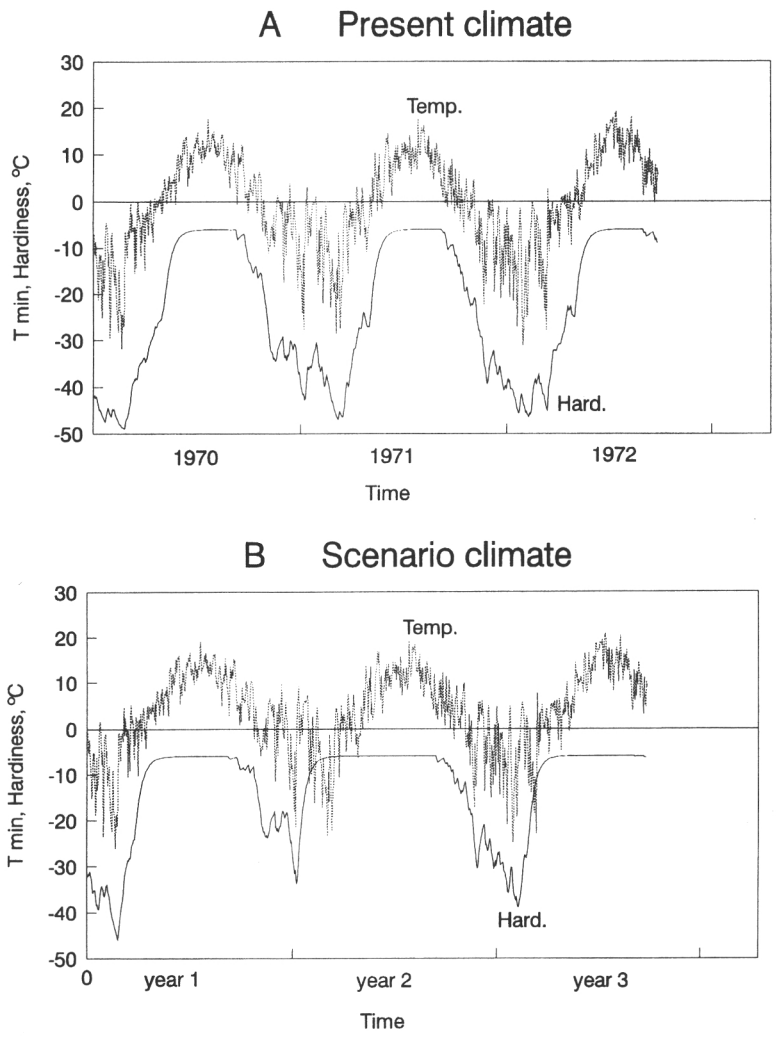


Fig. 2. Daily minimum temperatures and simulated frost hardiness of Scots pine trees over three years in Jyväskylä, central Finland, for (A) present climate and (B) scenario climate. Temperature data for the years 1–3 in (B) were constructed by increasing the daily mean and minimum temperatures for the years 1970–1972 according to the climatic scenario corresponding to a doubled level of atmospheric CO_2 (Table 1).

ing under elevated temperature conditions (Fig. 3b). With a few exceptions, the model considerably underestimated the needle frost hardiness of these saplings. For instance, the model predicted complete dehardening of the saplings during winter 1993–1994, when the needles of the real saplings were hardy down to –40 °C (Fig. 3b).

4 Discussion

The experimental results of the present study suggest that the climatic warming will not cause such catastrophic frost damage and mortality to Scots pine in southern part of Finland as predicted by computer simulations (Hänninen 1991, Kellomäki et al. 1995, Figs. 1,2b). This result

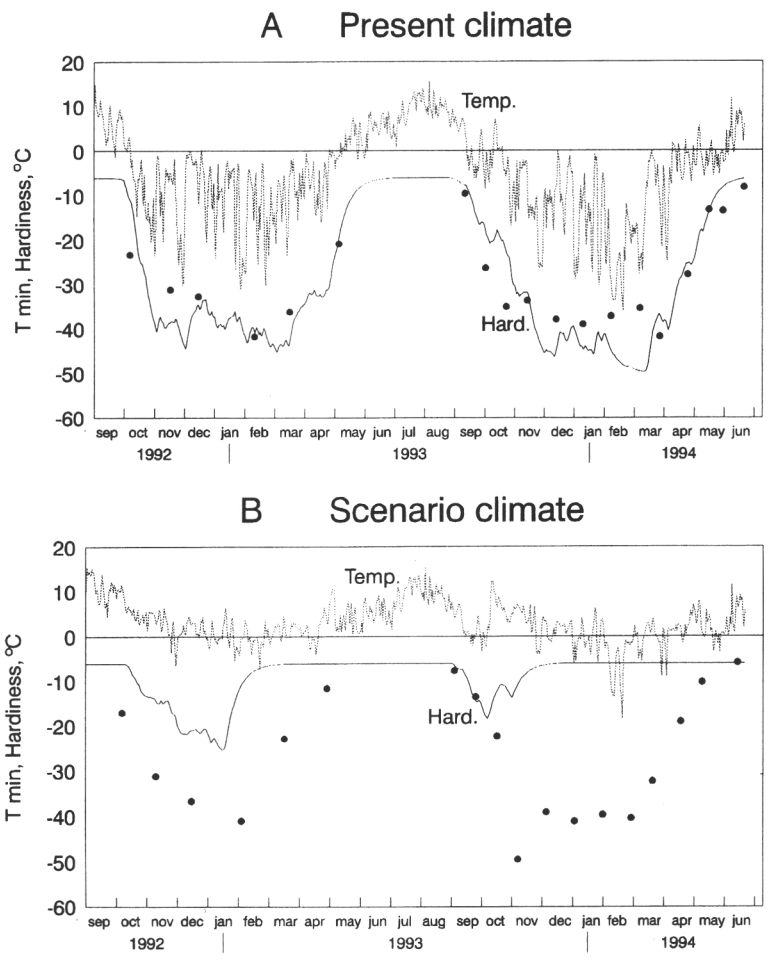


Fig. 3. Daily minimum temperatures (broken line), tree frost hardiness predicted by the overwintering submodel (solid line), and measured needle frost hardiness of Scots pine saplings (dots) in Mekrijärvi, eastern Finland. (A) Saplings growing under natural temperature conditions, (B) saplings growing in elevated temperature conditions, both in open-top chambers.

agrees well with the findings concerning the onset of height growth observed in the same experiment (Hänninen et al. 1993, Hänninen 1995a). More moderate frost damages, however, are possible, as the saplings under the elevated temperature conditions hardened later during autumn and dehardened earlier during spring, as compared with the saplings growing under natural conditions. During mid-winter there were no major differences between these two groups of saplings (Repo et al. 1996, Fig. 3).

Until now, only Kellomäki et al. (1995) and Kramer et al. (1996) have explicitly considered the overwintering of boreal forest trees in scenario analysis with forest ecosystem models. The present results from computer simulations and those from the open-top chamber experiment together demonstrate the need for such a consideration. The present overwintering submodel, however, has to be developed further in order to obtain reliable predictions of the development of boreal tree stands under changing climatic conditions.

The original models that were synthesized in the present overwintering submodel were developed on the basis of data from different tree species, concerning flower buds of adult trees or different tissues of 1–2 years old seedlings. The experimental results of the present study, on the other hand, concerned the frost hardiness of needles sampled from 20–25 year old saplings of Scots pine. This discrepancy may constitute one reason for the failure of the present overwintering model to predict the needle frost hardiness of the Scots pine saplings growing in scenario conditions. In further model development, the frost hardiness and damage should be addressed more specifically to different tree tissues and species.

Previous and current experimental work reveals three aspects of the frost hardiness model that require further development. First, the frost hardening during the rest phase is obviously influenced by both the shortening of the photoperiod and lowering of the temperature (Leinonen et al. 1995,1996), not only by temperature, as assumed in the present model. Second, the environmental response of needle frost hardiness does not change abruptly at the beginning of the active growth phase, as assumed in the present model (unpublished results from the present open-top chamber experiment). Third, the environmental regulation of growth onset is not properly described in the present model for the annual growth cycle (Hänninen et al. 1993, Hänninen 1995a).

The elevated temperature treatment of the present study was designed to correspond to an exceptionally warm winter under conditions of a doubled level of atmospheric CO_2 (Bach 1987, Kettunen et al. 1987, Hänninen 1991,1995a, Hänninen et al. 1993), i.e., the temperature fluctuated most of the time above zero (Fig. 3b). In this way the treatment provided a rigorous test of the hardening potential of the Scots pine saplings under changing climatic conditions. Contrary to the climatic scenarios, however, heavy intermittent frosts were generally not allowed in the treatments (Hänninen et al. 1993, Hänninen 1995a, Repo et al. 1996). In further model testing, temperature treatments more like the climatic scenarios should also be used.

The forest ecosystem model applied in the present study (Kellomäki et al. 1992a,b) fails to address the direct effects of elevated atmospheric carbon dioxide on the growth and development of the trees (e.g. Ceulemans and Mousseau 1994, Wang et al. 1995). In order to obtain more realistic assesments of the ecological implications of the climatic change, the overwintering sub-models should be introduced into forest ecosystem models considering also these effects (Kramer et al. 1996).

The ecological implications of the predicted climatic change are currently being assessed for a wide range of ecosystems by scenario analysis with ecological models (Shugart 1990, Ågren et al. 1991, Malanson 1993, Bonan 1993). This is actually the only possibility, since whenever we try to predict the future, we must resort to some kind of modelling approach. It should, however, be remembered that the scenario analysis only reveals the logical implications of the assumptions inherent in the ecological model applied. This basic fact calls for a rigorous examination of the validity of the ecological models. The results of the present study emphasize the importance of the concepts of model realism and model accurary (Levins 1966) for such an evaluation.

The present frost hardiness model had quite high *accuracy* for the present climatic conditions, i.e. its predictions agreed with independent observation in that case. Despite this, the model does not have high *realism*, i.e., its logical structure does not account for all the major factors regulating the frost hardiness development of the trees. A test under natural environmental conditions did not address the non-realistic weak points of the model, whereas the test under scenario conditions revealed their existence. This finding shows that the accuracy of a model in the case of natural conditions does not guarantee the realism of the model, nor for this reason, the accuracy of the model in predicted conditions. Thus, ecological models used for assessing the ecological implications of the climatic change should be exposed to continuous rigorous experimental testing in a wide range of environmental conditions. In this way the best possible predictions for the development of the ecosystems of the globe under changing climatic conditions can be obtained (Hänninen 1995b).

Acknowledgements

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Changes in Wood Production of *Picea abies* and *Pinus sylvestris* under a Warmer Climate: Comparison of Field Measurements and Results of a Mathematical Model

Egbert Beuker, Marja Kolström and Seppo Kellomäki

To project the changes in wood production of Norway spruce *Picea abies* (L.) Karst. and Scots pine *Pinus sylvestris* L. in Finland as a result of climate change, two separate studies were made. The first study, at the Faculty of Forestry, University of Joensuu, based its projections on mathematical models; the second one, at the Finnish Forest Research Institute, based projections on measurements of wood production in two series of aged provenance experiments. The results of the two studies were similar for both species: after a 4°C increase of the annual mean temperature a drastic increase in wood production in northern Finland, but little effect, or even some decrease in the southern part of the country.

However, the assumptions used in the two studies differed. One important difference was that in the models the temperature is assumed to be increasing gradually over the years; whereas in the provenance experiments, climate changed immediately when the seedlings were transferred to the planting sites. Another problem with the provenance experiments is that when material is moved in a north-south direction in Finland, not only temperature but also photoperiod changes markedly. To compare these two studies, site factors (e.g. soil type, temperature, precipitation) and silvicultural factors (e.g. plant spacing, survival, time of thinning, thinning intensity) from the provenance experiments were included as variables in the mathematical models.

Keywords Scots pine, Norway spruce, provenance trials, simulation model, global warming
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1 Introduction

To predict the growth of forests in the future, it is necessary to know how trees respond to climate warming. Different methods can be used to study this, for example, mathematical modelling or field trials. With modelling it is possible to separate various growth factors and to study the effects of rising temperature on each factor. It is also possible to predict long-term effects. It is, however, difficult to validate the results. Field trials give real values for the reactions of trees to elevated temperature. However, it is impossible to separate the different growth factors. In addition the trials are expensive to establish and they take time, especially when long-term reactions are to be studied. In provenance trials, which have been established in Finland since the early 1930's, trees have been grown for many decades in environments different from those to which they were adapted. These trials provide an unique opportunity to obtain data on the long-term effects of climate change on tree growth. Both types of studies can be used paralell to elaborate the outlines on how climate change could effect forest growth.

The aim of this study is to verify correspondence between results of simulations and of provenance trials by running the simulations using parameters from the trials. In this context two completely separate studies were utilized, both part of the Finnish Research Programme on Climate Change, SILMU (1990–1995). Both studies indicated the changes in wood production of Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.) as a result of climate change in Finland.

2 Material and Methods

2.1 Description of the two Studies

In the first study, which was carried out at the University of Joensuu by Kellomäki and Kolström (1994), projections of changes in wood production were based on model computations, using a gap type model (Kellomäki et al. 1992). This model, which was developed from the gap model of Pastor and Post (1985, 1986), has been adjusted to Finnish conditions and used to study how changing climate affects the yield of trees, species composition (Kellomäki and Kolström 1992b), soil factors (Kellomäki 1995), silviculture (Kellomäki, Hänninen and Kolström 1988, Kellomäki and Kolström 1992a, 1993) and frost damage to Scots pine (Kellomäki, Hänninen and Kolström 1995). It has also been used to study carbon sequestration in the forest ecosystem under changing climatic conditions (Karjalainen 1996a, b). The model has been further refined by Talkkari and Hypén (1996), among others, for different site and soil types. The growth factors included in the model are temperature, soil water, light and nitrogen. Growth and yield for different tree species were predicted for pure, even-aged stands over a rotation of the length commonly applied in forestry.

In the simulations only temperature was allowed to increase (Kellomäki and Kolström 1994). Precipitation was assumed to be the same as the current precipitation, because at that time estimations of future changes were still unreliable. The recalculated results of the simulations indicated that with rising temperature (0.04°C annually) the total yield of Scots pine in southern Finland could increase by a few per cent but in northern Finland by about 140%. The total yield of Norway spruce in southern Finland would remain unchanged but in northern Finland it may increase by about 200% (Table 1). These calculations are based on mean total production as calculated from 100 separate iterations over 160 years. An annual increase of 0.04°C corresponds with

Table 1. Comparison of the projections for the changes in wood production by the two studies.

		Simulations [1]	Provenance trials [2]
Scots pine	north	140 %	45 %
	south	5 %	–10 %
Norway spruce	north	200 %	300 %
	south	0 %	considerable decrease

[1] Calculated with a temperature increase of 0.04°C annually. The calculations are based on mean total production as calculated from 100 separate iterations over 160 years.
[2] Calculated with a 600 dd increase in annual mean temperature sum for a 27 years old stand for Scots pine and a 60 years old stand for Norway spruce.

an increase of the annual mean temperature with 4°C during 100 years, which is approximately the change which is projected for the next century (Kettunen et al. 1987, Carter et al. 1995).

The second study was carried out by Beuker (1994) at the Finnish Forest Research Institute. In this study a series of provenance experiments was used to assess the effects of a warming climate on the wood production of Norway spruce and Scots pine. In provenance experiments, plant material was moved to an environment different from that to which it was originally adapted. When the same geographical origins are represented at different sites in different climates, such experiments offer an opportunity to study the influence of climate on the performance of trees of various origins. For the purpose of these studies, trees of different origins transferred from north to south, into a warmer climate, are most interesting.

The Norway spruce series consisted of 7 sites throughout Finland, including a total of 29 origins from Fenno-Scandinavia and Central Europe. This series was established in 1931 by the late Prof. Olli Heikinheimo. The Scots pine series, established by Prof. Max Hagman in 1966, consists of 11 sites throughout Finland, including 32 Finnish origins. Both series were measured in 1991, and the total wood production per hectare was calculated for each origin at each site. With these data, models were developed which project the change in wood production as a function of the annual mean temperature sum at the location of the origin in question and the change in annual mean temperature sum as a result of the geographical transfer (Beuker 1994).

The results of the latter study show that wood production of Norway spruce could decrease in southern Finland, but increase by about 300 % in northern Finland after an increase of 600 degree days in annual mean temperature sum, which corresponds with an increase in annual mean temperasture of approximately 4°C. For Scots pine the projections are a minor decrease in southern Finland and a 40 % increase in northern Finland (Table 1). For southern Finland it is not possible to give accurate figures, because these results are obtained by extrapollation.

2.2 Comparison of the two Studies

To combine the model and the provenance trials, four sites from each of the two series used by Beuker (1994) were included, two sites in northern Finland and two in southern Finland. As much data as could be retrieved from the experiment archives of the Finnish Forest Research Institute were included in the model (Table 2).

Table 2. Location of the sites and the parameters used in the simulations.

Parameter	Pine				Spruce			
	Pieksämäki	Kuorevesi	Rovaniemi	Muhos	Vilppula	Punkaharju	Muhos	Kivalo
Latitude	62°22'	62°02'	66°27'	64°53'	62°03'	61°48'	64°52'	66°28'
Longitude	26°51'	24°50'	26°45'	26°06'	24°23'	29°18'	26°04'	26°39'
Altitude, m above sea level	140	140	180	70	140	100	70	210
Annual mean temp. sum, dd	1124	1158	863	1029	1161	1208	1033	852
Beginning growing season, julian day	120	119	130	123	118	116	123	130
End growing season, julian day	278	280	267	274	282	286	274	267
Forest type, Cajander	VT	VT	VT	VT	MT	OMT	MT	HMT
Soil type	Till	Till	Till	Till	Stony till	Stony till	Till	Stony till
Field capasity, mm	105	105	105	105	60	60	105	60
Wilting point, mm	45	45	45	45	9	9	45	9
Humus mass, t/ha	42	42	42	42	51	32.6	51	51
Nitrogen mass, t/ha	6.3	6.3	6.3	6.3	10.2	8.8	10.2	10.2
Planting spacing, m	2×2	2×2	2×2	2×2	1.5×1.5	1.3×1.5	1.5×1.5	2×2
Number of thinnings	0	0	0	0	5	6	1	1

For each location, temperature and precipitation data were calculated according to data of the Finnish Meteorological Institute. The beginning and end of the growing season were calculated according to Talkkari and Hypén (1996).

Soil type and forest type were obtained from the archives of the Finnish Forest Research Institute (Beuker 1994). For the site in Vilppula the soil data obtained were corrected from sand to stony till. The field capacity and wilting point for each soil type were taken from Talkkari and Hypén (1996, their Table 2). Data on thickness of the humus at the time of planting were calculated for each forest type by using the figures given by Tamminen (1991, his Table 16) and transforming them into figures for treeless sites, as done by Talkkari and Hypén (1996, their Table 3). Nitrogen concentrations were then calculated according to Talkkari and Hypén (1996, their Table 4).

Data on plant spacing, time of thinning and thinning intensity (for volume as well as number of stems) were also available from the archives. It was, however, not always clear what kind of thinnings had been carried out; usually the smallest individuals and suppressed trees were removed. In the simulations the trees were first devided into four height classes, whereafter the same percentage of trees was removed from each height class. The thinning percentage was equal to that used in the provenance trials. The height model of Näslund has different parameter values for northern and southern Finland (Talkkari and Hypén 1996), which affects the total production. Therefore different parameter values were used for the northern and southern sites in the simulations. The simulations were run until the ages at which the last measurements in the trials were made. For spruce this was at the age of 60 years; for pine it was at the age of 25 years (Beuker 1994).

The model was run for each site to project total wood production under present climatic conditions, thus without change in temperature. These projections were compared with the performance of the local origin at each site or the origin closest to the site in the field experiments. The development of the number of stems at each site was simulated and compared with the number of stems of local origin at each inventory made in the experiments.

3 Results

For Scots pine at age 25 the total production of wood projected by the simulations was considerably higher than the total production of the local origin at each site (Fig. 1). For Norway spruce at age 60 there was also a difference between the projections and the trial values, but the differences were less consistent. In two cases the trials had the highest total production of wood; in one case the simulation and the field results were almost the same (Fig. 2).

When the numbers of stems in the pine trials were compared (Fig. 3), it was found that at the sites in Rovaniemi and Pieksämäki the number of stems projected by the simulations was much higher than that in the trials; but at Muhos and Kuorevesi the number of stems in the trials was higher. For spruce (Fig. 4) the number of stems at the southern sites, Vilppula and Punkaharju,

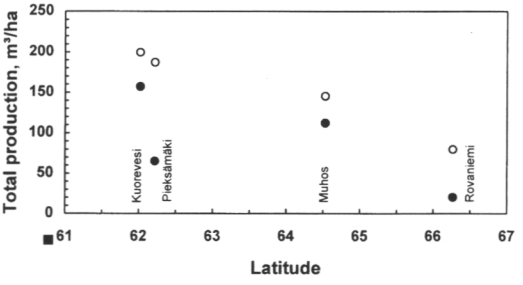


Fig. 1. The total wood production of the local origin at each of the four Scots pine sites (●), and the corresponding values obtained from the simulations (○).

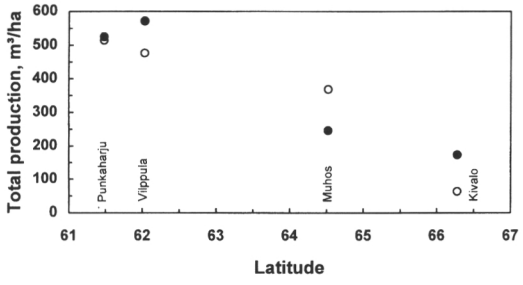


Fig. 2. The total wood production of the local origin at each of the four Norway spruce sites (●), and the corresponding values obtained from the simulations (○).

was close to that projected by the simulations. On the northern sites, the projections of the simulations were much lower than the trial values, although the number of stems at the site in Muhos has decreased drastically between the age of 35 and 57.

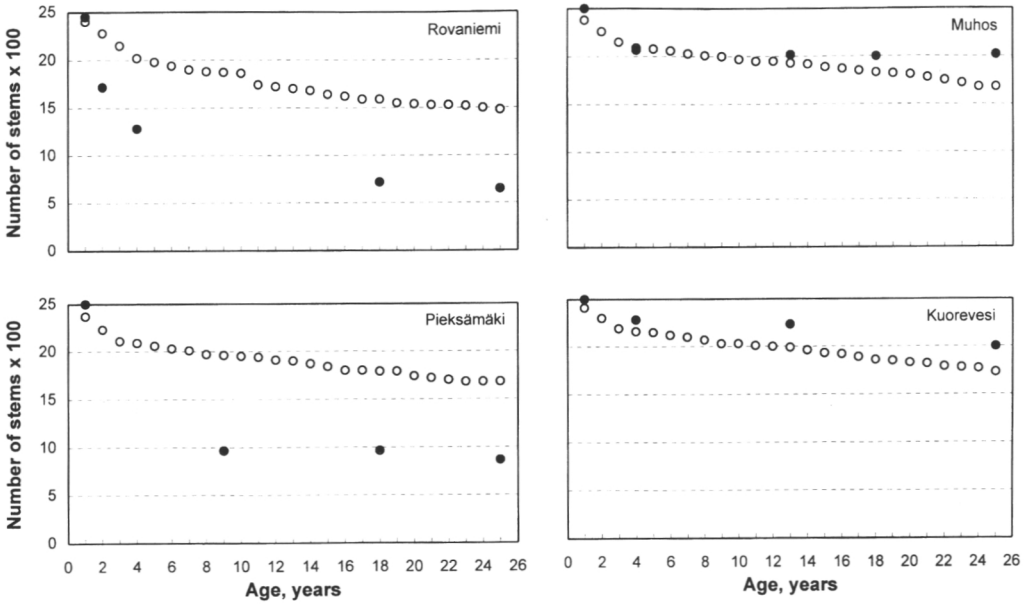


Fig. 3. The number of stems per ha, calculated for the local origin at each of the four Scots pine sites during the regular inventuries (●), and the projected number of stems for each year from the simulations (○).

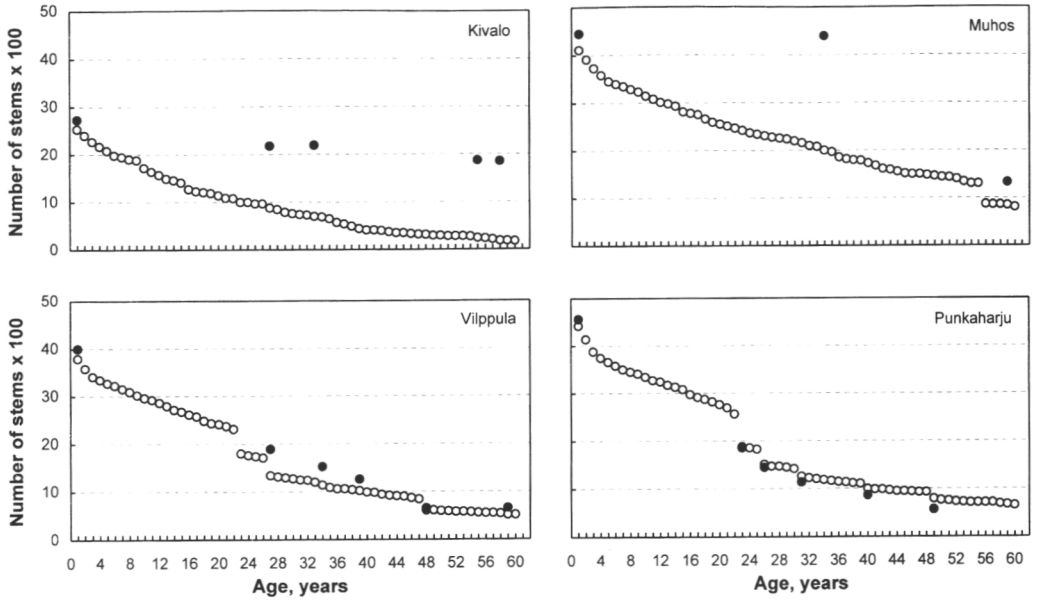


Fig. 4. The number of stems per ha, calculated for the local origin at each of the four Norway spruce sites during the regular inventuries (●), and the projected number of stems for each year from the simulations (○).

4 Discussion and Conclusions

The studies on changes in wood production of Scots pine and Norway spruce as a result of climate warming by Kellomäki and Kolström (1994) and Beuker (1994) resulted in similar projections, despite differences in methods and, as a result, differences in assumptions. In the model simulations the temperature was increased gradually over the years (0.00, 0.04, 0.06 or 0.08°C annually), whereas in the provenance trials climate changed at once when the material was transferred to the test site. Another problem with the provenance trials is the change in light conditions as a result of the geographical changes. When material is moved over long north-south distances at high latitudes such as in Finland, there are considerable changes in photoperiod and total radiation during the growing season (Meteorological Yearbook, 1993).

The most accurate comparison that could be made between these two studies was inclusion of the characteristics of the sites of the provenance trials into the simulations, which were run with a zero increase in temperature, and comparison of the results with the performance of the local origin at each site. The simulations were made for total wood production and for decrease in of stem number. The annual mean temperature sums for the sites used by Beuker (1994) were estimated using the program of Ojansuu and Henttonen (1983); whereas in the simulations, the estimations were made on the basis of climatic data. It was found that the estimations made by the simulations were higher than those of Ojansuu and Henttonen (Fig. 5), which might explain part of the differences between the simulations and the trial values.

The large difference in total wood production between the simulations and the Scots pine trial in Pieksämäki can, at least partly, be explained by the fact that this site has suffered from *Scleroderris* canker of pine (*Ascocalyx abietina* (Lagerb.) Schläpfer), which has caused considerable dieback in the trial. The difference at the Rovaniemi site, on the other hand, might be due to insufficient accuracy of the model. This model was developed mainly for southern Finnish conditions and may therefore give too high values for the northern part of the country. All the northern sites in this series (Beuker 1994) have very low production. The main reason for this seems to be a decrease in the number of stems to about 50 % during the first 4 years. Furthermore, survival in Scots pine provenance trials has been studied intensively in Northern Sweden (Eiche and Andersson 1974, Eriksson 1975, Eriksson et al. 1980, Persson and Ståhl 1990, 1993, Persson 1994). According to the results of these studies, there is much variation in the survival of trees of local origin at the different sites, and at those sites with the harshest climate, high mortality occurred during the early years of the trials (Persson and Ståhl 1990, 1993). The site in Rovaniemi is certainly harsher than that in Muhos. Muhos is not only situated 1.5° farther south, but is also close to the Gulf of Bothnia, which has a warming effect. In the trials on the sites in Kuorevesi and Muhos the wood production was lowest, despite the larger number of stems on these sites.

For Norway spruce the results were just the opposite. For this species the number of stems at the northern sites was greater in the trials than was projected by the simulations. These discrepancies resulted from differences in natural mortality in the early stage of stand development. Ruotsalainen (1987) found large variation in survival of the local origin in Norway spruce provenance trials in northern Finland. At one site, where two local seed sources were used, he found a survival of about 55 % for one source and about 75 % for the other. At the Muhos site, survival of the local origin was very high, at

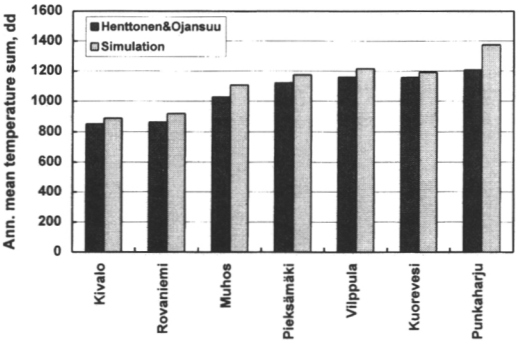


Fig. 5. Annual mean temperature sum in degree days (5°C thresshold) for each site, as they were calculated according to Henttonen and Ojansuu (1983) and by the simulations.

least until the stand reached 35 years of age. After that, there was a strong decrease in stem number, which cannot be explained only by the one thinning at age 55.

From these studies we conclude that a temperature elevation could increase the forest growth, especially in northern Finland. This conclusion is based on the combination of field experiments and model calculations. This involves, however, many problems as far as the assumptions and the methodology are concerned. In particular the genetic structure of the tree populations are poorly described in ecological models. In this respect the large number of provenance experiments provide unique opportunities to improve the interaction between ecologists and genetisists to improve our understaning on how climate change effects growth and development of forests.

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Regional Predictions Concerning the Effects of Climate Change on Forests in southern Finland

Ari Talkkari

A gap-model was used with forest inventory data in taking ground-true site, soil and tree characteristics into account in predicting the effects of climate change on forests. A total of 910 permanent sample plots established in the course of national forest inventory (NFI) in Finland and located on mineral soil sites in southern Finland were selected as the input data. The climatological input used in the simulations consisted of interpolated means of and deviations from long-term local temperature and precipitation records. The policy oriented climate scenarios of SILMU (Finnish Research Programme on Climate Change) were used to describe the climate change. The temperature changes in the climate scenarios were increases of ca. +1.1 °C (low), +4.4 °C (medium) and +6.6 °C (high) compared to the current climate in 110 years. The simulation period was 110 years covering the time years 1990–2100.

Southern Finland, divided into fifteen forestry board districts, was used as the study region. Regional development of stand volume, cutting yield, and total wood production of forests under different climate scenarios were examined. The annual average growth in simulations under current climate was close to that observed in NFI. Forests benefited from a modest temperature increase (Scenario 2), but under Scenario 1the growing stock remained at a lower level than under the current climate in all parts of the study region. In wood production and cutting yield there were regional differences. In the southern part of the study region wood production under Scenario 1 was ca. 10 % lower than under the current climate, but in the eastern and western parts wood production was 5–15 % higher under Scenario 1 than under the current climate. The relative values of total wood production and cutting yield indicated that the response of forests to climate change varied by geographical location and the magnitude of climate change. This may be a consequence of not just varying climatic (e.g. temperature and precipitation) and site conditions, but of varying responses by different kinds of forests (e.g. forests differing in tree species composition and age).

Keywords Gap-model, simulation, climate change, regional predictions
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1 Introduction

Changes in the mean climatic conditions and in the range of variability about the mean are likely. In the coming decades, these changes may be greater and more rapid than hitherto. It is predicted that the most drastic changes will take place in northern latitudes, which are mostly covered by boreal forests. The predicted global climate change is among the major factors affecting future forest development in the boreal zone. The majority of Finland's land area is located within the boreal zone. Thus, climate change may have great influence on forests and forestry in Finland. The most direct impacts are expected to occur on a local scale, but their effects will rapidly spread to regional, national and global levels (Robinson 1989). The future climate must be viewed in local light, because impact assessment must start with local direct impacts (Robinson 1989).

Research addressing the response of forest ecosystems to climate change has relied on historic changes in climate and computer simulations (Dale and Franklin 1989). Computer simulations provide possibilities to specify climate scenarios and to compute the response of forests over long time periods and at various locations (Dale and Franklin 1989). Recent simulation studies concerning the effect of climate change on forests in Finland (Kellomäki and Kolström 1993, Kellomäki and Kolström 1994, Kellomäki 1995) have relied on theoretical forests, e.g. even-aged seedlings and saplings of Scots pine have been used as the initial objects of study. When theoretical forests are used to provide the input in simulations, the resultant predictions are general by nature and cannot be used to produce local or regional predictions about the effect of climate change on forests. In order to produce realistic quantitative predictions of the effect of climate change on forests, predictions should be made at the local level and they should be based on ground-true forest data with known geographical locations and environmental conditions.

The aim of this study was to produce local predictions of the effects of climate change on forests in southern Finland using an existing climate sensitive forest growth model and by generalising the predictions to the regional level. This study examines regional development of stand volume, total wood production, and cutting yield of forests in southern Finland under different climate scenarios.

2 Material

The forest data used in this study consisted of data collected from 910 permanent sample plots in the course of the national forest inventory (NFI) carried out in 1990–1991 by the Finnish Forest Research Institute. The sample plots were located on mineral soil sites on forest land within boundaries of the fifteen forestry board districts in southern Finland (Fig. 1). No sample plots located on scrub land or waste land were included in these simulations. In accordance with the Finnish system of classification applied in forestry, scrub land is forestry land where the productivity of stem wood is less than 1 $m^3\ ha^{-1}\ a^{-1}$ and on waste land it is less than

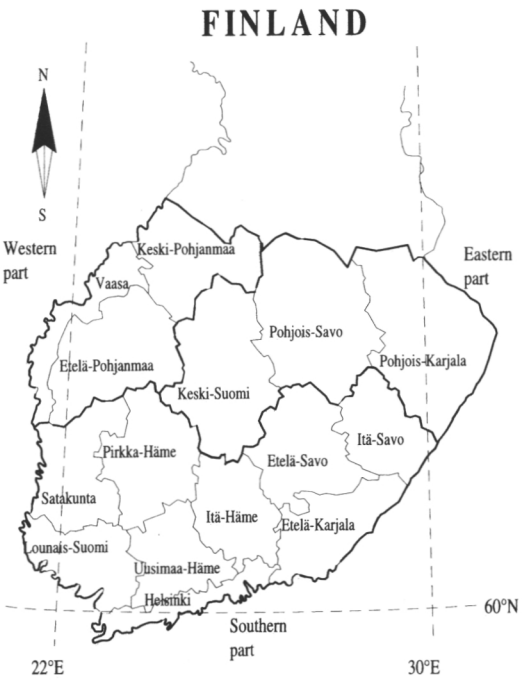


Fig. 1. The study area and the forestry board districts in southern Finland.

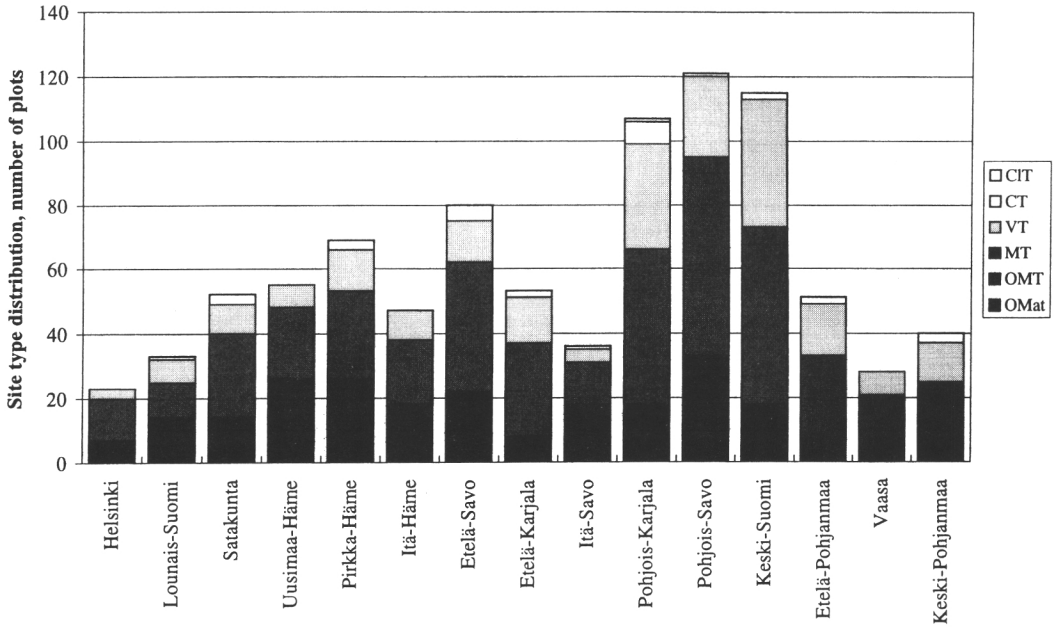


Fig. 2. Site type distribution in the simulation data.

1 m^3 ha^{-1} a^{-1}. The number of sample plots varied greatly by forestry board district (between 23 and 121).

In this study, the term "southern part" refers to the nine southernmost forestry board districts, "eastern part" refers to the forestry board districts of Pohjois-Karjala, Pohjois-Savo and Keski-Suomi, and "western part" refers to the forestry board districts of Etelä-Pohjanmaa, Vaasa and Keski-Pohjanmaa (Fig. 1).

Site types included in the data were, from richer to poorer, as follows: Oxalis-Maianthemum Type (OMaT, grove), Oxalis-Myrtillus Type (OMT), Myrtillus Type (MT), Vaccinium Type (VT), Calluna Type (CT), and Cladonia Type (CIT) (Cajander 1949) (Fig. 2).

The soil textures included in the data were coarse moraine, fine moraine, gravel, sand, fine sand, silt, and clay (Fig. 3). Unsorted soil textures, rough and fine moraine, covered most of the sample plots in the simulation data. Sand and fine sand were the most common sorted soil textures in the data (Fig. 3).

The tree species in the sample plot data represented Finland's six main current tree species. Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) were the commonest tree species in forests on mineral soil sites in Finland in 1990. The other four tree species included in the data were pendula birch (*Betula pendula*), pubescent birch (*Betula pubescens*), aspen (*Populus tremula*), and grey alder (*Alnus incana*).

The climatological input of the simulation model was based on recordings made at twenty-eight weather stations located at airports throughout Finland. The long-term monthly mean values were based on the daily means of temperature (°C) and precipitation (mm) recorded during the period 1961–1990 by the Finnish Meteorological Institute. Monthly mean temperature and precipitation and their deviations were needed in simulations. Weather data were interpolated to a grid of 10 km × 10 km throughout Finland by the Finnish Meteorological Institute.

Climate change in the simulations was described as changes in monthly mean values of temperature and precipitation. The climate scenarios used in this study were SILMU- policy scenarios based on a GCM (General Circulation Model) composite (Carter et al. 1995). The ex-

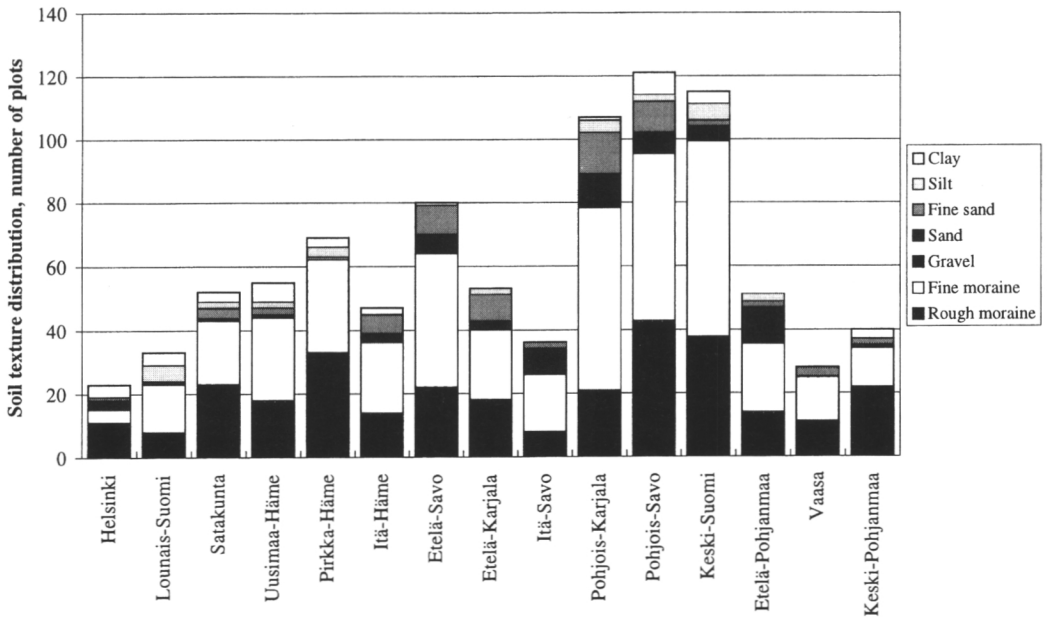


Fig. 3. Soil texture distribution in the simulation data.

ception was Scenario 0, which was based on the current climate with no temperature and precipitation changes. Scenario 1 (Medium) assumed emissions according to IS92a and a climate sensitivity of 2.5 °C, Scenario 2 (Low) assumed IS92c emissions and a climate sensitivity of 1.5 °C, and Scenario 3 (High) assumed emissions IS92f and climate sensitivity of 4.5 °C (Houghton et al. 1992). Climate sensitivity indicates how strongly the climate responds to increasing emissions of greenhouse gases. The rates of change in monthly mean temperature and precipitation were assumed to be uniform all over Finland and linear with respect to time (1990–2100) (Table 1). In practice, the scenarios presented above represent temperature changes of 4 °C (Scenario 1), 1 °C (Scenario 2) and 6 °C (Scenario 3) within a period of one hundred years.

3 Methods

The simulation model used in this study was a gap-type forest ecosystem model presented by Kellomäki et al. (1992), and further developed to utilise spatial ground-true data as input and assessed by Talkkari and Hypén (1996). Forest regeneration, thinnings and clear felling were included in this study's simulations. The growth of trees in the simulation model is based on diameter growth, which is controlled by light conditions, temperature, soil water, and the supply of nitrogen (Kellomäki and Kolström 1994).

Simulations were carried out using the site and tree data of each NFI plot as the input for the model. The site data consisted of site type and thickness of humus layer, which were used to determine the initial nitrogen content of the site, and soil texture on which the water holding capacity of the soil was based (see Talkkari and Hypén 1996). The data on trees (i.e. tree species and diameter at breast height) within a radius of 5.63 m (i.e. within an area of 100 m^2) from the centre of sample plot were included in simulations, because the current model used the plot size of 100 m^2. The height of trees in the model was calculated using the equation presented by Näslund (1937) with parameters presented by Talkkari and Hypén (1996) and the tree volume

Table 1. The SILMU policy oriented scenarios of seasonal temperature and precipitation changes over Finland, 1990–2100 (Carter et al. 1995).

	Temperature change (deg C/decade)			Precipitation change (percent/decade)		
	Scen1	Scen2	Scen3	Scen1	Scen2	Scen3
Spring (MAM)	0.400	0.100	0.600	0.500	0.125	0.750
Summer (JJA)	0.300	0.075	0.450	1.000	0.250	1.500
Autumn (SON)	0.400	0.100	0.600	1.000	0.250	1.500
Winter (DJF)	0.600	0.125	0.750	2.000	0.420	2.500

was calculated using the equations of Laasasenaho (1982). The data collected from the nearest point on the interpolated grid to the sample plot were used as temperature and precipitation data.

Felling rules were adapted from the management instructions for private, non-industrial forestry prepared by Forestry Centre Tapio (Luonnonläheinen... 1994). Thinning instructions vary by stand location (i.e. southern or northern Finland), site type, dominant species, and the limits are defined based on stand dominant height and basal area (Luonnonläheinen... 1994). Clear-felling limits are based on the mean stand diameter and they vary by stand location (i.e. southern or northern Finland), site type, and dominant tree species (Luonnonläheinen... 1994). No limitations to felling, e.g. reduced felling or conservation areas, were included in this study.

The simulation time covered the period 1990–2100. Since the model includes stochastic processes such as the birth and death of trees, each stand simulation was repeated fifty times in order to determine the prevailing tendency in stand development. Thus, the results for each sample plot are the means of fifty simulations.

The plotwise results of the model computations were stored in a database in order to generalise the predictions to apply each of the forestry board districts. The regional predictions were presented as the mean values of the simulation results for the sample plots located within each forestry board district. The regional results of this study were presented as sums of the results for the main tree species in Finland i.e. Scots pine, Norway spruce, pendula birch and pubescent birch.

4 Results

4.1 Initial Conditions

The regional stand volumes based on the simulation data at the onset of the simulation in 1990 varied from 75 $m^3\ ha^{-1}$ in the forestry board district of Keski-Pohjanmaa to 183 $m^3\ ha^{-1}$ in Lounais-Suomi (Table 2).

When compared to the inventory data, the regional stand volume based on the simulation data were systematically greater than stand volume based on the national forest inventory (NFI) re-

Table 2. Stand volumes by forestry board district at the onset of the simulations based on the simulation data and national forest inventory results (Kuusela and Salminen 1983, Salminen 1993).

Forestry board	Number of plots	Stand volume (simulation data) $m^3\ ha^{-1}$	Stand volume (NFI) $m^3\ ha^{-1}$
Helsinki	23	136	139
Lounais-Suomi	33	183	128
Satakunta	52	139	114
Uusimaa-Häme	55	155	150
Pirkka-Häme	69	125	127
Itä-Häme	47	172	140
Etelä-Savo	80	144	132
Etelä-Karjala	53	155	121
Itä-Savo	36	153	134
Pohjois-Karjala	107	102	85
Pohjois-Savo	121	125	96
Keski-Suomi	115	112	99
Etelä-Pohjanmaa	51	114	81
Vaasa	28	123	94
Keski-Pohjanmaa	40	75	65

sults. The simulation data consisted of data collected from sample plots located on mineral soil sites representing forest land, whereas inventory results are based on data collected from a great number of sample plots located on both mineral soil sites and on peatland, and this can lead to systematic differences. In two regions (Helsinki and Pirkka-Häme) the stand volume based on simulation data at the onset of the simulations was smaller than that based on inventory results, but the difference was only 2–3 m^3 ha^{-1}.

4.2 Regional Results

Regional predictions are presented using the mean values of the simulation results for sample plots located within each forestry board district. The regional mean values for stand volume, wood production and growth, and cutting yield under climate change scenarios at the end of the simulations were compared to those under the current climate.

The mean stand volume under the current climate (Scenario 0) varied between 125 m^3 ha^{-1} and 140 m^3 ha^{-1} in all the fifteen forestry board districts (Fig. 4). The stand volume under Scenario 2 at the end of the simulations was very close to that under the current climate, but under Scenarios 1 and 3 the growing stock remained at a clearly lower level than under the current climate. On comparing Scenarios 1 and 3, it was revealed that in the southern part of the study region the growing stock under Scenario 3 remained at a higher level than under Scenario 1, but in the eastern and western parts of the study region the situation was the opposite.

Annual average simulated growth under the current climate varied between 4.9 and 6.0 m^3 ha^{-1} and it was compared with annual growth given by the NFI results (Salminen 1993, Tapion Taskukirja 1991) (Table 3). The difference in annual growth between the simulations and the NFI results varied within the range of 0.2–2.1 m^3 ha^{-1} (Table 3). In the nine southernmost forestry board districts (from Helsinki to Itä-Savo) the relative difference in growth varied between 3.6 % and 14.0 %. In eastern and western parts the relative difference in growth varied between 17.7 % and 68.5 % (Table 3). The large differ-

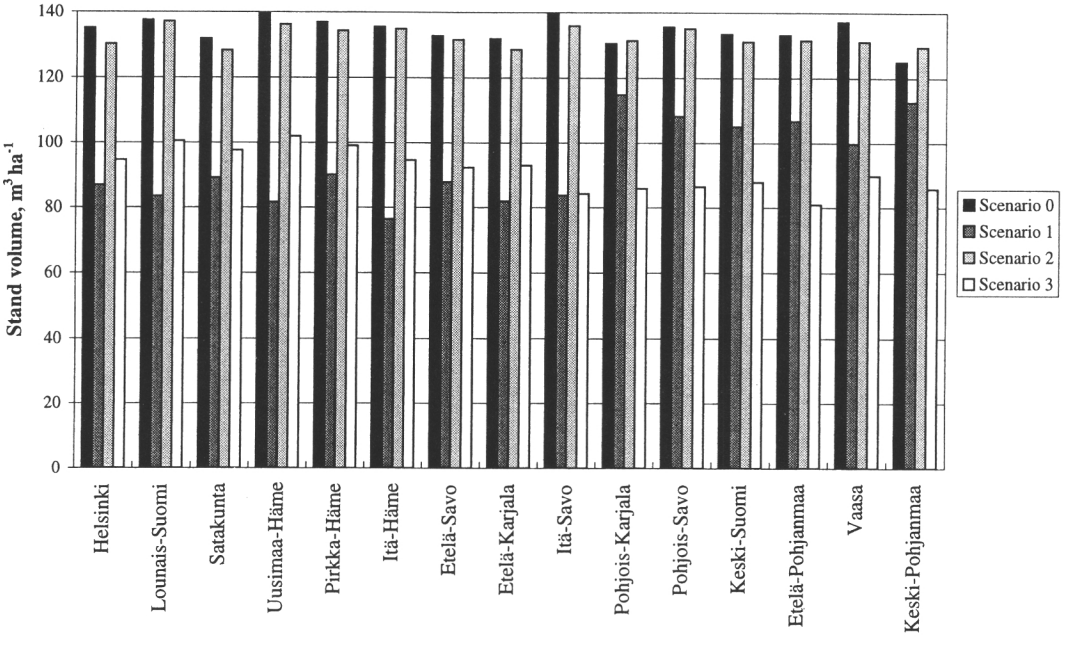


Fig. 4. Stand volume at the end of the simulations in year 2100.

Table 3. Annual average simulated growth under the current climate as compared to national forest inventory results (Salminen 1993, Tapion Taskukirja 1991).

Forestry board	Simulation $m^3\ ha^{-1}$	Inventories (NFI) $m^3\ ha^{-1}$	Difference $m^3\ ha^{-1}$	Difference %
Helsinki	5.8	6.1	–0.3	–5.3
Lounais-Suomi	6.0	5.7	0.3	5.5
Satakunta	5.8	5.1	0.7	14.0
Uusimaa-Häme	5.9	6.7	–0.8	–12.1
Pirkka-Häme	5.8	5.5	0.3	5.5
Itä-Häme	5.9	6.3	–0.4	–6.7
Etelä-Savo	5.7	6.2	–0.5	–7.5
Etelä-Karjala	6.0	6.2	–0.2	–3.6
Itä-Savo	5.3	5.8	–0.5	–8.6
Pohjois-Karjala	4.9	4.2	0.7	17.7
Pohjois-Savo	5.2	4.4	0.8	19.3
Keski-Suomi	5.4	4.4	1.0	23.2
Etelä-Pohjanmaa	4.9	3.4	1.5	45.5
Vaasa	5.5	3.6	1.9	52.3
Keski-Pohjanmaa	5.1	3.0	2.1	68.5

ences in growth between simulations and the NFI results in Etelä-Pohjanmaa, Vaasa and Keski-Pohjanmaa are probably due to the large proportion of poorly growing peatland forests in those parts of the study region. According to Kuusela and Salminen (1983), the proportions of peatlands in Etelä-Pohjanmaa, Vaasa and Keski-Pohjanmaa are 39.6 %, 29.9 % and 40.9 %, respectively. Furthermore, both forest land and scrub land stands are included in the NFI-based growth in the eastern and western parts of the study regions (i.e. from Pohjois-Karjala to Keski-Pohjanmaa). Therefore, the simulation model appears to overestimate forest growth in those three forestry board districts, but elsewhere simulated growth appeared to be realistic. The average annual growth in the southern part of the study region in the simulations was 5.8 $m^3\ ha^{-1}$ and in NFI results it was 6.0 $m^3\ ha^{-1}$. Thus, the quantitative estimate of average annual growth in the nine southernmost forestry board districts, where the proportions of peatlands and scrub lands are low, is very close to national forest inventory results (Salminen 1993).

Total wood production under the current climate (Scenario 0) in the nine southernmost forestry board districts varied between 583 $m^3\ ha^{-1}$ and 662 $m^3\ ha^{-1}$ (Fig. 5). In the eastern and western parts of the study region, total wood production remained 50–100 $m^3\ ha^{-1}$ lower than in the southern part, varying between 544 $m^3\ ha^{-1}$ and 603 $m^3\ ha^{-1}$ (Fig. 5). According to Koivisto (1959), wood production in managed pure stands in southern Finland amounts to 582 $m^3\ ha^{-1}$ in Scots pine stands with a rotation of 90 years, 688 $m^3\ ha^{-1}$ in Norway spruce stands with a rotation of 110 years, and 491 $m^3\ ha^{-1}$ in pendula birch stands with a rotation of 80 years. Total wood production in the southern part of the study region under Scenario 1 remained at a lower level than under the current climate, but the results under Scenario 2 were similar to those achieved under the current climate in southern parts of the study region (Fig. 5). In eastern and western parts of the study region total wood production reached higher levels than under the current climate in all the scenarios.

In the southern part of the study region the cutting yield varied between 356 $m^3\ ha^{-1}$ and 463 $m^3\ ha^{-1}$, and in eastern and western parts it varied between 281 $m^3\ ha^{-1}$ and 348 $m^3\ ha^{-1}$ under the current climate (Fig. 6). According to

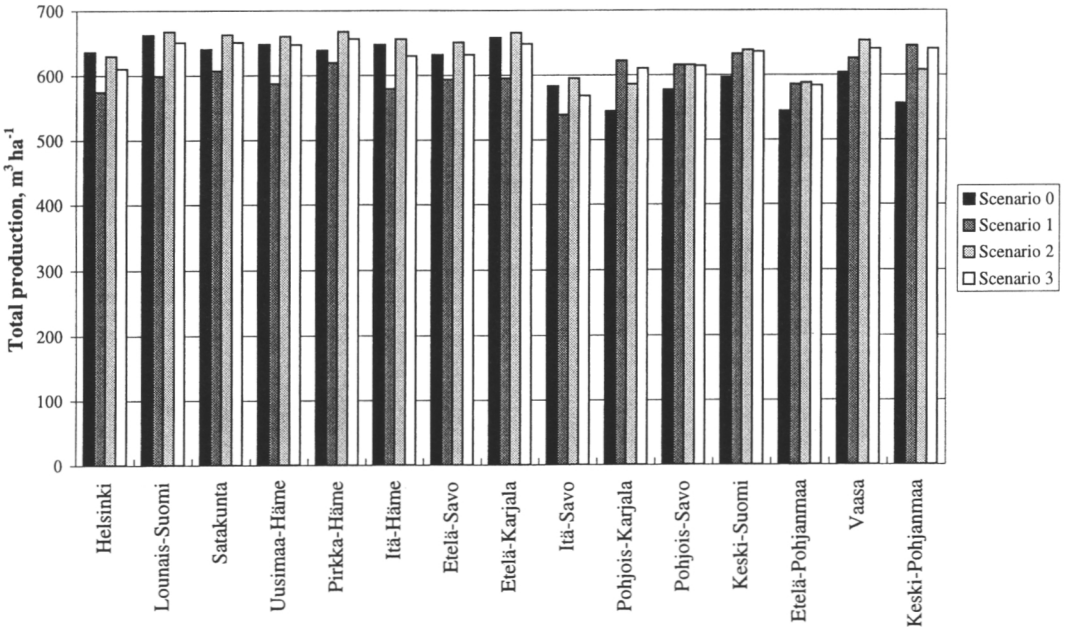


Fig. 5. Total wood production during the simulation period 1990–2100.

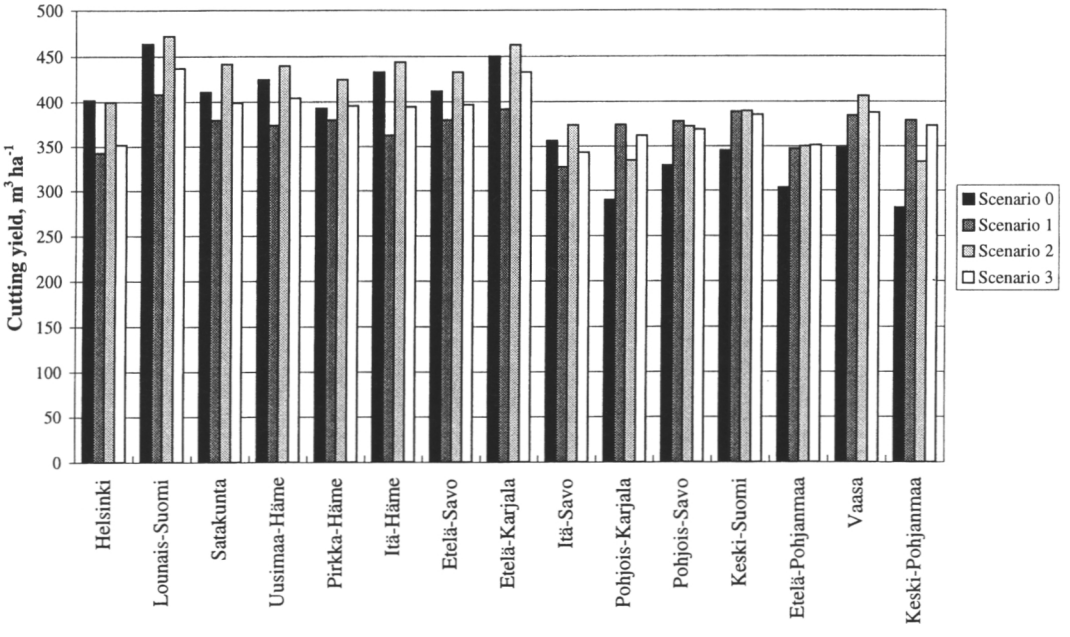


Fig. 6. Cumulative cutting yield during the simulation period 1990–2100.

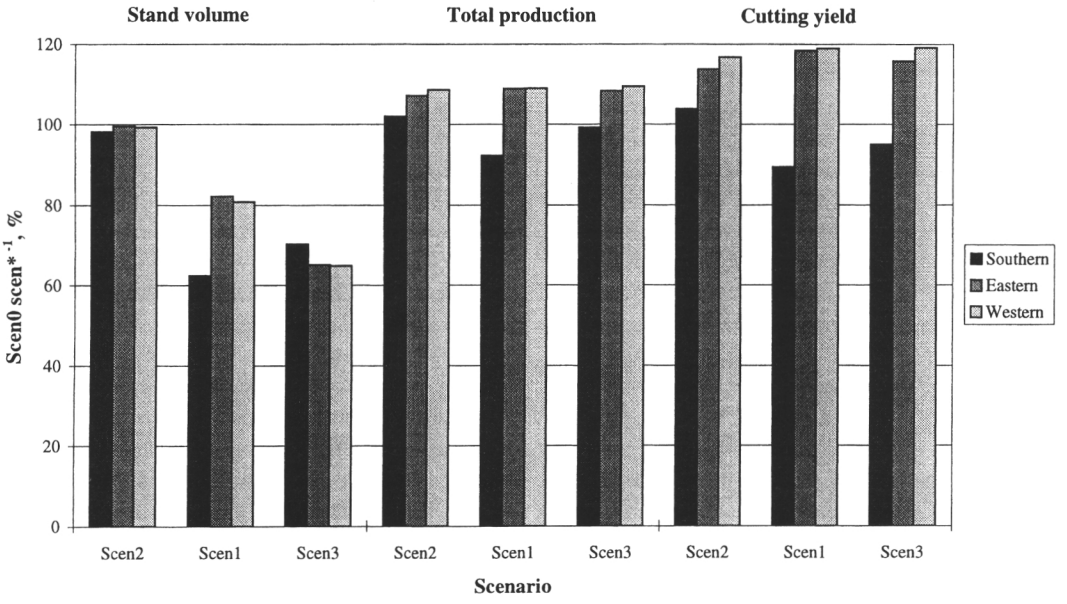


Fig. 7. Relative stand volume, total wood production, and cutting yield under climate change scenarios by southern, eastern and western parts of the study region.

Koivisto (1959), the cutting yield in managed pure stands in southern Finland is 320 m^3 ha^{-1} in Scots pine stands with a rotation of 90 years, 423 m^3 ha^{-1} in Norway spruce stands with a rotation of 110 years, and 316 m^3 ha^{-1} in pendula birch stands with a rotation of 80 years. The temperature increase in Scenarios 1 and 3 decreased the cutting yield in the southernmost part of the study region, but increased that in the eastern and western parts (Fig. 6). In most of the study region, the modest temperature increase of Scenario 2 had a positive effect on the cutting yield. In all parts of the study region the development of the cutting yield followed the development of total wood production. The diameter, basal area, and dominant height limits applied in the felling rules were reached earlier under those scenarios, where growth increased due to temperature increase.

The relative values of stand volume, total wood production, and cutting yield under the climate change scenarios as compared to the situation under the current climate by southern, eastern and western part are presented in Fig. 7. The relative values varied by part of the study region, i.e. in the southern part the relative total wood production and cutting yield remained at a lower level than in the other parts. These relative values indicate that the response of the forest to climate change varied according to geographical location and the magnitude of climate change (Fig. 7).

5 Discussion

Ground-true forest inventory and climate data were used in simulations to produce regional predictions about the effect of climate change on forests. The results of these simulations under the current climate were compared to national forest inventory results (Salminen 1993, Kuusela and Salminen 1983) and to growth and yield tables (Koivisto 1959). The quantitative regional predictions of forest annual growth, total wood production, and cutting yield under the current climate were very similar to forestry statistics data. The greatest difference occurred in stand volume. The data in this study consisted of a subset of NFI's permanent sample plots located

on mineral soil sites representing forest land. The results of forest statistics comprise data on forest stands on both mineral soils and peatlands. Thus, the simulations gave overestimations compared to forest statistics. Furthermore, the comparison of simulations and inventory results was even more difficult when scrub land sites were also included in the inventory results concerning the eastern and western parts of the study region.

Only natural regeneration was included in the simulation model, i.e. the establishment of new seedlings was controlled by environmental conditions without any man-made tree species selection. This can alter the tree species composition, which was not, however, examined in this study. The felling rules applied were adopted from the management instructions for private, non-industrial forestry (Luonnonläheinen... 1994). There were no restrictions to felling; i.e. stands were thinned or clear-felled once the limits were reached. This can increase the cutting yield more than happens in practice.

However, the realistic predictions achieved under the current climate indicated the model's ability to work with forest inventory data and it provided a basis for comparing the climate scenarios. The predictions under Scenario 2 (Low) were similar to those under the current climate. In many forestry board districts forest growth was slightly higher under Scenario 2 than under the current climate. This indicated that forests derived a little benefit from the temperature increase of 1 °C in the space of one hundred years. Greater differences were observed between the current climate and Scenario 1 (Central). The growing stock remained at a lower level under Scenario 1 than under the current climate in all parts of the study region.

In wood production and cutting yield there were regional differences. In the southern part of the study region wood production under Scenario 1 was ca. 10 % lower than under the current climate, but in the eastern and western parts wood production was 5–15 % higher under Scenario 1 than under the current climate. This indicated that forests in the central part of Finland could increase their growth due to climate change. The results under Scenario 3 were similar to those achieved under Scenario 1; the exception was that stand volume at the end of the simulations remained at a clearly lower level in the eastern and western parts of the study region and slightly higher level in the southern part. This may be due to increased growth of birch caused by temperature increase.

The relative values of total wood production and cutting yield indicated that the response of forests to climate change varied by geographical location and the magnitude of climate change. This may be a consequence of not just varying climatic (e.g. temperature and precipitation) and site conditions, but of varying responses by different kinds of forests (e.g. forests differing tree species composition and age). Thus, further computations concerning possible changes in tree species distribution and response of tree species to climate change could clarify the results presented above.

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Assessment of CO_2 Fluxes and Effects of Possible Climate Changes on Forests in Estonia

Malle Mandre, Hardi Tullus, Vaike Reisner and Jaan Kõšeiko

The present study is the first attempt to carry out an inventory of greenhouse gas (GHG) fluxes in the forests of Estonia. The emission and uptake of CO_2 as a result of forest management, forest conversion and abandonment of cultivated lands in Estonia was estimated. The removal of GHG by Estonian forests in 1990 exceeded the release about 3.3 times. Changes in the species composition and productivity of forest sites under various simulated climate change scenarios have been predicted by using the Forest Gap Model for the central and coastal areas of Estonia. The computational examples showed that the changes in forest community would be essential.

Keywords climate change, forest composition, Forest Gap Model, forestry, greenhouse gases

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1 Introduction

Climate change and a realistic assessment of CO_2 release from and uptake by forests have been considered major environmental problems during the last decades. Although the problem has a global importance, it is particularly essential for countries rich in forests.

The total area of the Republic of Estonia, including areas of inland water, is 4 523 000 hectares, of which land area is 4 310 000 hectares (Statistical Yearbook 1994, Karoles et al. 1994). On 1 January 1994, the area of productive forest land was 2 016 600 ha, of which about 1.9 Mha was actually forested (Forestry... 1995). During the last half-century the area of forest stands has more than doubled and will be increasing in the nearest future. In 1993 the forest cover was 47.7 %. The current total increment of solid wood over bark in forests is estimated at 9.6 Mm^3/yr, corresponding to about 4.8 m^3/ha/yr on productive forest land. The area of forest land has been gradually increasing (Fig. 1) mainly due to abandonment of agricultural lands.

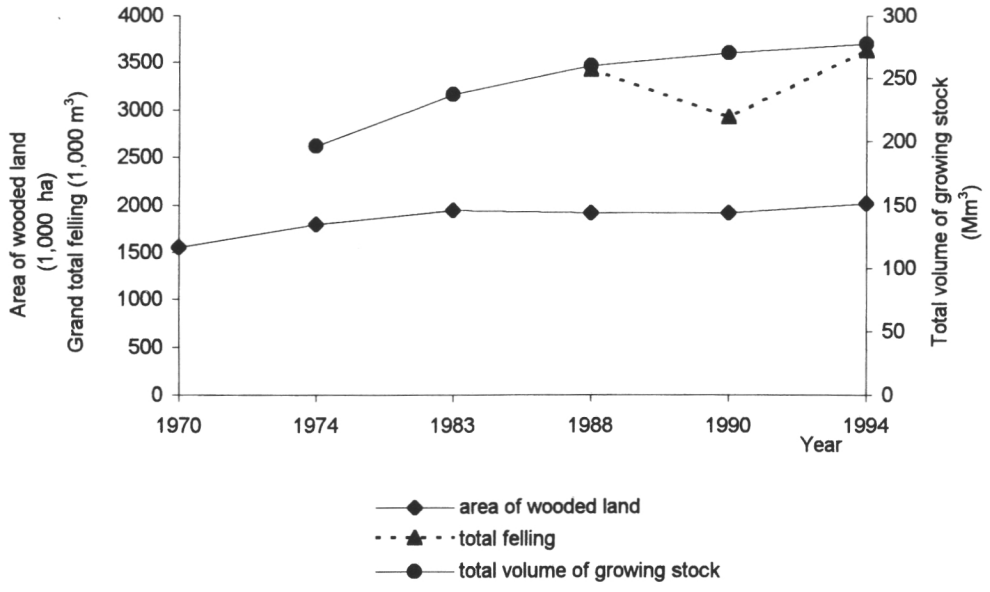


Fig. 1. Changes in wooded land, volume of growing stock and grand total felling (Karoles et al. 1994, Statistical yearbook 1994, Forestry... 1995).

In 1993 the total volume of standing growing stock in closed forests was reported to be 277 Mm^3. Coniferous forests make up 63 % of the total area of the Estonian forests and 66 % of the total forest yield and deciduous forests 37 % and 34 % respectively (Statistical Yearbook 1994) (Fig. 2).

At the present time 87 native and over 500 introduced tree and shrub species have been recorded in Estonia (Karoles et al. 1994). The main coniferous tree species are Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst.). Deciduous trees are represented by several species of birches (*Betula pendula* Roth, *B. pubescens* Ehrh.), speckled alder (*Alnus incana* (L.) Moench), aspen (*Populus tremula* L.) and black alder (*Alnus glutinosa* (L.) Gaertn.). Other broad-leaved trees, e.g. oak (*Quercus*), ash (*Fraxinus*), linden (*Tilia*), elm (*Ulmus*) make up only 1 % of the standing volume (Supply, production and costs... 1994) (Fig. 2).

During the last decade (from 1980 to 1991) the average annual cut reached 3.2–3.4 Mm^3. After that the harvested volume decreased and was estimated at about 2 Mm^3 for 1992 but in 1994 the cut increased again and was estimated at about 3.6 Mm^3 (Fig. 1).

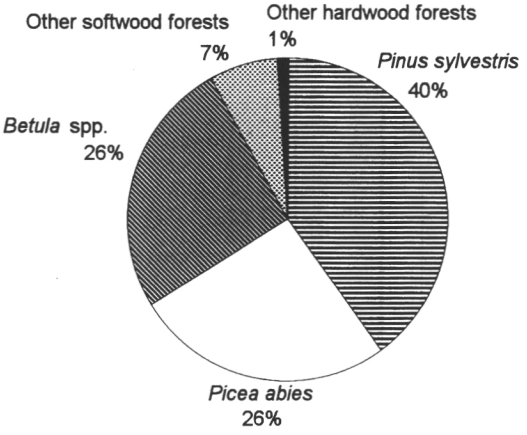


Fig. 2. Distribution of predominant forest tree species according to yield in Estonia.

About 100–200 000 ha has been reported as former agricultural land, abandoned during the last decades and covered mainly with bushes.

The aims of present study were to assess the release and uptake of CO_2 by forests in Estonia at the present time, to evaluate possible changes in the species composition and productivity of

forests under doubled atmospheric CO_2 and climate warming predicted for the future. The study was launched in 1994 as a part of the U.S. Country Studies Program by using the calculation methods and Forest Gap Model recommended by the program (IPCC... 1994, Guidance for... 1994).

2 Assessment of CO_2 Release and Uptake

Principles and Methods

There are notable uncertainties in all the current methods for estimating fluxes of greenhouse gases from forests and land use change. The simplified method for the estimation of CO_2 and other GHG fluxes which has been recommended by the IPCC/OECD Programme on the Development of a Methodology for National Inventories of Net Greenhouse Gas Emissions was used in the present study (IPCC guidelines... 1994).

In the calculations of the CO_2 budget in Estonian forests three main factors were considered:

1. changes in forest and other woody biomass stocks
2. forest conversion
3. abandonment and natural or artificial afforestation of former farm lands.

1990 ± 1 is designated as a base year for the calculation of CO_2 emission and uptake. Since radical changes have been taking place in Estonian economy from 1990, the inventory of CO_2 fluxes was also carried out in 1994 and comparative dynamics of processes was estimated. The data of the Estonian Forest Department, Estonian Forest Survey Centre, Estonian Forest Institute and Faculty of Forestry of the Estonian Agricultural University have been used in the inventory calculations. According to the methodological requirements current emissions of CO_2 from biomass left to decay were estimated over the previous decade (1980–1990). Emissions from soils due to conversions were estimated over previous 25 years (1965–1990). For the immediate release from burning the data of 1990 were used. In 1994 no forest conversion took place and thus no immediate release from burning occurred. To estimate the CO_2 release from abandoned managed lands for a base year the data for 1970–1990 and for 1994 the data for 1974–1990 were used.

In the 1990 inventory the areas converted under ditches with forest roads have been considered as forest conversion because of absence of other conversion types in Estonian land use. In 1994 the situation was completely changed: under the new economic situation the drainage and road building in forests had stopped. This is due to the uncertainties in the fate of forest land because of the continuous process of returning lands to private owners is under way. Forest conversion did not take place during the period of privatization and the ongoing process of restructuring the socio-economic system offers good possibilities for decreasing CO_2 emission.

Due to the changes in forest management the volume of fellings had grown in 1994 in comparison with the base year (1990) mainly because of the increased consumption of fuel wood. Accordingly, the total felling in 1994 was 3626.2 thousand m^3 (Fig. 1), out of which 1414.3 thousand m^3 was used for fuel. Unfortunately the methodology used does not consider the fate of harvested material except of those used as fuel wood. Compared to 1990 the growth in total felling is 24 % and in fuel consumption 33 % (Forestry... 1995).

The calculations used:

1. Annual biomass C uptake (t C/yr):
   $U = AP \times GP \times CP$
   where
   AP = area of managed forests (ha)
   GP = annual biomass growth rate (t dm/ha/yr)
   CP = C fraction for managed forests (t C/t dm) (biomass C fraction = 0.45; default value from IPCC guidelines (1994))

2. Annual biomass C removal (t C/yr):
   $R = ((RW \times EF) + FW + OW - FC) \times C$
   where
   RW = roundwood harvest (m^3/yr)
   EF = biomass conversion/expansion factor (t dm/m^3) (default values for converting volume data to tons are 0.65 t dm/m^3 for deciduous trees and 0.45 t dm/m^3 for conifers (IPCC guidelines 1994); 2/3 of

the Estonian forests are coniferous (Statistical Yearbook 1994), hence the conversion ratio = $2/3 \times 0.45 + 1/3 \times 0.65 = 0.5$)

FW = annual fuel wood consumption (t dm/yr)
OW = other wood use (t dm/yr)
FC = wood removed from forest clearing and burned off-site (t dm/yr)
C = C fraction (t C/t dm)

3. Total C released by burning aboveground biomass on- and off-site (t C/yr):
$COn = A \times (BB - BA) \times FBn \times FOn \times C + A \times (BB - BA) \times FBf \times FOf \times C$
where
A = area converted annually (ha/yr)
BB = biomass density before conversion (t dm/ha)
BA = biomass density after conversion (t dm/ha)
FBn = fraction of biomass burned on site
FOn = fraction of biomass oxidized on site (fraction of biomass oxidized during burning both on- and off-site = 0.90; default value from IPCC guidelines (1994))
FBf = fraction of biomass burned off site
FOf = fraction of biomass oxidized off site
C = C fraction (t C/t dm)

4. Total C released by decay of aboveground biomass (t C/yr):
$CD = AA\text{-}10 \times (BB - BA) \times FD \times C$
where
AA-10 = 10-year average annual area converted (ha/yr)
BB = biomass density before conversion (t dm/ha)
BA = biomass density after conversion (t dm/ha)
FD = fraction left to decay
C = C fraction (t C/t dm)

5. Total C released from soil (t C/yr):
$CS = AA\text{-}25 \times SC \times FR$
where
AA-25 = 25-year average annual area converted (ha/yr)
SC = soil C fraction before conversion (t C/ha) (C in soil per unit forest area = 185 t C/ha; although, in Estonian forests the soil carbon content ranges from 44 to 192 t/ha (Kylli 1988) the default value recommended by IPCC guidelines (1994) has been used in calculations)
FR = fraction released over 25 years (fraction C released from soil following forest conversion = 0.5/25 yrs; default value from IPCC guidelines (1994))

6. Annual C uptake in soils, ≤ 20 years (t C/yr):
$CSL = AY \times RS$
where
AY = total area abandoned and regrown during last 20 years (ha)
RS = annual rate of C uptake in soils (t C/ha/yr) (average annual soil C accumulation per unit area regenerating = 1.8 t C/ha/yr; default value from IPCC guidelines / 1994/)

7. Annual C uptake in aboveground biomass, ≤ 20 years (t C/yr):
$CBL = AY \times RB \times C$
where
AY = total area abandoned and regrown during last 20 years (ha)
RB = annual rate of aboveground biomass accumulation (t dm/ha/yr)
C = C fraction of biomass (t C/t dm)

Results

The calculation results showed that CO_2 uptake by Estonian forests in 1990 exceeded 3.3 times its emission.

It became evident that while compared to 1990 the emission of CO_2 has decreased and removal has increased during these four years. CO_2 emission due to commercial harvest and fuel wood consumption had increased by 7 % (Table 1). Taking into account the changes over the four year period, the emission from Estonian forests had increased by 1 %. Annual removal of CO_2 from Estonian forests in 1994 was 11089 Gg. This is 2 % lower than in 1990 (Table 1).

Net CO_2 uptake by Estonian forests in 1994

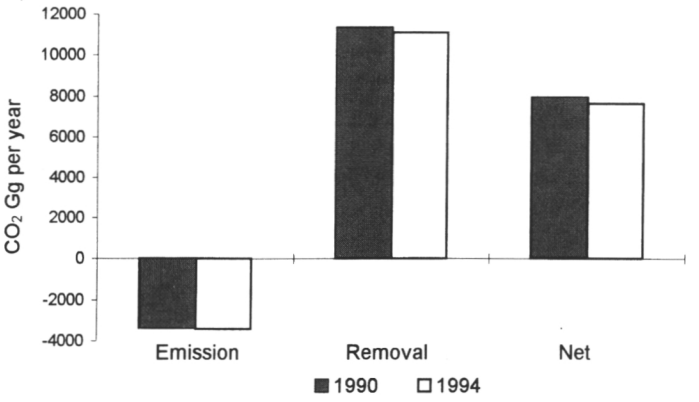


Fig. 3. CO_2 emission and removal.

Table 1. Dynamics of removals/emissions (Gg) of CO_2 due to forestry and land use change from 1990 to 1994.

		1990		1994	
		Removal	Emission	Removal	Emission
Forest management	Biomass growth increment	7438.27	-	8602.47	-
	Harvest	-	2791.01	-	2989.14
Forest conversion	On- and off-site burning	-	62.73	-	0
	Decay	-	33.82	-	19.32
	Soil	-	508.75	-	420.57
Abandoned managed lands	Aboveground biomass	1642.70	-	1045.04	-
	Soil	2265.78	-	1441.44	-
Total		11346.75	3396.31	11088.95	3429.03

was estimated at 7660 Gg, which is 4 % lower than in 1990 (7950 Gg CO_2) (Fig. 3).

Although the net emission of CO_2 in 1994 had not changed in comparison with 1990, great differences in the balance of land use and forestry categories were observed (Table 1). The ratio removal/emission was 3.34 in 1990. In 1994 it was 3.23. The 3 % decrease in the ratio removal/emission indicates a possible growing trend in the CO_2 emission.

3 Prognosis of the Dynamics of Forest Community under Climate Change

Atmospheric CO_2 concentrations are the net result of continuous emissions and sequestration that occur through natural processes and human activity. Models of global climate change suggest a doubling of the present atmospheric CO_2 with a 4 °C mean rise in global temperature within the next 100 years (Manabe and Wetherald 1980).

The importance of climatic factors in the function and structure of the boreal forests is well

Table 2. Basic parameters used to define species attributes in the FGM.

Species	Max. observed diameter, m	Max. observed age, yr	Max. observed height, m	SEDmax	L	minPET ratio
Picea abies	1.5	350	47	50	1	0.94
Pinus sylvestris	1.7	450	40	40	3	1.20
Quercus robur	2.5	999	39	20	2	1.10
Betula pendula	0.7	150	31	100	3	0.98
Betula pubescens	0.6	120	25	100	2	0.97
Populus tremula	1.0	200	34	40	3	1.00
Alnus glutinosa	1.2	200	30	20	2	0.94
Alnus incana	0.5	70	20	40	1	0.98

Max. diameter (Laas 1967, Paal et al. 1989).
Max. age (Laas 1967, Tappo 1982, Paal et al. 1989).
Max. height (Laas 1967, Paal et al. 1989).
SEDmax – maximum yearly seedling establishment scaled to plot (Laas 1967, Holdridge 1967).
L – light response category: 1 – shade tolerant, 2 – intermediate, 3 – shade intolerant (expert estimation).
minPET ratio – potential evapotranspiration (PET) allowing tree growth, as species specific bioclimatic index of drought tolerance. It is the quotient of PET and average annual precipitation (Holdrige 1967).

Table 3. Incremental climate change scenarios for central Estonia and coastal area of Western Estonia.

Regions, climatic parameters	Location	Scenario 0: present climatic conditions*	Scenario 1: +4 °C	Scenario 2: +4 °C, –10 % AP	Scenario 3: +4 °C, +10 % AP
Tudu	59°12' N 27°00' E				
GDD		2257	3264	3264	3264
PETratio		0.72	0.88	0.98	0.8
AP		670	670	604	737
Virtsu	58°36' N 23°30' E				
GDD		2503.7	3609.9	3609.9	3609.9
PETratio		0.82	1.01	1.12	0.92
AP		620	620	560	682

GDD – annual sum of growing-degree days = yearly sum of daily mean temperatures above 0 °C.
PETratio – potential evapotranspiration ratio, mm/mm.
AP – annual precipitation, mm.
* Data of J. Jaagus from the Institute of Geography, University of Tartu.

known and applied in managing forest resources. The trend of climate warming would greatly affect the plants and plant communities.

Generally the computer simulations have indicated that doubling of the atmospheric CO_2 and climatic warming could increase the productivity of tree stands in the boreal zone (Kellomäki et al. 1988, Kellomäki and Kolström 1992, Solomon and Leeman 1990), although some simulations showed a decrease in total forest biomass (Pastor and Post 1988, Overpeck et al. 1990, Lasch and Lindner 1995). It is logical that the character of forest responses to climate changes depends on the physiological tolerance of tree species and several edaphic factors.

Plant communities could respond to changes in climate and increased CO_2 as a function of changing competitive advantages among species (Solomon and Cramer 1993). Given that long sets on forest timescale dynamics are incomplete

in simulations what yet facilitate the study of forest growth and demography. Using the Forest Gap Model for simulating a range of the dynamics of forest composition and diversity under various exogenous disturbance climatic regimes are found. We examined the sensitivity of forest trees to climate warming and changes which may occur under doubled CO_2.

Model Description and Species-Specific Parameters

In determining the responses of predominant species of Estonian forests to changes in environmental conditions (doubling of CO_2, increase of temperature and annual precipitation) the simple version of the Forest Gap Model (FGM) (Botkin et al. 1972, Shugart 1984), recommended by the U.S. Country Studies Program was used. The Holdridge Life Zones Classification Models mapping in triangular coordinate system (Holdridge 1967) was also used to determine the potential evapotranspiration ratio for forest ecosystem types and species.

The FGM evaluates changes in the species composition and productivity of species in forested sites of areas smaller than 1 ha. FGM simulates the establishment, growth and mortality of individual trees on a forest stand on an annual time step and is capable of simulating stands with mixed-species and mixed-age population.

The potential growth of each tree is estimated from species-specific optimal growth curves, derived from silvicultural data on maximum tree size and longevity (Botkin et al. 1972, Shugart 1984). The environmental conditions on the plot (e.g. light, available moisture, resource depletion, temperature) modify the optimal growth of the tree in a stand. The interaction of responses of yearly diameter increment to the changing environmental conditions is computed through the product of all growth factors.

Main attention was paid to the evaluation of the changes in the species composition and of the tolerance of forest trees under various climate change scenarios in Central Estonia (Tudu) and in the coastal area of Western Estonia (Virtsu), which differ in the present climatic and landscape character.

The parameters of eight predominant forest trees (species) in Estonia that were used in the FGM for modeling biomass and species composition dynamics under the potential climate changes for both regions are given in Table 2. Stand simulations were done with nine plots for each region with yearly time step during 250 years.

Into the modeling framework four climate change scenarios were incorporated (Table 3). According to FGM possibilities the transient climate change was applied before forest growth and the forest development began from bare ground under already changed climate.

Results

In the simulation of long-term forest development (250 years) our analyses showed significant potential changes in forest community structure for two different regions of Estonia under various climatic conditions (Fig. 4). Competition, succession and changes in species composition as a function of time and climate may be predicted by the given version of FGM under the baseline scenario.

1. *Scenario 0.* In certain points of investigation the present climatic conditions have been used. The results of modeling showed an intensive growth of forest during the first 50–70 years, which is in accordance with the real data on mature and overmature forests in Estonia (Tappo 1982, Yearbook of Forest 1995). A slight decline in the stand and biomass followed after 100 years. In the first period of forest development the pioneer community consisted mainly of birch. After 100 years the predominance of deciduous trees will be replaced by Norway spruce in Central Estonia or by mixed stands in the coastal area.

2. *Scenario 1.* The warming of climate by 4 °C causes essential changes in forest structure. Scots pine seems to the most tolerant to warming of climate and would appear in Central Estonia as a predominant species. During the first one hundred years the high number of birch and aspen could be noticed, but their share decreases with the ageing of forest. In the coastal area the warming of climate favours only the development of

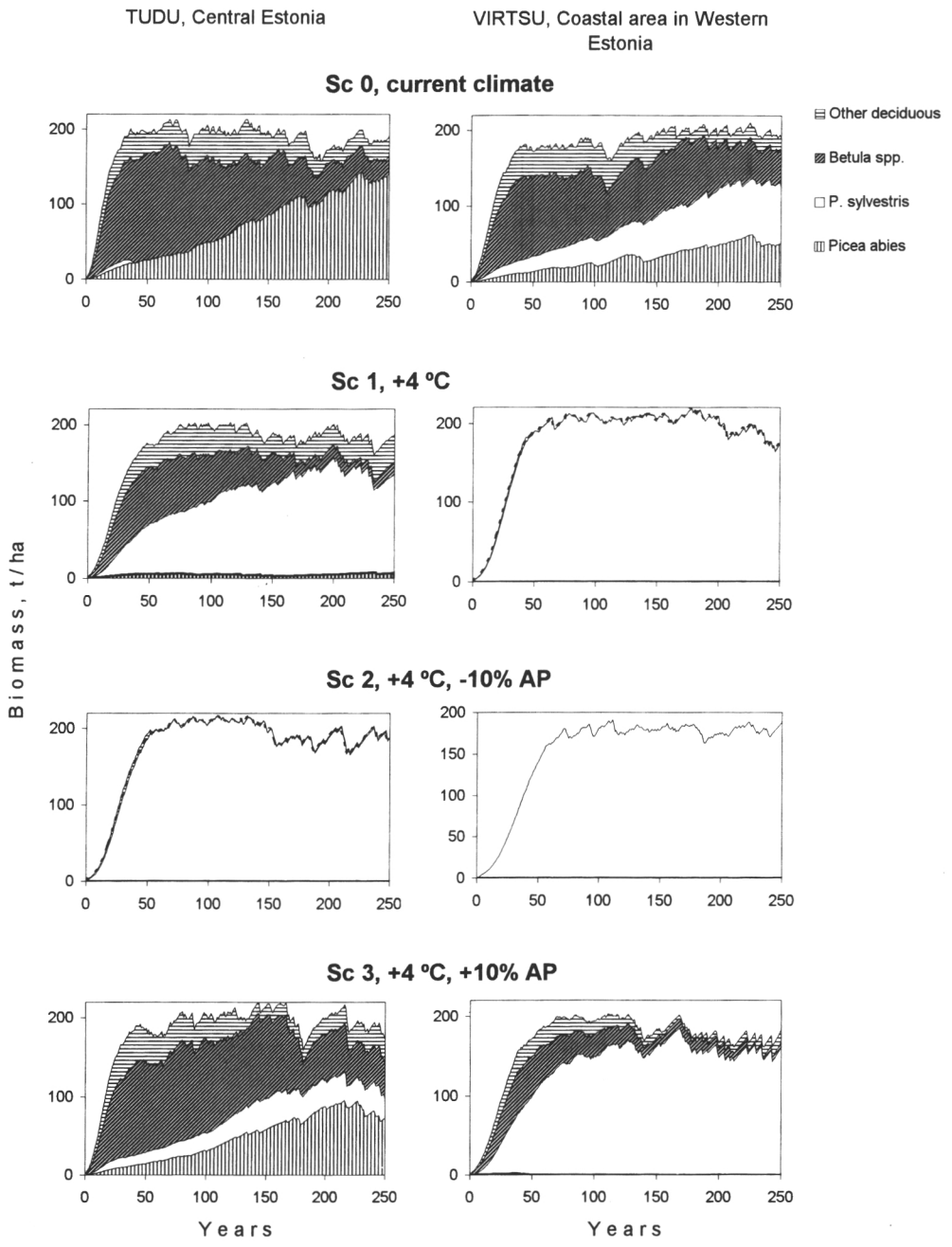


Fig. 4. Possible alterations in the forest community structure under simulated scenarios of climate change in Estonia.

Scots pine with an inconsiderable share of oak.

3. *Scenario 2*. At the increase of temperature and decrease of annual amount of precipitation the growth of the most drought tolerant species should be possible – Scots pine and oak in Central Estonia, Scots pine in the coastal area.

4. *Scenario 3*. Increase in both temperature and the amount of precipitation favours an intensive growth of deciduous trees during the first 120–170 years. In Central Estonia during the later development of the forest ecosystem deciduous trees will be replaced by Norway spruce. Here is an analogy with scenario 0. In the coastal area the predominant trees in the forest site are Scots pine and deciduous trees to some extent.

It can be seen in the simulations of climate changes that the effect may be considerable on forest species composition. Scots pine, oak and birch seem to be rather tolerant to the increase of temperature and changes in the amount of precipitation level.

4 Discussion

The calculation results showed that CO_2 uptake by Estonian forests exceeds its emission at the present time. The prognosticated doubling of the CO_2 concentration and the accompanying climate change raise the question of the capability of forests of counteracting the increased amounts of CO_2 and surviving under the changed climatic conditions. A number of models and scenarios have been compiled to forecast possible changes in forests.

The used FGM summarizes the results with respect to the ecology of tree species. In our modeling framework only predominant native species occurring in Estonia were used. Exotic and rare native ones were avoided.

Our results suggest that *Pinus sylvestris*, having a broad ecological area of distribution, showed the highest tolerance to climate warming and decreasing amount of precipitation (Scenarios 1, 2). An increase of the mean temperature by 4 °C and of precipitation by 10 % may result also in an increase of the biomass of several deciduous tree species (*Betula* spp., *Quercus robur, Populus tremula*) (Scenario 3), although the total biomass of sites may decrease in all modelled scenarios. Decreasing of forest biomass by climate changes may lead to disturbances of the balance of CO_2 emission and removal. Changes in forest structural composition and possible inhibition of forest biomass formation raised problem of sequestration facilities of enhanced CO_2 by forests in the future.

Although the results of modeling by FGM show some inhibition of forest biomass and serious changes in species composition, we are afraid that projections presented in this paper should not be interpreted as realistic predictions of future forest dynamics.

A logical consequence of such a situation would be the replacement of the present species in forest ecosystems by those of more southern distribution. If the mean annual temperature increased by 4 °C and the mean annual precipitation by 10 %, which is generally predicted, the climate in the region of Estonia could resemble that of southern Poland or central Germany. The replacement of contemporary species may take place and the area of hardwood forests may thus become wider in Estonia. The possible immigrants to Estonian forests community may be *Fagus silvatica, Carpinus betulus, Quercus petraea* and *Ulmus carpinifolia*. The forest communities in Estonia will probably change towards the *Fagion, Carpinion* or *Quercion* types and the total biomass of forest may increase.

Although gap models have been used and modified by several authors (Botkin et al. 1972, Shugart 1984, Urban et al. 1991, Urban and Shugart 1992), some shortcomings in the simulation of forest dynamics by FGM may lead to unsatisfactory results. Lasch and Lindner (1995) conclude from a comparison and modification of two gap models that with currently available models realistic forest dynamics within different climatic zones cannot be simulated without quite substantial model modifications. In Estonia, the heterogeneity of the landscape, particularly the distribution of various soils, will become an important factor determining forest responses to climate change. The incorporation of some vital parameters such as characteristics of landscape, soil and other nutritional factors controlling forest productivity into the model could help overcome these shortcomings. As the applied FGM

simulates the growth and mortality of individual tree species in sites, the seasonal timing of morpho-physiological processes, physiological tolerance of species to frost in boreal zones might be suitable to improve the forest succession simulations.

Our calculations reflected a strong response of forests to climate warming, revealed in both the composition and age structure of forest stands. The simulation of possible impacts of climate change for Estonian forests is only preliminary and prior to taking any preventive measures it is advisable to continue with improved climate scenarios and further model development.

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Economic Impacts of Carbon Sequestration in Reforestation: Examples from Boreal and Moist Tropical Conditions

Anssi Niskanen, Olli Saastamoinen and Tapio Rantala

The impact of carbon sequestration on the financial profitability of four tree plantation cases in Finland and the Philippines were examined. On the basis of stem wood growth; the accumulation of carbon in forest biomass, the formation and decomposition of litter, and the carbon flows in wood-based products were assessed for each reforestation case representing boreal (Finland) and moist tropical conditions (the Philippines). Using different unit values for carbon sequestration the profitability of reforestation was estimated for a fixed 100 year period on a per hectare basis. The financial profitability of reforestation increased notably when the sequestered carbon had high positive values. For example, when the value of carbon sequestration was set to be Twenty-five United States Dollars per megagram of carbon (25 USD/Mg C), the internal rate of return (IRR) of a reforestation investment with spruce (*Picea abies*) in Finland increased from 3.2 % to 4.1 %. Equally, the IRR of reforestation with mahogany (*Swietenia macrophylla,* King) in the Philippines increased from 12.8 % to 15.5 %. The present value of carbon sequestration ranged from 39–48 % and from 77–101 % of the present value of the reforestation costs in Finland and the Philippines, respectively, when a 25 USD/Mg C shadow price and a 5 % discount rate were applied. Sequestration of one Mg of carbon in reforestation in Finland and the Philippines was estimated to cost from 10.5–20.0 and from 4.0–13.6 USD, respectively.

Keywords plantation forestry, carbon, profitability, environment, boreal, tropical, Finland, Philippines

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1 Introduction

The potential of forest plantations in the global stabilisation of the carbon dioxide balance of the atmosphere has been discussed and outlined in many contexts (e.g. Sedjo 1989, Vitousek 1991, Woodwell 1992). If forest plantations were used purposefully to sequester carbon the impact on the CO_2 balance could be substantial. In theory, it is even possible to compensate for all of the carbon released in fossil fuel combustion and deforestation by plantations. According to Vitousek (1991) that would require afforestation of approximately 800 million hectares, assuming that forest plantations can sequester carbon at a rate of 7.5 Mg C/ha/yr.

The role of forest plantations in carbon sequestration have been examined in some country specific studies. In New Zealand, the annual storage of carbon for 1988–89 in forest plantations of 1.24 million hectares was estimated to be 3.6 million tonnes after harvest, equivalent to 70 % of New Zealand's total fossil fuel emissions, but less than 0.1 % of the total global fossil fuel emissions (MacLaren et al. 1993). Similarly in Britain, the rate of carbon removal by 1.3 million hectares of plantation forests in 1990 was estimated to be 2.5 million tonnes, representing only 1.5 % of Britain's annual carbon emissions (Cannell and Dewar 1995). The carbon storage capacity of short rotation tropical plantation species has also been examined (e.g. Schroeder 1992).

Technically, the flows of carbon associated with reforestation are dependent on similar factors to those in natural forest management: carbon stored in the woody biomass of living, growing trees, accumulation of carbon on soil and timber products, and the cumulative emissions of carbon lost as a result of energy consumed in forest management and wood processing (Matthews 1993). In Fig. 1 major carbon fluxes and carbon storage sites in forest plantations are presented, excluding the energy processes in forest management and wood processing.

The role that forest plantations could play as a global sink for carbon will depend less on the technical factors of carbon sequestration than on economic expediency. The area under forest plantations could be technically expanded rather easily if it was considered socially and environmentally feasible and economically profitable. Although the role of forest plantations in carbon sequestration has been investigated from the economic point of view (see Nabuurs 1994), there seem to be few studies as of yet which have examined the problem from the perspective of plantation profitability, especially in boreal and tropical zones. One such study done in British Columbia (van Kooten et al. 1993) estimated that the profitability of reforestation of inadequately stocked lands was improved when the

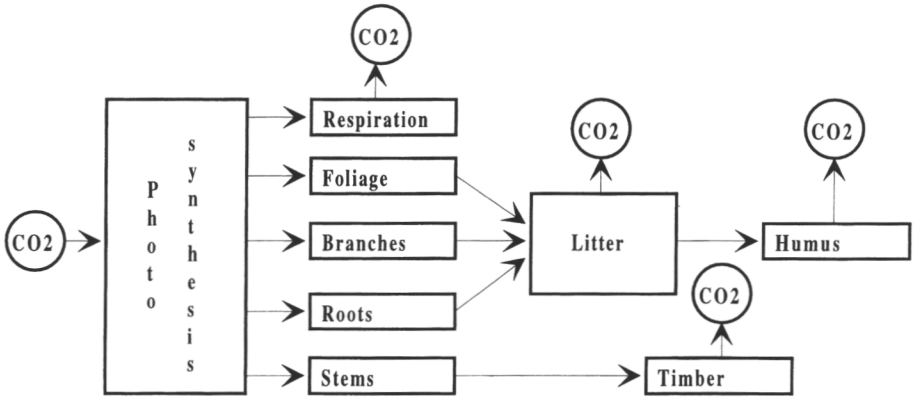


Fig. 1. A simplified diagram of fluxes and stocks of carbon in a forest ecosystem. CO_2 refers to a release of carbon to the atmosphere either through respiration or decomposition (Nabuurs and Mohren 1993).

economic impacts of carbon sequestration were included in the profitability analysis.

Finland and the Philippines were selected to represent distinctly different but typical examples from boreal and moist tropical conditions respectively. The Philippines represents a case of a developing tropical country, where after a long period of large scale deforestation and forest degradation recent extensive goals and programs of reforestation have been established to slow environmental damage and secure a future timber supply. In many respect Finland represents an opposite case: an industrialized country where forests and the forest industry provide a backbone for the economy and where a long-term commitment to forest management and silviculture has resulted in expanding its forest resources. The growth and yield possibilities for planted trees, and the economic environments for plantation forestry do differ in these countries at least as much as they generally do for boreal and tropical conditions. However, both countries share the concern for the stabilisation of the atmospheric carbon dioxide balance and the new challenges and opportunities that forest plantations may offer in this global issue.

The purpose of this study was to examine the impacts of carbon sequestration on the profitability of reforestation in Finland and the Philippines. More specifically, the aim was to examine the impacts of varying growth and yield conditions, rotation cycles and end-use patterns on the quantity and timing of carbon flows, in addition to assessing their impacts on the economic value of carbon sequestration and the profitability of reforestation.

2 Methodology of the Study

2.1 Profitability Analysis

Net present value (NPV) and internal rate of return (IRR) were the two criteria used to indicate the profitability of reforestation investments. The NPV is the current value of the sum of the annual costs and revenues with a given discount rate. The IRR is the discount rate at which the NPV is equal to zero. Profitability analyses were first calculated solely for reforestation investments (a formal financial profitability analysis), and then for reforestation investments where the carbon flows were valued and included in the profitability analysis. The latter approach represents an environmental economic profitability at the firm level, in a case when shadow prices are given by the society. Various unit values for carbon flows in United States Dollars per megagram of carbon (USD/Mg C) and two discount rates were applied.

2.2 Reforestation Options

Both in Finland and in the Philippines one reforestation option studied represented fast-growing (short rotation), and the other slow-growing (long rotation) tree plantation. It was assumed that reforestation is done on bare land. In other words, the previous vegetation was assumed to have no influence on the growth and yield of a forest plantation, or on the carbon flows in the future. Therefore, the opportunity cost of land in terms of carbon sequestration was assumed to be zero.

In Finland, reforestation of former agricultural land with birch (*Betula pendula*) was considered as an example of a tree plantation with fast growth. Plantation establishment costs were the average costs in field afforestation (Aarnio and Rantala 1994), and growth and yield data, including two thinnings (30 %) at the ages of 20 and 30 years were applied from Oikarinen (1983, 45). Reforestation with spruce (*Picea abies*) after a clear felling on a moderately fertile soil (blueberry type), was considered as a slow-growing tree plantation. For spruce, the average planting costs in reforestation (Yearbook of forest statistics 1993–1994), and the average growth and yield data, including two thinnings (30 %) at the ages of 45 and 70 years, were applied (Vuokila and Väliaho 1980, 147) (Table 1).

In the Philippines, reforestation with *Acacia auriculiformis* using a 15 year rotation period and with mahogany (*Swietenia macrophylla,* King) using a 25 year rotation period were considered as a fast- and slow-growing tree plantations, respectively. The basic cost data for reforestation was the same as used in the national forestry sector planning (DENR 1990). Since only scattered data

Table 1. Studied reforestation options.

Species	Rotation (yr)	MAI (m^3/ha/yr)	End-use of stem wood
Betula pendula	50	8	66 % plywood, 34 % chemical pulp & paper
Picea abies	100	5	77 % saw timber, 23 % mechanical pulp & paper
Acacia auriculiformis	15	12	100 % chemical pulp & paper
Swietenia macrophylla, King	25	10	70 % saw timber, 30 % fuelwood

on forest plantation growth and yield on different soils were available, the growth and yield estimates had to be based on different sources (Firewood crops... 1980, Pandey 1983, Ten-year development... 1988, Master plan... 1990, Forestry sector... 1994). The average mean annual increments in the Philippines (MAI) were estimated without thinnings (Table 1).

2.3 Carbon Sequestration

2.3.1 Accumulation of Carbon on Growing Biomass

In this study, photosynthesis and respiration were not explicitly considered. Instead, the carbon increment rates were estimated indirectly from the stem volume increments (Nabuurs and Mohren 1993). The assessment of carbon fluxes and carbon storage structures via stem volume increment was based on an assumption that the total weight of foliage, branches, and roots have a high correlation with the stem diameter and the volume of stem wood (e.g. Evans 1992).

Specific values for the carbon content, the assimilate allocation, decomposition, and the residence time of carbon in the litter for *Acacia auriculiformis* and mahogany were the same as used for *Albizia* spp. plantations in the tropics. The specific values for spruce and birch plantations were the same as those used for spruce forests in the Boreonemoral zone of Russia and for poplar plantations on former agricultural land in Europe, respectively (Nabuurs and Mohren 1993).

The stem volume increment was converted into a stem biomass increment using specific conversion factors for basic density (oven dry weight per fresh volume). The oven-dry stem biomass was further converted into the mass of carbon using the values for the carbon content in oven-dry structural biomass (Appendix 1, Table A).

The allocation of forest biomass on various structures (foliage, branches and roots) during the stand development was, as mentioned earlier, based on stem wood increment. The specific factors used for conversion are presented in Appendix 1, Table B. Turnover rates of biomass structures (Appendix 1, Table C) were used to assess the formation of litter. Finally, the residence time of various biomass compartments in litter was assessed using the values presented in Appendix 1, Table D.

Since the formation of humus as well as its decomposition are relatively slow processes, and the study was limited to studying the carbon flows during the first 100 years after reforestation, they were both excluded from the analysis.

2.3.2 Carbon Flows in Wood-Based Products

In addition to the biological carbon processes, the carbon flows in wood-based products were also estimated. On the whole, the residence time of carbon in the wood-based products was assumed to be higher for sawn wood and plywood than for paper products or fuelwood. The residence time of carbon in the wood-based products was estimated using life span equation (Karjalainen et al. 1994). The life span indicates the average time over which products in a given category are in use. Similarly, a certain amount of carbon is removed from use in subsequent years as

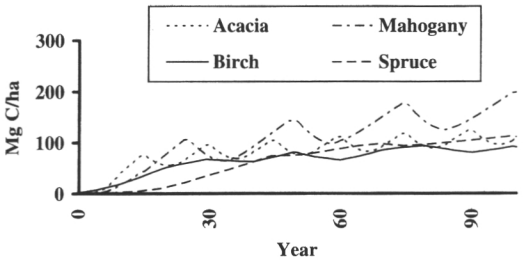


Fig. 2. Carbon sequestration (Mg C/ha) on studied tree plantations over a 100 year period.

$$pu = [d - (a / 1 + b \times e^{-cxt})] \times 100$$

where pu is the proportion of products still in use of the original cohort at a given time. Values for the parameters for different wood-based products are presented in Appendix 1, Table E.

In general, the carbon flows were followed, first, up to the decomposition of litter; and second, up to the assumed decomposition of the end products (see Fig. 1). To illustrate the estimated carbon flows, the accumulation of carbon in different tree plantations is presented in Fig. 2, where the trends and cycles in the accumulated carbon are due to the rotation and thinning cycles.

2.4 Valuation of Carbon Sequestration

Crucial to the economic analysis is whether carbon sequestration can be treated as an economic benefit or not. If it can be treated as a benefit, what will be the proper unit price level (shadow price) for the carbon sink that forests will provide?

The shadow price of a unit of CO_2 is the value of the external damage caused by an emission. Determinations of the shadow price level for emission control, however, vary strikingly according to the method of pricing the external damages or the costs of preventing them (Table 2). Since the unit values of carbon emissions are usually presented as present-valued lump sums the shadow prices of CO_2 depends also on the discount rate used. In conclusion, the shadow price of carbon dioxide emission can be assumed to be positive, although it seems impossible to objectively determine any exact or core estimates.

Theoretically, it has been shown that when market distortions are rejected, marketable emission permits will minimise the total costs used for pollution control if limitations for a maximum pollution level are given (Randall 1987). This theory was assumed here to be relevant also in the valuation of carbon sequestration: Since forests clearly offer an opportunity for emission control investments (e.g. in industry and energy production) emission control costs can be assumed to describe the value of carbon sequestration in plantation forests. Consequently, the recommendation made by Andersson and Williams (1994) that the Global Environmental Facility (GEF) should apply 25 USD/Mg shadow price for carbon in GEF funded projects (e.g. afforestation projects) for 1993, increasing by 10 % per

Table 2. Unit value for carbon emission control.

Method of pricing CO_2	Unit value (USD/Mg C)	Reference
Cost of damages in global warming	20	Frankhauser (1992), cf. Pearce and Brown (1994)
Marginal cost of abatement	1–6	Falk and Mendelson (1993)
Eight various methods	1–380	Price and Willis (1993), Price (1994)
Marginal cost of limiting C emissions in energy production	25–120	Andersson and Williams (1994)
Direct subjective estimation of nine experts (interview)	113 (s.d. 150)	Schauer (1995)
Reforestation costs	1–60	Sedjo et al. (1995)

s.d. standard deviation

annum until the year 2010, was considered most relevant for this study. The shadow price for carbon flows – 25 USD/Mg – was assumed constant as were wood prices. Sensitivity analyses were made with shadow prices between 1 and 50 USD/Mg C.

3 Results

3.1 Profitability of Reforestation and Costs of Carbon Sequestration

Reforestation with fast-growing tree species was estimated to be financially more profitable than reforestation with slow-growing species both under boreal and moist tropical conditions. The profitability of reforestation increased more in the Philippines than in Finland when the environmental benefits of carbon sequestration were included in the profitability analysis (Table 3).

In general, the greatest impacts on the profitability were by; the growth and yield data, the plantation establishment costs, the rotation period, the end-use of wood products, and the discount rate. For example, when a 10 percent discount rate was applied, reforestation in Finland was unprofitable even if the environmental value of carbon sequestration was included in the profitability analysis. The environmental value of carbon sequestration also decreased when the discount rate was increased (Table 4). Sequestration of one Mg of carbon in boreal and moist tropical forest plantations was estimated to cost 10.5–20.0 and 4.0–13.6 USD, respectively (Table 5).

Table 3. Internal rate of return (%) of reforestation investments with and without carbon sequestration (25 USD/Mg C) calculated for a 100 year period.

	Birch	Spruce	Acacia	Mahogany
Financial profitability	5.2	3.2	15.3	12.8
Profitability with carbon sequestration	6.6	4.1	20.3	15.5

3.2 Sensitivity Analysis

An increase in the shadow price of carbon sequestration by one USD/Mg C increased the NPV of the reforestation investment by 35, 20, 46 and 47 USD/ha in birch, spruce, acacia and mahogany plantations, respectively, when a five percent discount rate was applied (Table 6). When the shadow price of carbon sequestration was set to be higher than 47 and 66 USD/Mg C, reforestation with spruce (5 % discount rate) and birch (10 % discount rate), respectively, generated a positive NPV for the reforestation investment.

The present value of carbon sequestration was estimated to be equal to 48, 39, 77 and 101

Table 4. Net present value of reforestation investments (USD/ha) with and without carbon sequestration (25 USD/Mg C) calculated for a 100 year period.

Discount rate (%)	Birch	Spruce	Acacia	Mahogany
Financial profitability				
5	171	–927	4041	5039
10	–1282	–1150	888	648
Value of carbon sequestration				
5	870	501	1159	1191
10	491	160	684	560
Profitability with carbon sequestration				
5	1041	–426	5200	6230
10	–791	–990	1571	1209

Table 5. Costs (USD/Mg C) of carbon sequestration using reforestation.

Discount rate (%)	Birch	Spruce	Acacia	Mahogany
5	20.0	11.4	13.6	5.9
10	17.2	10.5	8.4	4.0

percentages of the present value of the plantation establishment costs for birch, spruce, acacia, and mahogany plantations, respectively, when a five percent discount rate and a 25 USD/Mg C shadow price were applied. More generally, an increase in the shadow price of carbon sequestration by one USD/Mg C covered approximately 1–2 and 3–4 percentages of the present values of the plantation establishment costs in Finland and the Philippines, respectively (Table 7).

4 Discussion and Conclusions

For a forest plantation in general, the better the growth and yield is, the more carbon that can be sequestered on trees. Similarly, in general, the longer the rotation period is, the more carbon that is sequestered on forest biomass. Further-

Table 6. Net present value of reforestation investment (USD/ha) with different shadow prices for carbon sequestration calculated for a 100 year period.

Species	Discount rate (%)	Shadow price of carbon sequestration (USD/Mg C)				
		0	1	10	25	50
Birch	5	171	206	519	1041	1912
	10	–1282	–1262	–1086	–791	–299
Spruce	5	–927	–907	–727	–426	75
	10	–1150	–1143	–1086	–990	–829
Acacia	5	4041	4087	4504	5200	6359
	10	888	915	1161	1571	2255
Mahogany	5	5039	5086	5515	6230	7421
	10	648	671	873	1209	1769

Table 7. Value of carbon sequestration relative to the plantation establishment costs (%).

Species	Discount rate (%)	Shadow price of carbon sequestration (USD/Mg C)				
		0	1	10	25	50
Birch	5	0	2	19	48	96
	10	0	1	13	31	63
Spruce	5	0	2	16	39	79
	10	0	1	5	14	27
Acacia	5	0	3	31	77	155
	10	0	3	29	73	147
Mahogany	5	0	4	40	101	202
	10	0	3	28	70	139

more, the end-use pattern of wood products and the factors that affect decomposition in general, also influence the amount of sequestered carbon.

Basically, the same factors that influence the amount of sequestered carbon, also influence the value of carbon sequestration. However, there are smaller than expected differences in the value of carbon sequestration between the Philippines and Finland due to the discounting and assumed patterns of end use. It seems that discounting greatly reduces differences in end-use, for example, making them almost insignificant in the case of a spruce plantation in Finland.

It seems (Table 3) that the profitability increase (measured in percentage increases of IRR) due to carbon sequestration is higher in the Philippines, where the financial profitability of plantations is already much higher than in Finland. However, the relative improvements in IRR (measured in relative increase of IRR) vary in the same range (21–35%) in both countries.

When the profitability was measured by NPV (Table 4) the lower discount rate (5 %) resulted in higher relative profitability changes in Finland than in the Philippines. However, with the higher discount rate (10 %) the opposite was true. In general, the assumed shadow price of carbon sequestration (25 USD/Mg C) increased the profitability of reforestation significantly, similar to the IRR results.

As demonstrated by the sensitivity analysis, the impact of carbon sequestration on the profitability of reforestation largely depends on the assumed level of the shadow price for carbon fixation. The uncertainties related to the determination of the proper unit price for carbon fixation may help to describe the wide range of the results in the sensitivity analysis.

It can be assumed that reforestation is one of the most cost-effective ways to control the concentration of carbon dioxide in the atmosphere, since the more traditional benefits of reforestation (financial, economic, and other environmental) in many cases fully or partially cover the costs of the investment. For example, even if the financial revenues from harvested timber were not included, the sequestration of one Mg of carbon was estimated to cost only 4.0–20.0 USD.

The present value of carbon sequestration was estimated as higher with fast-growing tree plantations than with slow-growing tree plantations, although the total growth within the 100 year period did not vary much between these types of plantations. This leads to a discussion on the role of discounting when the value for carbon sequestration is assessed.

Discounting makes the future harvest values commensurate to the present plantation establishment costs. The choice of a proper discount rate is a known sustainable headache for forest economists. In assessing the economic importance of carbon sequestration, the time factor and discounting play similar crucial, and perhaps an even more complicated role than in traditional economic calculations. The discount rate holds the crucial balance between the immediate benefits of burning fossil fuels, and the uncertain consequences of releasing CO_2 over centuries (Price and Willis 1993). Price and Willis (1993) suggest, among other things, that the uncertainty of climatic change should be a reason for an increased weight on the future. In response to that, we think that a selective reduction of the discount rate for the carbon values could be appropriate. This consequently, would contribute significantly to the benefits of forestry.

When considering the other implications of the improved profitability of forest plantations, one should keep in mind that in practice forest owners who plant the trees rarely will have any financial compensation (transfer payments) for the carbon sequestration. Therefore, carbon sequestration does not improve the financial profitability unless there is an appropriate incentive provided. In addition, the assumption that forest plantations decelerate deforestation in the tropics, therefore also decreasing carbon emissions from the destruction of the natural forests, provides that the grounds for incentives seem to be especially relevant (Andrasko et al. 1991).

Appropriately planned tree plantations (from farm level agroforestry to watershed and industrial plantations) will produce wood products, employment, and income, while at the same time counteracting land degradation and soil erosion, reducing pressure on natural forests and sequestering carbon from the atmosphere. Of course, some negative environmental impacts are related to tree plantations in the developing world and the profile of the impacts of forest planta-

tions may be in some respects quite different from what it is in industrialised countries. For all these reasons, among which the carbon sequestration potential may play a major role, the economics of the multiple role of forest plantations in developing and developed countries certainly deserves more intensified research efforts.

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Total of 33 references

Appendix 1

Table A. Conversion factors from fresh volume to oven dry matter (kg/m^3) and carbon content in oven-dry structural biomass (%) for the studied tree species.

Species	Conversion factor to oven dry matter (kg/m^3)	Carbon content (%)
Acacia	460[1)]	50.0[4)]
Mahogany	550[2)]	50.0[4)]
Birch	490[3)]	50.5[5)]
Spruce	385[3)]	51.9[5)]

1) Saquino (1991), 2) Gimoto (1992), 3) Kellomäki et al. (1992), 4) Nabuurs and Mohren (1993), 5) Karjalainen et al. (1994)

Table B. Assimilate allocation during stand development, relative to stem oven dry weight (Nabuurs and Mohren 1993).

Age (yr)	0	5	10	20	30	40	50	60	70	80	100
Acacia & mahogany											
– foliage	0.7	0.7	0.4	0.4	0.4	-	-	-	-	-	-
– branches	0.6	0.4	0.4	0.4	0.4	-	-	-	-	-	-
– roots	0.7	0.7	0.4	0.4	0.4	-	-	-	-	-	-
Birch											
– foliage	2.5	1.0	0.3	0.5	0.8	0.9	1.2	-	-	-	-
– branches	1.5	0.8	0.2	0.35	0.4	0.5	0.5	-	-	-	-
– roots	2.0	0.8	0.1	0.3	0.35	0.4	0.5	-	-	-	-
Spruce											
– foliage	1.0	1.0	1.0	0.75	0.65	0.65	0.65	0.65	0.65	0.7	0.7
– branches	1.0	1.0	0.4	0.25	0.23	0.22	0.22	0.21	0.21	0.2	0.2
– roots	1.0	1.0	0.9	0.8	0.6	0.6	0.6	0.5	0.5	0.5	0.5

Table C. Turnover rates of biomass structures (yr^{-1}) (Nabuurs and Mohren 1993).

Plantation species	Foliage	Branches	Roots
Acacia & mahogany	0.5	0.05	0.06
Birch	0.3	0.03	0.07
Spruce	1.0	0.06	0.1

Table D. Average residence time of dead branches, roots and foliage in various plantations (yr) (Nabuurs and Mohren 1993).

Plantation species	Residence time, branches and roots	Residence time, foliage
Acacia & mahogany	10	1
Birch	10	1
Spruce	30	6

Table E. Basic values for parameters in the product lifespan equation and assumed distribution of products into lifespan categories (Karjalainen et al. 1994).

Product lifespan category	Parameters for product lifespan equation a	b	c	d	Sawn goods	Plywood	Mechanical pulp & paper	Chemical pulp & paper	Fuelwood
Short	120	5	0.5	120	-	-	34	14	100
Medium–short	120	5	0.15	120	-	-	66	86	-
Medium–long	120	5	0.065	120	50	50	-	-	-
Long	120	5	0.03	120	50	50	-	-	-

A Mechanistic Perspective of Possible Influences of Climate Change on Defoliating Insects in North America's Boreal Forests

R.A. Fleming

There is no doubt that tree survival, growth, and reproduction in North America's boreal forest would be directly influenced by the projected changes in climate if they occur. The indirect effects of climate change may be of even greater importance, however, because of their potential for altering the intensity, frequency, and perhaps even the very nature of the disturbance regimes which drive boreal forest dynamics.

Insect defoliator populations are one of the dominating disturbance factors in North America's boreal forests and during outbreaks trees are often killed over vast forest areas. If the predicted shifts in climate occur, the damage patterns caused by insects may be considerably changed, particularly those of insects whose temporal and spatial distributions are singularly dependent on climatic factors. The ensuing uncertainties directly affect depletion forecasts, pest hazard rating procedures, and long-term planning for pest control requirements. Because the potential for wildfire often increases in stands after insect attack, uncertainties in future insect damage patterns also lead to uncertainties in fire regimes. In addition, because the rates of processes key to biogeochemical and nutrient recycling are influenced by insect damage, potential changes in damage patterns can indirectly affect ecosystem resilience and the sustainability of the multiple uses of the forest resource.

In this paper, a mechanistic perspective is developed based on available information describing how defoliatoring forest insects might respond to climate warming. Because of its prevalence and long history of study, the spruce budworm, *Choristoneura fumiferana* Clem. (Lepidoptera: Tortricidae), is used for illustrative purposes in developing this perspective. The scenarios that follow outline the potential importance of threshold behavior, historical conditions, phenological relationships, infrequent but extreme weather, complex feedbacks, and natural selection. The urgency of such considerations is emphasized by reference to research suggesting that climate warming may already be influencing some insect lifecycles.

Keywords *Choristoneura fumiferana*, phenological relationships, plant quality, natural selection, extreme weather, thresholds, historical factors, *Abies balsamea*
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1 Introduction

The greatest impact of climate change on ecosystem composition and function within North America's boreal forest will probably be mediated through changes in disturbance regimes such as insect outbreak and fire systems (Price and Apps 1995). In this perspective insects are seen as important contributors to carbon and nutrient cycling, to biomass decomposition, and to energy flow (Szujecki 1987, Haukioja et al. 1988, Haack and Byler 1993). For instance, insect feces decompose faster than leaf litter and, in attacked trees, defoliation hastens nutrient leaching from damaged foliage and litterfall. Consequently Chapin (1993) and Schowalter et al. (1986) argue that chemical elements like nitrogen, calcium, potassium, and phosphorus cycle faster through forest ecosystems than they would if there were no pests present.

Insects are also a major influence on forest productivity in North America. Annual forest losses from tree mortality and reduced growth due to insect attack in Canada, alone, are estimated at 51.6 million m^3 per year. These losses are 1.4 times those due to wildfire and amount to 32 % of the annual harvest volume (Hall and Moody 1994). In addition, because of their vast scales, such disturbances are thought to affect physical climatic processes on a regional and perhaps even on a global level (e.g., Bonan and Shugart 1989, Price and Apps 1995).

This paper reviews research on possible climate change effects on insect defoliators in North America's boreal forests. Because of both the complexity and immensity of the problem, the literature on the subject has been necessarily fragmentary (e.g., Fleming and Volney 1995, Fleming 1996). Although this review extends and updates this earlier work, it is still incomplete: in fact, detailed consideration of the response of each defoliating insect species in North America's boreal forests to climate change would be an overwhelming task. A more practical approach is to adopt certain species as "representative types" and to try to anticipate how the hypothesized future climatic conditions might affect the insect defoliator-boreal forest systems as they are currently understood. Because of its prevalence and long history of study (c.f. Morris 1963), the spruce budworm, *Choristoneura fumiferana* Clem. (Lepidoptera: Tortricidae), is an ideal candidate for a "representative type". My goal is to organize current knowledge in order to clarify the complex of mechanisms by which climate change is most likely to affect this insect. These mechanisms provide a basis for exploration and conjecture to describe some of the possible responses of boreal forest insect defoliators to climate change.

2 Spruce Budworm

The range of the spruce budworm mirrors that of white spruce, *Picea glauca* (Moench) Voss., in North America's boreal forest and records of severe defoliation extend to within 150 km of the arctic circle (Volney and Cerezke 1992). Hall and Moody (1994) attribute 53 % of all insect-caused losses in forest productivity in Canada to the spruce budworm. This native insect attacks spruce, *Picea* spp., and balsam fir, *Abies balsamea* (L.) Mill., and often kills most trees in dense, mature fir stands when outbreaks are not controlled. Such outbreaks, during which population densities can reach 10^8 fourth instar larvae/ha typically last 5–15 years; between outbreaks the budworm usually remains rare (10^5 fourth instar larvae/ha) for 20–60 years (Crawford and Jennings 1989) and this allows the spruce-fir forests to regenerate (Mattson et al. 1988).

Partly because it competes so effectively with industry for the forest resource, many consider the spruce budworm to be the pre-eminent pest of North America's boreal forests. Nonetheless, it is possible that the spruce budworm's pest status may diminish in a warmer climate. An economic analysis of climate warming impacts on the U.S. forest sector (Mills and Haynes 1995) suggests that gains in productivity (due to predicted changes in temperature and precipitation patterns, and due to increases in available carbon) could substantially increase the supply/demand ratio for wood products and thus limit prices. Under this scenario, the spruce budworm may cause less annual economic loss in the future than it does now, even if the annual volume lost were greater. But this is only one possible

scenario: the assumption of gains in forest productivity is based on a study (McGuire and Joyce 1995) which explicitly omitted any consideration of how vegetation distributions and disturbance regimes might respond to climate change.

The life cycle provides a useful framework for developing an understanding of how animal and plant populations might respond to climate change. The spruce budworm has one generation a year. In mid-August, 2–3 weeks after the eggs are laid, the non-feeding first instar larvae hatch and move to overwintering sites on the branches. They overwinter as a tiny second instar larva and resume activity in early May. They then pass through four feeding instars before pupating in late June. Mating, moth dispersal, and oviposition occur in July. The spruce budworm's potential for causing tree mortality and growth loss is due, in part, to its high fecundity (of about 170 eggs per female) and rapid growth rate. A mature sixth instar larva, which weighs about 100 mg (fresh weight) and is about 20–30 mm long, is roughly 1500 times larger than it was as a second instar larva just 6–9 weeks earlier.

Climate change may affect insect defoliator populations directly through their per capita growth rates or indirectly through interactions and feedbacks with other species and abiotic components of the environment. Although climate directly affects spruce budworm survival (Lucuik 1984), and to some extent, fecundity (Harvey 1983b), competitive interactions among individuals is expected to modify the extent to which climate-induced gains in survival and fecundity produce gains in the per capita growth rate. Competition among spruce budworm, however, seems to have little impact except among feeding larvae at very high densities (e.g., Sanders 1991). Therefore, limitations on climate-induced changes in the spruce budworm's rate of population growth must come mainly through indirect effects such as those associated with trophic interactions. In the past the net result of these indirect effects has been a tendency for per capita growth rates to increase during warm, dry years (Wellington 1948).

3 Species Movement

3.1 Integrated Movement

The importance of the possible indirect effects of climate change, particularly those effects which are imparted through interactions with other species (Kingsolver 1989), depends on how ecosystems as integral units (Holling 1992a) respond to climate change. The simplest assumption is that as climatic zones move poleward (and to higher altitudes), species assemblages, and the ecosystems in which they are embedded, will track suitable environmental conditions from one geographic region to another as complete integrated units (e.g. Farrow et al. 1993). This implies that although the geographic distribution of pests may shift in response to climate change, their impact (in terms of volume lost per unit area) should change little because they will remain embedded within the same ecosystems (and hence subject to the same feedback structure) as before. To some extent this assumption is a basis for all inductive approaches (reviewed by Sutherst et al. 1995) for predicting insect pest responses to climate change. Such approaches predict a species' (or ecosystem's) response to climate warming by matching projected future climates with certain key aspects of the climatic regime observed in the species' (or ecosystem's) present geographical distribution.

3.2 Individualistic Movement

Another possible response to climate change is that species, or even certain age groups of a species, may move north individualistically (Hengeveld 1990) rather than as fully integrated components of an entire ecosystem which is moving in unison. In fact, Davis (1981) reports evidence that the conifer species which comprise today's boreal forest in North America migrated northwards individualistically in the Late Glacial. Individualistic movement under future climate warming could result from (a) basic differences in the migratory potential of different tree (e.g., Solomon and Leemans 1990, Gear and Huntley 1991) and different insect (e.g., Elias 1992, Stinner et al. 1989) species, (b) the appearance of

'green bridges' (plants which, once the climate warms, become hosts or provide favorable overwintering sites for exotic pests which previously were incapable of surviving the winter in that region [Porter et al. 1991]), and (c) the destabilization of resident ecosystems (Perry et al. 1990).

The dynamic models of trophic interactions of forest-pest systems derived by Antonovsky et al. (1990) explicitly represent possibility (c) directly above. One of their models is specifically used to represent the spruce budworm-balsam fir system. In this model the tree population has two age classes and only the older trees are attacked by the insect. Fig. 1 is a schematic illustration of the (logarithm of the) steady state densities of the insect (solid lines) and tree species (dashed lines) in the model when the rates of tree senescence and regeneration are allowed to vary, and when the other parameters are assigned values estimated for spruce budworm and balsam fir. The model system experiences four qualitatively different types of long-term behavior as the ratio of tree senescence to regeneration increases: persistence at a Stable Equilibrium when the ratio is near its lower limit (in area SE of Fig. 1); system persistence (or extinction) if Tree densities are above (or below) a Threshold density (area T_T); Insect eXtinction and survival (or extinction) of the tree species above (or below) a Threshold Tree density (area T_TI_X); and when the senescence/regeneration ratio is highest, System eXtinction (area SX). The threshold densities for balsam fir are not shown explicitly in Fig. 1, but their effect is evident in the trajectories of the model system as explained further below.

The threshold tree density in the model is due to an assumption that regeneration success is greatest at intermediate densities of the older age-class of the trees. This assumption is supported by considerations of light competition and soil processes. At high densities of mature host trees of the spruce budworm, the thick canopy tends to suppress regeneration by limiting the light reaching the undergrowth. At very low densities of mature trees on fertile soils, fast growing plant competition (grasses, shrubs, deciduous species) can overtop the spruce-fir seedlings and limit their rate of regeneration through light limitation. At intermediate densities of mature host trees, the canopy can shade out competing weeds and at the same time allow the more shade-tolerant fir seedlings to regenerate. On the relatively barren sites of the tundra-boreal forest ecotone, spruce leaf litter improves soil fertility (Pastor 1993) so regeneration success can be expected to increase if mature host trees increase from low to intermediate densities. At the same time, the chemistry of this leaf litter inhibits further improvements in soil fertility to the point that herbaceous plants and deciduous trees can easily compete (Chapin 1993).

As an illustration of how individualistic movement might result from destabilization of resident ecosystems consider the spruce budworm–forest system depicted in Fig. 1. A densely forested southerly site which is at steady state densities would be located somewhere along the lines in area SE. As the climate warms, the expectation is that the senescence and regeneration rates of boreal trees will increase and decrease, respectively, near the southern boundary of the boreal forest (Rizzo and Wicken 1992). But because seedling mortality is usually high in hot, dry weather (e.g., Sims et al. 1990), many established trees are expected to survive (albeit in less than ideal environmental conditions) after almost all regeneration has died (e.g., balsam fir can live up to 150 years in the absence of fire and budworm). In effect, the model predicts that the seedlings will 'retreat' north before established trees (and before the spruce budworm which prefers older host trees). Thus different age-classes of host trees are expected to move north individually from the southern boundary of the spruce budworm–forest system in response to climate warming. This scenario is supported by Payette's (1993) study of the response of boreal tree populations to climatic changes in the Holocene in northern Quebec-Labrador. He remarks , "Once a species became established at a site, it remained there well after the conditions propitious for its establishment disappeared. ... Instead of being latitudinally displaced, the population sizes (densities) were reduced".

4 Spruce Budworm–Forest Dynamics

Returning to the spruce budworm–forest system depicted in Fig. 1, the southerly site becomes less favorable for boreal tree species as a result of the warming and their regeneration rates decline and their senescence rates increase. If these changes are not too abrupt, they may 'pull' the system (arrows pointing to the right on the dashed and solid lines) into area T_T in Fig. 1. The tree population exceeds its low density threshold in this area, so both the tree and the insect populations can persist here. In reality, there would be a danger at this stage that a severe outbreak might so devastate the forest that the population of host trees falls below the threshold density. Since the tree population cannot renew itself once it falls below its threshold density in area T_T, the spruce budworm–forest system effectively goes locally extinct under these circumstances.

If the spruce budworm–forest system survives in area T_T, then the model suggests that the tree species can persist without the insect if further slow warming 'pulls' the system into area T_TI_X. By the time the conditions at the site have entered area T_TI_X of Fig. 1 the warming has reduced the population density of host trees to the point that they can no longer sustain the budworm. At this point the host trees can be expected to occur in disconnected pockets in a fragmented landscape. Under these circumstances, the remaining budworm may experience large losses in dispersal and critical patch size effects (Van Raalte 1972, Ludwig et al 1979) may become important. Additional warming, which causes further increases in the senescence to regeneration rate at the site, eventually 'pushes' the model system into area SX where gradual local extinction of the boreal species occurs.

Now consider a northerly site where climate warming decreases the senescence to regeneration ratio. If the model represents a site which is initially north of the northern boundary of boreal tree species (where regeneration rates are negligible and senescence rates would presumably be high if there were any trees), both the insect and the tree species are locally extinct (area SX of Fig. 1). Assuming that the cold climate contributes to making the site unfavorable for trees,

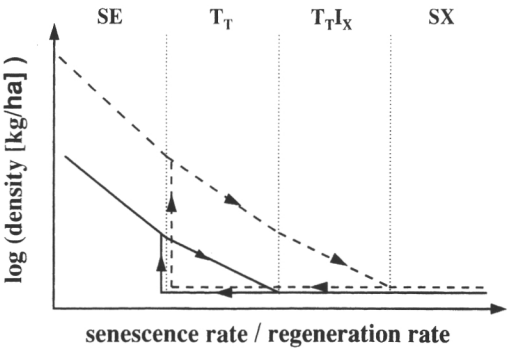


Fig. 1. Schematic of the dynamics of a forest:insect model (Antonovsky et al. 1990) in which the insect attacks only older trees . The dashed and solid 'curves' represent the (logarithm of the) steady state biomass densities of the tree and insect populations, respectively. Depending on the ratio of the rates of tree senescence to tree regeneration (horizontal axis), the system undergoes four qualitatively different dynamics. In area SE the system is attracted to a stable equilibrium; in T_T the system approaches a stable equilibrium provided the tree population exceeds a low density threshold (not shown), otherwise the system becomes extinct. In T_TI_X the forest can survive above a low density threshold but the insect goes extinct; in SX the entire system eventually becomes extinct. The small arrows pointing diagonally down towards the (lower) right indicate the response of the model when it leaves area SE as the senescence to regeneration ratio increases; the small arrows pointing up or to the left indicate the response when the ratio decreases and the system leaves area SX (see text).

increasing rates of regeneration and decreasing rates of senescence can be expected (Rizzo and Wicken 1992), to at least some extent (Jacoby and D'Arrigo 1995), as the climate warms. Consequently, changes in the suitability of this northern site for the host tree species can be represented by a shift from right to left in Fig. 1. As climate warming continues, the senescence to regeneration ratio continues to fall and the steady state populations follow the lower trajectories into area T_TI_X and then area T_T. (The lower trajectories are followed in areas T_TI_X and T_T

because the tree population density at this northerly site has not been able to exceed the low density threshold needed for establishment). The tree and insect populations establish themselves only after more warming causes further decreases in the senescence to regeneration ratio and 'pushes' the populations up to their steady state densities in area SE.

The last three paragraphs suggest that chance, historical factors and threshold effects (which have been deduced in many theoretical forest-pest systems [e.g., Isaev and Khlebopros 1979], including the spruce budworm [Holling 1992b, but see Fleming and Shoemaker 1992], and occasionally reported in North American forest ecosystems [e.g., Griggs 1946, Bergeron and Dubuc 1989, Perry et al. 1989, MacDonald et al. 1993]) may determine the nature of the prevailing condition of the ecosystem as destabilization occurs. For instance, depending solely on whether the tree's senescence to regeneration ratios are increasing or decreasing as the model system enters area T_T, the fate of the tree:insect model (if the system remains in this area) ranges from persistence to extinction for both populations. Thus the model implies that for identical 'intermediate' values of this ratio, two different steady states are possible for the forest-pest system. The steady state actually imposed depends on whether the density of boreal trees is above or below a threshold density when the system is first 'pushed' into area T_T by local climate warming. If a new (warmer) climate began to persist in a southern site when the population density of boreal trees was initially low, then their regeneration could not overcome the other plants competing for the site, so neither the spruce budworm nor the boreal tree species which it attacks could become established. This steady state involves (local) extinction for the boreal forest-pest system.

On the other hand, if the population of boreal trees on the site were already dense and well-established when such a new climate began to persist, then the budworm–forest assemblage might hold the site indefinitely, assuming the boreal forest's canopy shaded out competing vegetation (and allowed the more shade-tolerant seedlings of boreal species to continue to regenerate). In this case the model system would eventually settle at a stable equilibrium at which both the boreal forest and the budworm coexisted. Competing vegetation would not become a factor unless changes in the senescence and regeneration rates of boreal tree species eventually opened the overstory to the point where invading competition suppressed seedling regeneration.

Ergo, two sites encountering similar climates (and which, as a result, have identical rates of tree senescence and regeneration) could theoretically be occupied by quite different ecosystems solely because (tree) population densities were different when that climate arrived. Observations (e.g., Griggs 1946, Payette 1993) and modelling studies (e.g., Shugart et al. 1980, Pastor and Post 1993) suggest that such situations should not be unexpected in North America's forests. In these situations, climate-matching might be deceiving: differences in ecosystem composition between the two sites might easily be attributed to differences in the values of irrelevant climatic variables rather than to the historical population densities of key species.

5 Phenology

The previous section showed that direct climate-induced changes to tree senescence and regeneration rates could destabilize forest-pest systems and lead to individualistic movement of the system in response to climate change. This next section suggests that climate change could also destabilize forest-pest systems by disrupting the phenological relationships between trophic levels.

5.1 Synchrony with Host Plants

In its life history, the spruce budworm, has synchronized its greatest nutritional demand with the time when developing, rather then mature, host plant foliage is most available. (This is typical of many herbivores, including close to 50 % of forest insect pests [Martineau 1984]). As balsam fir needles mature, their growth slows but photosynthesis continues, and the result is often increased leaf carbohydrate content relative to nitrogen concentration (Shaw and Little 1977).

Often the surplus carbon is stored as secondary metabolites (Bryant et al. 1983) which either through design (e.g., Rhoades and Cates 1976, Haukioja 1980), or accident (Tuomi et al. 1988), can impede herbivory. Moreover, because animal tissue typically requires nitrogen concentrations of 7–14 % while plants provide only 0.5–4 %, Mattson (1980) and White (1994) have suggested that dietary nitrogen can limit herbivore growth. Hence, developing plant tissue may offer the advantage to the herbivore of being low in fibre (which can limit digestibility), high in nitrogen (nutritional value), and low in secondary metabolites (defensive chemicals).

Foliage will probably develop faster in a warmer climate, and this should reduce the length of the time interval when herbivores can find young foliage. Because poikilothermic herbivores also develop faster at higher temperatures, however, the net effect is in doubt. For example, simulation of the phenological development of the spruce budworm and its host tree's foliage suggest that the insect is well synchronized with white spruce (Volney and Cerezke 1992). The results of a second simulation study suggest that the budworm is so well synchronized with balsam fir that defoliation is largely unaffected by shifts in weather patterns (Régnière and You 1991).

5.2 Synchrony with Natural Enemies

Of the current theories of budworm population dynamics, the most popular (Royama 1992) claims that a 'complex' of numerically responding invertebrate natural enemies drives the budworm outbreak cycle, almost as though it were a classic predator-prey relationship. Miller and Renault (1976) found that the prevalence of the particular natural enemy species that comprise this complex varies from region to region and from one phase of the budworm's outbreak cycle to another. Two univoltine parasitoids are among the natural enemies identified as important members of this 'complex' (Royama 1992).

One general tactical approach to studying how climate change might affect host-parasitoid dynamics relys on simple mathematical models. For example, Hassell et al. (1993) developed a model in which both the host insect and its parasitoid have a four stage lifecycle: egg, larva, pupa, and adult. The larva is the only host lifestage susceptible to attack and only the adult parasitoid is capable of attack. Hence, the attack rate depends on the synchrony between the appearance of the parasitoid's adult stage and the host's larval stage. Hassell et al. (1993) assumed that, due to differences in the biological constraints on parasitoid and host physiology, the host larvae emerge earlier and earlier relative to the emergence of adult parasitoids as the climate warms. This effectively provided a 'temporal refuge' in which many hosts completed their susceptible larval stage and pupated before the first adult parasitoid emerged, thus totally escaping any possibility of attack. In time the model's host and parasite populations settle at a stable equilibrium, but the sooner the host completes its phenological development relative to the parasitoid, the greater the host's equilibrium density. At the extreme, the entire host population could escape parasitoid regulation altogether in the model by completing its development before the first parasitoid emerged.

6 Extreme Weather

6.1 Drought

Under climate change, North America's boreal forest, especially its most southwestern part, can expect generally drier conditions with an increased probability of heat waves and droughts (Hengeveld 1995), and some insect pests may prosper in such a climate (e.g., Solbreck 1991). Insect herbivores such as the spruce budworm may gain from modifications of host plant physiology brought on by drought stress (but see Larsson 1989). One possible example of such a gain involves sucrose concentration. It acts as a feeding stimulant to late-instar spruce budworm larvae and thus prompts the insect to grow larger (Harvey 1974), and possibly also helps the insect find and accept suitable host material. Sucrose concentrations in balsam fir are typically near 0.004M, but can rise to almost three times this level in moisture-stressed trees (Mattson and

Haack 1987). As a result, sucrose concentrations in moisture-stressed fir are in the range of the peak feeding response of sixth-instar spruce budworm larvae, which occurs between 0.01–0.05M (Albert et al. 1982). This offers some explanation for Mattson et al.'s (1983) observation that spruce budworm larvae grow larger on host plants suffering low to moderate moisture stress.

There is another reason why insect pests may do very well in drier, hotter conditions. The temperature regime of drought stressed plants is often ideal for insect pests, partly because stomatal closure decreases transpirational cooling so that plants enduring drought stress are frequently 2–4 °C warmer than well-watered plants (Mattson and Haack 1987), and partly because of the higher air temperatures and lower humidities generally associated with drought. For example, as the microhabitat of the spruce budworm larva warms towards its optimum, the insect tends to develop more quickly (e.g., Lysyk 1989), suffer less early instar mortality due to cool wet springs (e.g., Lucuik 1984), and increase its fecundity (e.g., Sanders et al. 1978). Besides, budworm mortality from natural enemies may also fall during droughts because the temperature optimum for budworm development of about 26.6 °C (Hudes and Shoemaker 1988) exceeds that of many of its natural enemies [e.g., the entomophthoralean fungal pathogen *Erynia (Zoophthora) radicans* (Perry and Fleming 1988), the microsporidian parasite *Nosema fumiferanae* (Wilson 1974), and the solitary endoparasitoid *Apanteles fumiferanae* (Nealis and Fraser 1988)]. Hence, there are reasons to anticipate greater survival and fecundity of the spruce budworm if the climate becomes generally warmer, drier, and more drought-prone, as predicted. This may not influence the insect's population dynamics in the long-term other than to increase average densities, and consequently, the chronic levels of defoliation.

Increases in chronic defoliation combined with a drier, warmer climate, however, may well add to tree stress, and this could have important consequences. For instance, Wein (1990) hypothesizes a chain of cause and effect relationships whereby increased tree stress leads to greater tree mortality, which in turn, results in faster short-term fuel loading and ultimately in more frequent and severe forest fires.

More frequent occurrence of drought could also change the spruce budworm's outbreak dynamics. Mattson and Haack (1987) argue that synergistic interaction between drought induced changes in the insect's thermal environment and in host plant quality will permit budworm populations to enhance their survival and reproductivity. These authors suggest that given sufficient increase in the insect's survival and reproductivity, budworm populations will be able to 'escape' the regulation of natural enemies more easily and rise to outbreak levels more often. This change in insect outbreak patterns can also be expected to aggravate fire regimes (Stocks 1987).

6.2 Late Spring Frosts

For as long as records have been kept, the white spruce forests of western Canada have endured chronic spruce budworm outbreaks. Because the end of these outbreaks is associated with late spring frosts, Cerezke and Volney (1995) suggest that these frosts contribute to the abrupt collapses of spruce budworm populations on a regional scale. The concern is that, as the climate warms, late spring frosts will become less frequent, and as a result, spruce budworm outbreaks will last even longer (Fleming and Volney 1995). However, as Martinat (1987) and Myers (1988) have pointed out, an association of particular weather patterns with certain phases of the outbreak cycle is not strong evidence of cause and effect, especially when the association is based on patterns among uncontrolled and poorly quantified variables.

7 Natural Selection

"There is good evidence that natural selection continues to 'tune' insect populations to changing environments" (Price 1987, p. 288–289). Many insect species will already have some genotypes preadapted to climate change because of their immense populations. For instance, a 'low density' spruce budworm population has approximately 100 000 fourth instar larvae/ha (Craw-

ford and Jennings 1989), and since outbreaks involve densities 1000 times greater (Royama 1994) and may extend over as much as 72 million ha (Hardy et al. 1986), outbreak populations contain approximately 7.2×10^{15} insects! When such huge population sizes are considered in terms of mutation rates typical for insects (10^{-5} to 10^{-4} [Sager and Ryan 1961]), it is clear that millions of rare genotypes will be produced each generation. Hence, even if all common genotypes, and the vast majority of rare genotypes, prove to be poorly adapted as the climate warms, by force of numbers alone it is clear that at least a few of these rare genotypes are bound to be 'preadapted' to their new, warmer environment.

More common genotypes are also subject to natural selection. For instance, some species with large ranges may be composites of regionally adapted populations (Ayres and Scriber 1994) so common genotypes in the warmer areas may be able to successfully establish in the cooler areas as the climate warms. Harvey (1983a,b), for instance, discovered a genetically-based cline in spruce budworm fecundity and egg weight which appears to be an adaptation to winter conditions. Females from northern sites tend to lay fewer (150 versus 250 per 100 mg moth) but larger (0.22 versus 0.16 mg) eggs than females from southern sites. In the north the larger egg lets the young insect store enough energy to survive the long winters (Harvey 1985). If climate warming shortens northern winters, however, and differences in photoperiod (Taylor and Spalding 1986) do not prove insurmountable, one can expect selection in the north to favor the 67 % fecundity advantage of the southern genotypes, all else being equal. Hence, incidents of devastating mortality need not characterize the impact of natural selection in a changed climate. It may be subtle, non-lethal effects that cause many of the predicted shifts in the abundance and distribution of insect populations. Spectacular events of mass mortality, if they do occur, may be relatively trivial to the overall influence of natural selection in a warming climate.

The global circulation models (GCMs) are projecting a protracted trend to a warmer climate (Intergovernmental Panel on Climate Change 1994). This will allow many generations of directional selection, particularly for insects, since many have at least one generation per year. In this situation, those genotypes which are best adapted to warmer environments are expected to constitute an ever growing fraction of insect populations, and the populations are expected to become incrementally better adapted to warmer climates. This has ramifications for closed environment experiments in which organisms of interest are instantaneously placed in conditions imitating future climates. The results may underrate a species' capability to handle those projected climates because the typically very short duration of the experiments allows little opportunity for genetic changes to occur.

Some suspect that certain insect populations have already reacted to warmer climates. In the northern hemisphere, Jones and Wigley (1990) report that average temperatures are about 0.4 °C higher than they were in 1964. In pursuing this question, Fleming and Tatchell (1994, 1995) studied the Rothamsted Insect Survey's records for daily suction trap catches. The data on five of the most exhaustively sampled aphid species at each of the eight longest operating traps were studied to check if aphid flight periods were occurring sooner in the flight season in more recent years. The authors discovered that these flight periods had moved forward by an average of approximately 3–7 days in the previous 25 years. As anticipated for climate warming, on an individual basis most of the trends lacked statistical significance, but when the trends for all species-site associations were considered simultaneously, the consistency in trend direction toward earlier flight periods was statistically significant ($P < 0.0001$).

8 Summary and Conclusion

Climate warming's greatest impact on ecosystem function and composition in the boreal forest of North America will likely be brought about by changes in disturbance regimes such as fire and insect outbreaks. One practical approach to trying to forecast such changes is to focus on the lifecycles of "representative types" of insect species.

Because it has been the more exhaustively

studied than any other insect defoliator of North America's boreal forest, the spruce budworm, *Choristoneura fumiferana* was selected as a "representative type". It was argued that limitations to climate-induced changes to its population growth rate would be mediated as indirect effects through interactions with other trophic levels in the spruce budworm–forest system. Consideration of the migratory potential of different components of this system, and of this system's dynamics as a whole, suggested that the distributions of established and regenerating spruce and fir may move separately in response to climate change. A simple model of such a system was used to demonstrate the potential importance of threshold and historical effects and the difficulties such effects pose for forecasting. It was suggested that in particular circumstances severe spruce budworm outbreaks could destroy the ability of tree populations to renew themselves and this could lead to local extinctions. For the spruce budworm key uncertainties centre on how disruptive episodes of extreme weather might be and on what influence climate warming might have on natural enemy interactions. Natural selection may not exert itself quickly, but it may become the dominant process if the climate continues to warm for some time.

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Total of 92 references

Need for Integrated Policy Oriented National Research Programmes:

the Second Phase (1995–2001) of the Dutch National Research Programme on Global Air Pollution and Climate Change NRP

Renaat S.A.R. van Rompaey

1 Introduction

As a follow-up on acid rain programmes many countries (Heij and Erisman 1995), e.g. Finland, the Netherlands, Sweden, launched national research programmes on Climate Change by the end of the eighties. Other countries centred new programmes on Global Change, such as Belgium, United Kingdom, Germany, Canada. Also the European Community included the climate issue in the research programme 'Environment & Climate'.

The conclusions of the Intergovernmental Panel on Climate Change (IPCC) shifted in the successive assessment reports (IPCC 1990, 1992, 1996) from possible climate change to actual climate change and will maybe attain quantified climate change in a couple of years.

The Netherlands decided in 1989 to strongly support research efforts in this field (Schneider et al. 1994), because they realised the vulnerable position of the 'Low countries by the sea' in case of sea level rise or changes in hydrological regimes of large rivers like Rhine and Meuse. The Dutch are very conscious about environmental issues as their country is very densely populated.

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Much of the wealth of the country and of its environmental care is based on fossil fuel consumption and the availability of a large resource of natural gas. The climate change problem undermines the unlimited use of fossil fuel by asking for drastic reductions in CO_2 emissions. Even a rich country like the Netherlands has a very hard time to deal with the pollutant CO_2.

2 Evaluation of the First Phase (1990–1995) of the Dutch Climate Change Research Programme NRP

2.1 Organisation

In total 145 research contracts were signed with a total additional funding of 60 Mf (= 29 Mecu). Some projects were considered too small, containing only one PhD researcher. Collaboration between projects on related subjects was facultative and not included in the contract. International collaboration was in many projects not really developed. Project leaders referred to core projects of the large international programmes WCRP, IGBP and HDP, but there have been few international activities organised. A number of projects produced only a report, whereas only publications in international journals comply with

the programme's objective to have impact in the international science arena.

In the same way, international participation in the closing conference of the first phase in Maastricht, 6–9 December 1994 was rather limited (Zwerver et al. 1995).

2.2 Research Themes

Five themes were identified in 1990: climate system, causes of climate change (greenhouse gases), impacts of climate change, integration and assessment, solutions. There appeared to be close links between the themes climate system and causes. Indeed, greenhouse gases are part of the system. A number of projects on the impact of increasing UV radiation because of loss of stratospheric ozone have been included in the programme under theme 'impacts'.

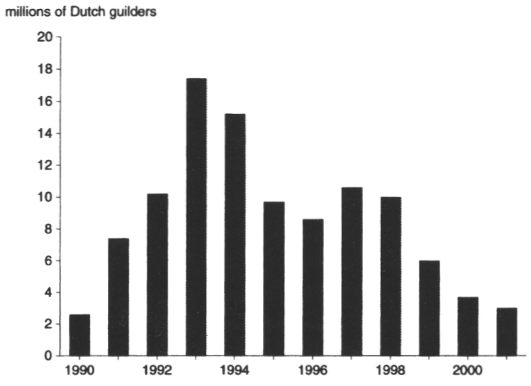


Fig. 1. Availability of funds in the Dutch Climate Change Research Programmes, first phase 1990–1995 and second phase 1995–2001 (foreseen).

3 New Directions for NRP Second Phase (1995–2001)

3.1 Organisation

The number of projects will be more restricted, only about 50 for a total additional funding of 45 Mf (22 Mecu). By October 1995, already 25 contracts had been signed. This time, projects are larger, including several research institutes. In this way, collaboration is included in the contract, as is integration of knowledge. Participation in international programmes will be controlled by the Programme Office. A list of intended publications is included in the contract.

The management of NRP is carried by RIVM Bilthoven, the Dutch National Institute for Public Health and the Environment, in cooperation with NWO, the Netherlands Organisation for Scientific Research, The Hague (NRP Programme Office 1995).

3.2 Research Themes

Based on the experience of the first phase, the themes 'climate system' and 'causes of climate change' have been merged into the single theme 'climate system'. The theme 'impacts of climate change' has been reoriented towards 'vulnerability of society and ecosystems to climate change'.

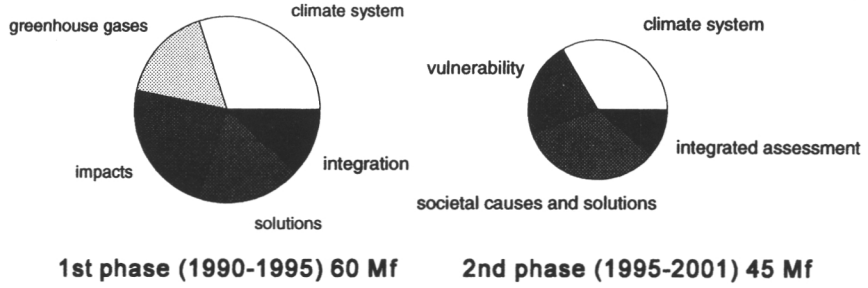


Fig. 2. Distribution of funds over research themes in first and in second phase of NRP.

The theme 'solutions to the climate change problem' is now called 'societal causes and solutions', and the fourth theme deals with 'integrated assessment of the climate change problem' and also integrates knowledge from the first three themes.

A considerable shift occurred in the funds earmarked for natural sciences towards social sciences (see Fig. 2). In the Programming Memorandum (Berk et al. 1994) it is stated that research projects must be less targeted on detailed experimental work, but must work at higher levels of integration. Within the theme 'vulnerability' research should not be limited to dose-effects studies, but perform a complete system analysis and analyse the contribution of climate change as a supplementary stress. This involves that methods shift from single factor analysis to multi-stress approaches.

3.3 Selection of Research Topics for 1995–2001

From April 1994 to June 1995, NRP went through a process of selection of tenders and proposals following the first of three calls for proposals (21 Mf = 10 Mecu available; Berk et al. 1995). Initially 209 tenders were submitted with a demand for funds exceeding 10 times the available budget. Selected tenders were grouped and 65 potential project leaders were asked to write full proposals. These have been peer reviewed by both foreign and national reviewers.

The selection committees decided to propose 25 projects for funding. These cover the following topics:

- theme 'climate system': methane and regional upscaling, CO_2 fluxes between oceans and atmosphere and between grasslands and atmosphere, aerosols and clouds in relation to the radiative balance of the Earth, ocean circulation modelling, continental ice sheets, modelling of decadal climate variability
- theme 'vulnerability to climate change': tidal flats and coastal aquatic and terrestrial ecosystems, Rhine basin modelling, nutrient poor forest ecosystem development, fresh water wetlands, productivity and water balance of forests
- theme 'solutions': causes of tropical deforestation, biomass as fuel, material systems, energy efficiency, household consumption patterns, tradeable CO_2 permits
- theme 'integrated assessment': development and user interface of the IMAGE model, land use change modelling

From January 1996 to June 1996, NRP will launch a second call with 13 Mf (= 6 Mecu) available. The third call is foreseen for 1997 with a last 11 Mf (= 5 Mecu). These calls are more policy steered than the first call. Dutch policy makers from several ministries will state clearly which knowledge needs they have and the programming committees are asked to translate these needs into feasible terms of reference of research projects. Research teams will then be invited to tender for these projects.

4 Perspective for Research in the Field of Man and Environment: towards a Programme on Sustainable Global Development

I hope that in this way climate change research in the Netherlands will contribute to national and international policy development to cope with the serious problem of climate change. A more intensive dialogue between scientists and decision makers is essential in this process.

I also hope that NRP funding will trigger the formation of international research teams and networks that can deal with the environmental problems of the 21st century. NRP is also a unique forum for natural and social scientists to meet and to discuss the problems of the present and next generations. This forum should be continued after the end of NRP in 2001. Mankind is facing a series of threatening, undesired and unstable developments with inevitably touch all regions and all nations on this earth. Moreover mankind has to choose between welfare and quality of life now, and reasonable welfare for the next generations.

Science has never been so much oriented to-

wards the entire earth, and even more intriguingly, towards the next century. The future is our major concern, and surviving the next century will be the challenge of human genius.

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Part II
Biodiversity

Effects of Intensity and Frequency of Harvesting on Abundance, Stocking and Composition of Natural Regeneration in the Acadian Forest of Eastern North America

John C. Brissette

In a silviculture experiment in east-central Maine, USA, natural regeneration was sampled to measure the effects of: (1) a range of partial harvest intensities, and (2) repeated partial harvest at one intensity. Under the first objective, five treatments were compared with residual basal areas ranging from 15 to 24 m^2 ha^{-1} for trees ≥1.3 cm diameter at breast height. For the second objective, regeneration was evaluated after four harvests at 5 year intervals. Prior to harvests, the overstory of all the treated stands was dominated by *Tsuga canadensis* (L.) Carr., *Picea* spp. A. Dietr., and *Abies balsamea* (L.) Mill. Eleven species or species groups were identified among the regeneration: *A. balsamea*, *T. canadensis*, *Picea* spp., *Thuja occidentalis* L., *Pinus* spp. L., *Betula papyrifera* Marsh., *Acer rubrum* L., *Betula populifolia* Marsh., *Populus* spp. L., *Fagus grandifolia* Ehrh. and *Prunus serotina* Ehrh. Regeneration abundance was measured as counts of seedlings or sprouts taller than 15 cm but with diameters less than 1.3 cm at breast height (1.37 m). Regardless of harvest treatment, total regeneration was profuse, ranging from over 25 000 to nearly 80 000 trees ha^{-1}. Regeneration was dominated by conifers with a total angiosperm component of 10 to 52 percent approximately 5 years after harvest and 11 to 33 percent after 10 years. Consequently, in forests of similar species composition, tree regeneration following partial harvests should be sufficiently abundant with an array of species to meet a variety of future management objectives.

Keywords natural regeneration, harvest intensity, partial harvest, repeated harvests, silviculture

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1 Introduction

In eastern Canada the boreal forest extends south to about latitude 47°N. In the northeastern United States the northern boundary of the broadleaf forest is at about 42°N. Between is a mixed-species forest dominated by conifers. Gymnosperms include boreal species such as balsam fir (*Abies balsamea* (L.) Mill.) and a number of spruces (*Picea* spp. A. Dietr.). Also included are species at the northern limit of their ranges, like eastern hemlock (*Tsuga canadensis* (L.) Carr.) and pines (*Pinus* spp. L.). East of the Great Lakes, this region is termed the Acadian Forest (Rowe 1972). Here stand-replacing fires are less frequent than in other boreal and temperate forests (Wein and Moore 1977, 1979). Other common natural disturbances are insect epidemics and wind storms that often cause sporadic, partial mortality. Such disturbances may occur only once during the life of the relatively short-lived fir, but several times during the life of spruce, hemlock or pine.

Selective logging for high value products was common during the 18th and 19th centuries. The rate of harvesting accelerated in the early 20th century as the pulp and paper industry expanded in the region. Following a severe outbreak of spruce budworm (*Choristoneura fumiferana* Clemens) that started in the mid-1970s, clearcut harvesting has become a common silvicultural practice (Seymour 1992). In recent years, however, impacts of production silviculture on forest ecosystems have been questioned from a number of perspectives, including diversity (Hunter 1990) and sustainability (Rowe 1994). Alternative approaches to forest management have been proposed which recommend patterning silvicultural systems after natural disturbance regimes, placing a greater emphasis on species and age class diversity (Seymour and Hunter 1992), and exploring a broad range of silvicultural options (Burton et al. 1992). Such strategies rely on partial harvests to provide needed wood products while retaining a more or less continuous forest canopy.

A critical question for today's forest manager is: What are the impacts of partial harvesting on natural regeneration? A number of attributes of regeneration are important. Abundance is a count by species or of the total. Stocking is the proportion of the site occupied by a species or in total. Both of these measures are meaningful, abundance indicates how many seedlings or sprouts there are in the area of interest, while stocking expresses how well they are distributed throughout that area. Composition gives an indication of what species will likely be in the future stand.

What is certain about the Acadia Forest is that natural reproduction is prolific (Smith 1991), although not always of the species most desired by managers; and that advance regeneration is essential to ensure timely stand establishment following cutting (Seymour 1995). However, little is known about how the intensity and frequency of partial harvesting affects natural regeneration. The objectives of this paper are to: (1) describe impacts of a range of partial harvest intensities on abundance, stocking and species composition of natural regeneration, and (2) examine effects of repeated partial harvesting on those attributes of regeneration.

2 Study Site

This study is part of a silviculture experiment at the Penobscot Experimental Forest (PEF) located in the towns of Bradley and Eddington, in Penobscot County, Maine. The PEF is 1540 ha in size and its center is at approximately 44°52'N, 68°38'W. It was established in 1950 for the purpose of conducting timber management research in the northeastern spruce-fir forest type. History of the PEF prior to 1950 is not well documented. What is known is that only a small portion was ever cleared for agriculture or grazing and that most of the area was cut lightly in the recent past (perhaps 20 to 40 years before 1950) for pine, hemlock and spruce sawlogs. Earlier cutting may have been heavier; presence of charcoal and old burned stumps in some areas indicate fires following cutting of pine stands (Safford et al. 1969). In 1950, stands on the PEF were 60 to 100 years old with a few older individual trees scattered throughout the area.

Under a recent ecological land classification, the PEF is located in the Central Maine Coastal and Interior Section of the Laurentian Mixed

Forest Province (McNab and Avers 1994). Prevailing winds are from the west, but the Atlantic Ocean is less than 100 km east; consequently, weather is influenced by both continental and maritime air masses. The highest elevations between the PEF and the ocean are highlands less than 400 m, so orographic lifting has little influence on weather in the area. The elevation of the PEF itself is less than 75 m above sea level.

The 30-year (1951–1980) normal (i.e. mean annual) temperature for nearby Bangor, Maine, is 6.6 °C. The warmest month is July with a normal temperature of 20.0 °C; this is higher than the 18 °C mean July isotherm that Kuusela (1990) used to define the southern boundary of the boreal coniferous forest. The coldest month in Bangor is January with a normal temperature of –7.7 °C. Normal precipitation is 1060 mm per year, with 48 percent of that falling from May through October.

Glacial till is the principal soil parent material on the PEF. Soil types vary from well-drained loams and sandy loams on glacial till ridges to poorly and very poorly drained loams and silt loams in flat areas between these low-profile ridges. Along water courses are deposits of marine sediments. Very few sand and gravel deposits are present. A few organic deposits also occur. Till ridges, flats and streams are often in close proximity, resulting in extremely variable site conditions on relatively small areas.

A list of woody plants (trees and shrubs) of the PEF includes 103 species in 60 genera (Safford et al. 1969). Of those, 41 are trees, 13 of which grow to become large trees; i.e., >61 cm diameter breast height (DBH measured at 1.37 m).

The silviculture experiment that is the focus of this research occupies about 160 ha in the most conifer-dominated part of the experimental forest, none of it in that portion that had been cleared for agriculture or grazing. The experiment is concentrated on somewhat well-drained to somewhat poorly-drained soils; however, even within the study, soil type and drainage class can vary markedly.

The forest canopy within the silvicultural experiment is dominated by a mixture of species. Gymnosperms include: eastern hemlock; spruce, mostly red (Picea rubens Sarg.) with some white (*P. glauca* (Moench) Voss); balsam fir; northern white-cedar (*Thuja occidentalis* L.); eastern white pine (*Pinus strobus* L.); and, infrequently, tamarack (*Larix laricina* (Du Roi) K. Koch) or red pine (*P. resinosa* Ait.). The most common angiosperms are: red maple (*Acer rubrum* L.); paper birch (*Betula papyrifera* Marsh.); gray birch (*B. populifolia* Marsh.) and aspen, both quaking (*Populus tremuloides* Michx.) and bigtooth (*P. grandidentata* Michx.). Individuals of sugar maple (*Acer saccharum* Marsh.), yellow birch (*B. alleghaniensis* Britton), American beech (*Fagus grandifolia* Ehrh.), white ash (*Fraxinus americana* L.), black cherry (*Prunus serotina* Ehrh.), northern red oak (*Quercus rubra* L.,) and American basswood (*Tilia americana* L.) are scattered throughout the study area.

3 Methods

The silviculture experiment was established between 1952 and 1957. A number of treatments were imposed, including both even-age and uneven-age regimes. The treatments were assigned to compartments at random and replicated twice, each replicate or compartment averaging 10 ha. The experiment has eight treatments; this paper focuses on five that incorporate partial harvests: fixed and modified diameter limit cutting, and selection silviculture with 5-, 10-, and 20-year harvest intervals; FDL, MDL, S05, S10 and S20, respectively (Table 1).

In the diameter limit treatments, trees are harvested when they reach specified diameters and those diameters vary with species (Table 1). The most commercially valuable species have the largest diameter limits. In FDL compartments, the diameter limits are strictly adhered to and the harvest interval varies, depending on when a compartment regrows to its initial volume. Harvesting has occurred at 21-year intervals so far. Under the MDL treatment, diameter limits are guides, allowing the research forester to adjust for density and tree quality. Furthermore, the harvest interval does not vary, instead periodic growth is harvested every 20 years.

The selection compartments are managed with goals for species composition, density and diameter-class distribution (Table 1). *Picea* spp. is

Table 1. Experimental prescriptions for five partial harvest treatments at the Penobscot Experimental Forest, east-central Maine, USA.

Treatment	Harvest interval	Experimental prescription
FDL	When regrowth volume reaches stand volume before first harvest (i.e. 148 m^3 ha^{-1})	At harvest trees are cut if DBH exceeds: *Pinus* spp., 29 cm *Picea* spp. and *Tsuga canadensis*, 24 cm *Betula papyrifera*, 22 cm *Thuja occidentalis*, 19 cm all other species, 16 cm
MDL	Every 20 years, harvest not to exceed periodic growth	At harvest most trees are cut if DBH exceeds: *Pinus* spp. and *Picea* spp., 37 cm *Tsuga canadensis*, 32 cm *Betula papyrifera*, 24 cm *Thuja occidentalis*, 19 cm *Abies balsamea*, 16 cm all other species, 14 cm These limits are modified to capture mortality or to leave trees as seed sources or to provide wind protection.
S05	Every 5 years	*Stand structural goals*: post-harvest basal area, 26.4 m^2 ha^{-1}; maximum diameter before harvesting, 51 cm; quotient (q) between 2.54 cm diameter classes, 1.4. *Species composition goals* (percent basal area of trees ≥1.3 cm DBH): *Picea* spp., 35–55; *Tsuga canadensis* and *Abies balsamea*, 15–25; *Pinus* spp., *Thuja occidentalis*, *Betula papyrifera*, and all other species combined, each 5–10. *In practice*, cutting has emphasized capturing mortality, improving stand quality and species composition over strict adherence to residual basal area, maximum diameter and q goals.
S10	Every 10 years	Same as S05 except post-harvest basal area goal is 23.0 m^2 ha^{-1}.
S20	Every 20 years	Same as S05 except post-harvest basal area goal is 18.4 m^2 ha^{-1}.

favored over all other trees. Density goals for the beginning of an operating interval (i.e. following harvest) are highest for S05, lowest for S20, and intermediate for S10. From the maximum DBH goal of 51 cm for all selection treatments, the desired number of trees in each successively smaller 2.54 cm DBH class is defined by a multiplier, or "q", of 1.4.

These five treatments differ in two major respects, harvest intensity and harvest frequency (Table 1). Because S05 is harvested at 5-year intervals, S10 at 10-year intervals and the other treatments at or near 20-year intervals, there have been two periods when all the compartments were harvested over relatively short time spans: at the start of the experiment in the mid-1950s and 20 years later in the mid-1970s (Fig. 1). A third such period is underway at present but will not be complete until after the 1997 growing season.

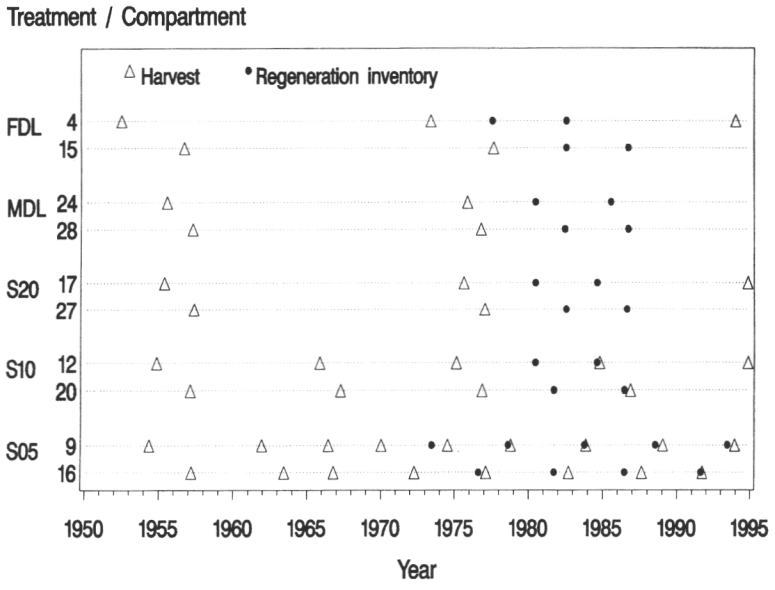


Fig. 1. History of partial harvest and regeneration inventories for selected treatments and their replicates at the Penobscot Experimental Forest, east-central Maine, USA.

Periodic measurements of stand composition and structure are taken on a series of permanent plots established in each compartment on a grid with a random start. These plots are a series of two concentric circles of different sizes with the same plot center. All trees with DBH ≥ 1.3 cm are measured on 0.20 ha plots. All trees with DBH ≥ 11.4 cm are measured on 0.81 ha plots. The number of such plots ranges from 13 to 23 per compartment with the 0.81 ha plots representing an average 15.2 percent sample and the 0.20 ha plots an average 3.8 percent of the compartment area.

Regeneration inventories did not begin until the 1960s, when three 4.05 m^2 plots were established on the circumference of the 0.20 ha plots (an average 0.23 percent sample of the compartment). On each regeneration plot, counts are made by species of each tree ≥15 cm tall but with a DBH < 1.3 cm. In treatment S05, regeneration plots are measured pre- and post-harvest. In other treatments, plots are measured before and after cutting and at about 5-year intervals between harvests.

The purpose of this paper is to examine post-harvest natural regeneration responses; consequently, I chose the most recent period, 1973 to 1977, when all the treatments were logged to compare the effects of harvest intensity on regeneration (Fig. 1). Treatment effects for both first and second inventories after harvest were compared, about 5 and 10 years post-harvest, respectively. To examine impacts of repeated partial cutting, four harvests between 1970 and 1987 in S05 were compared (Fig. 1).

Because a tree had to be at least 15 cm tall to be counted in this study, at the first inventory most would have been advanced regeneration; i.e., established seedlings at the time of harvest or developed from seed or sprouts from trees in the pre-harvest stand. At the second inventory, some of the smaller regeneration would likely have originated from trees in the post-harvest stand.

Besides differences in harvest intensity and frequency, there were differences among compartments in species composition and size structure prior to the mid-1970s harvest (Table 2). *Tsuga canadensis* and *Picea* spp. dominated the overstory of all the compartments. Thus, throughout the study area, they were the most likely seed

Table 2. Structure and composition of likely seed producing tree species or species groups prior to partial harvest in selected treatments at the Penobscot Experimental Forest, east-central Maine, USA.

Species/ DBH (cm)	Treatment[1] / Compartment									
	FDL		MDL		S05		S10		S20	
	4	15	24	28	9	16	12	20	17	27
	Trees ha^{-1}									
Tsuga canadensis										
11–20	92	83	112	62	86	82	59	19	57	22
21–30	32	6	66	58	53	66	45	13	61	29
31–40	1	1	5	4	19	45	17	14	34	12
>40	1			1	10	1		1		
Picea spp.										
11–20	96	41	95	62	48	36	103	84	43	63
21–30	31	9	60	80	55	37	87	85	53	54
31–40			3	22	13	18	15	17	17	21
>40					1	1		1	1	<1
Abies balsamea										
11–20	113	104	68	112	136	66	227	107	59	111
21–30			1		2	3	13	6		
31–40										
>40										
Thuja occidentalis										
11–20	50	62	45	52	16	43	53	54	35	47
21–30	3	8	5	1	6	6	4	5	8	4
31–40			1					<1		
>40										
Pinus spp.										
11–20	1	1		4						
21–30	2	1	3	2	4	1	1	2		<1
31–40			3	4	4		1	1		<1
>40					9			<1	2	
Acer rubrum										
11–20	75	24	73	30	25	17	87	43	14	15
21–30	3	3	1	9	15	3	20	5	1	2
31–40				1		2				
>40				1						
Betula papyrifera										
11–20	71	4	16	13	27	2	32	3	10	6
21–30	1		5	3	20	5	7	4	3	1
31–40					1			<1		
>40										
Other angiosperms										
11–20	27	6	21	4	4	1	6	1	1	1
21–30		1	1		5		3			
31–40	1									
>40					1					

[1] Treatments: FDL = fixed diameter limit; MDL = modified diameter limit; S05 = selection, 5-year harvest interval; S10 = selection, 10-year harvest interval; S20 = selection, 20-year harvest interval.

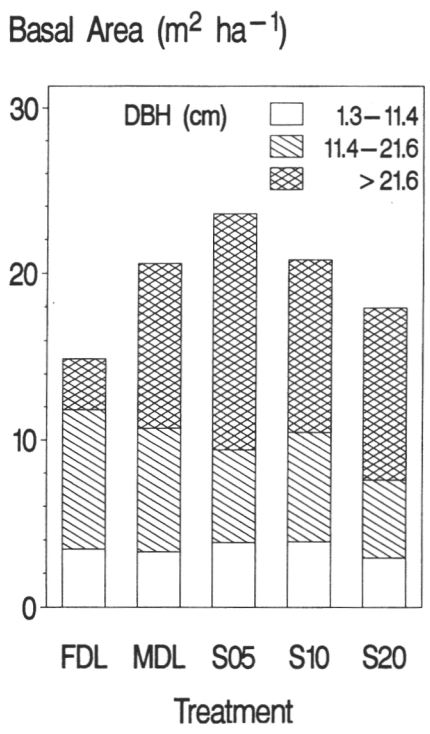


Fig. 2. Residual basal areas for three size classes of trees following harvesting stands under: fixed diameter limit cutting (FDL), modified diameter limit cutting (MDL), and selection silviculture with 5- (S05), 10-(S10), and 20- (S20) year harvest intervals.

producers contributing to regeneration that was present following harvest. However, the number of trees of various species in each size class differed markedly, even between compartments within a treatment.

Following the mid-1970s harvest, residual basal areas varied among treatments except between MDL and S10, which were nearly identical (Fig. 2). S05 had the greatest residual basal area and the most in large trees. FDL had the least total basal area and the least in large trees; in fact, basal area of trees larger than 21.6 cm DBH was less ($p = 0.01$) in FDL than in the other treatments. There were no differences among the smaller size classes, however.

Harvests were conducted by commercial logging crews that felled trees using chainsaws, delimbed them at the stump, and transported logs roadside with rubber-tired skidders. Harvesting in the various compartments occurred during different seasons of the year and permanent plots were treated no different than the rest of the stand.

3.1 Data Collection and Analyses

Comparisons among silvicultural treatments were made with analysis of variance (ANOVA) for a completely random experimental design. Treated compartments (replicates) were the experimental units and plots were sampling units. Treatment and inventory, first and second (except for S05) after harvest, were the independent variables. Response variables were abundance and stocking values by species or species groups. Separate analyses were conducted for each species or species group, and for total gymnosperms, total angiosperms and total regeneration. Differences among treatment means were evaluated using Duncan's New Multiple Range Test (Steel and Torrie 1980).

To analyze the effect of repeated partial harvesting in S05, an ANOVA for each species, group or total was conducted with harvests as the independent variable, and number and stocking as response variables. For species or groups where the effect of harvest was significant ($p \leq 0.05$), the relationship was examined by partitioning harvest sums of squares by orthogonal polynomials (Steel and Torrie 1980).

Eleven tree species or species groups are identified in this study: *Abies balsamea*, *Tsuga canadensis*, *Picea* spp., *Thuja occidentalis*, *Pinus* spp., *Betula papyrifera*, *Acer rubrum*, *Betula populifolia*, *Populus* spp., *Fagus grandifolia*, and *Prunus serotina*. Because young *Picea* seedlings can be difficult to identify to species, they were grouped. However, based on saplings and larger trees, it is clear that *P. rubens* is the dominate spruce with *P. glauca* occasionally present and *P. mariana* rarely found on the sites in this study. Although *Pinus* species are also grouped, *P. strobus* is the dominate pine with *P. resinosa* seedlings seldom present. Small *Populus* seedlings or sprouts can also be difficult to identify to species, so they too were grouped.

4 Results and Discussion

4.1 Treatment Effects on Tree Regeneration

Total regeneration was profuse (Table 3). There were over 27 000 trees ha^{-1} in the least abundant treatment (FDL) at the first inventory (Inv 1), and it increased to over 42 000 trees ha^{-1} at the second (Inv 2). At Inv 1, treatments S10 and S20 had significantly more regeneration than the other treatments. S20 and S10 still had the most regeneration at Inv 2, but S10 no longer differed from MDL. Not only was regeneration prolific, it was well distributed within the treated compartments (Table 4). Even in the poorest stocked treatment (MDL), 93 percent of the area was regenerated at Inv 2.

Coniferous species dominated regeneration in all treatments. With conifers comprising 90 percent of total regeneration, S05 had the most gymnosperms at Inv 1. Among the five treatments, only in S20 was the number of regenerating angiosperms greater than gymnosperms, 52 versus 48 percent of total regeneration. However, that was just at Inv 1, by Inv 2 conifers clearly dominated with 67 percent of the total. Treatment S20 had the lowest stocking of gymnosperms at Inv 1 (70 percent of the area), but the highest at Inv 2 (95 percent) (Table 4).

In total abundance of angiosperms, there were no differences among treatments with an average of 28 percent of all regeneration at Inv 1 and 23 percent at Inv 2 (Table 3). Yet, there were differences in stocking (Table 4). At Inv 1, S05, with 34 percent stocking of angiosperms, had less than other treatments except S10. S10 still had the least stocking of angiosperms (61 percent) at Inv 2, but differed only from S20, which had the most (84 percent).

Overall, *Abies balsamea* was the most abundant species and also had the greatest stocking at both inventories, although in MDL and S05 *Tsuga canadensis* was more prevalent (Tables 3 and 4). Among species or species groups, only *Thuja occidentalis* exhibited a difference in abundance with S05 having significantly more than the other treatments. Stocking of *T. occidentalis* at Inv 1 differed only between S05 and MDL. Treatments differed in stocking of *Betula papyrifera* and *B. populifolia* as well. S20 had the greatest stocking of both species at both inventories; however S20 only differed from the other selection treatments, not from the diameter limit treatments.

The three most common gymnosperms, *Abies balsamea*, *Tsuga canadensis* and *Picea* spp., accounted for an average of 71 percent of regeneration at Inv 1 and 75 percent at Inv 2 (Table 3). Availability of seed producing parent trees, site characteristics and seed attributes all contributed to the success of these species.

Abies balsamea, *Tsuga canadensis* and *Picea* spp. were the most common overstory species prior to the partial harvests, providing a ready seed source. However, *A. balsamea* trees were much smaller than the other two species, almost all in the 11–20 cm DBH size class (Table 2).

Seedlings of all three species are well adapted to growing in a shady, cool and moist understory; consequently, all of them are classified as very tolerant (Spurr and Barnes 1980). Shade provided by residual trees was apparently adequate to provide numerous germination sites, as there were no differences in abundance or stocking for these species among the treatments.

Seeds of *Abies balsamea* are 2 to 3 times heavier, on average, than those of *Picea rubens* or *Tsuga canadensis* (Franklin 1974, Safford 1974, Ruth 1974). Larger seeds provide greater reserves which may account for more rapid and deeper penetration of roots of *A. balsamea* seedlings compared to *P. rubens* (Frank 1990). Seeds of all three are wind disseminated and those of *A. balsamea* and *P. rubens* often disperse 100 m or more (Frank 1990, Blum 1990). However, because of their small wings, most seeds of *T. canadensis* fall within one tree height (i.e., 20 m or less at the study site) of the parent tree (Godman and Lancaster 1990). Thus, seed characteristics, which affect early seedling development, probably account for why *A. balsamea* was more common than *T. canadensis* or *Picea* spp.

Among common regenerating angiosperm trees, understory tolerance ranges from very intolerant (*Betula papyrifera*, *Populus* spp.) to tolerant (*Acer rubrum*) (Spurr and Barnes 1980). It is notable that the very intolerant *B. papyrifera* and the tolerant *A. rubrum* were the most abundant angiosperms (Table 3) as well as those with

Table 3. Regeneration abundance following partial harvest in selected treatments at the Penobscot Experimental Forest, east-central Maine, USA.

Species/ Inventory	SE[2]	Treatment[1]					Mean[3]
		FDL	MDL	S05	S10	S20	
		Trees ha^{-1}					
Abies balsamea							
1	5389	10131	9551	10129	27071	10535	13856
2	6539	14782	15404	[4]	32708	18227	20622
Tsuga canadensis							
1	4085	6014	10220	15636	11399	9537	10446
2	4817	9616	18059		15202	25723	16933
Picea spp.							
1	1782	2600	3822	4267	9233	4933	5061
2	1910	4563	6952		12596	8389	8208
Thuja occidentalis							
1	87	156b[5]	83b	1041a	392b	125b	351
2	385	536	672		1441	1037	934
Pinus spp.							
1	361	136	156	792	117	0	229
2	100	211	178		98	77	140
Total gymnosperms							
1	9518	19036	23831	31867	48214	25127	29944
2	9934	29739	41265		62044	53456	46845
Betula papyrifera							
1	6666	1976	5041	535	1932	17467	5324
2	6653	4460	4829		1078	16069	6434
Acer rubrum							
1	1097	3864	4878	2544	5234	3141	3968
2	991	4225	4640		5411	5417	4929
Betula populifolia							
1	526	1583	424	0	363	1706	833
2	1224	2801	588		667	2801	1723
Populus spp.							
1	1107	83	391	21	167	2440	612
2	683	62	166		99	1399	419
Fagus grandifolia							
1	719	475	697	73	0	1513	542
2	524	560	380		0	935	458
Prunus serotina							
1	55	21	83	0	59	170	66
2	134	84	378		69	105	151
Total angiosperms							
1	7649	8115	11660	3352	7753	26800	11501
2	8085	12430	11276		7322	26215	14119
Total regeneration							
1	3052	27153b	35490b	35218b	55968a	51928a	41446
2	4983	42170c	52539bc		69365ab	79671a	60964

[1] Treatments: FDL = fixed diameter limit; MDL = modified diameter limit; S05 = selection, 5-year harvest interval; S10 = selection, 10-year harvest interval; S20 = selection, 20-year harvest interval.
[2] Pooled standard error from analysis of variance.
[3] Weighted by area in each treatment.
[4] In this treatment, only one inventory is taken between harvest intervals.
[5] Within species and inventory, values with different letters are significantly different ($p \leq 0.05$); if there are no letters, differences are not significant at that level.

Table 4. Regeneration stocking following partial harvest in selected treatments at the Penobscot Experimental Forest, east-central Maine, USA.

Species/ Inventory	SE[2]	Treatment[1]					Mean[3]
		FDL	MDL	S05	S10	S20	
		percent stocking					
Abies balsamea							
1	13.43	70.6	54.8	77.2	76.6	56.5	67.4
2	8.11	76.1	69.6	[4]	89.7	78.7	79.0
Tsuga canadensis							
1	14.02	61.0	60.2	75.6	51.2	57.6	60.7
2	8.14	70.8	67.4		57.6	84.7	69.8
Picea spp.							
1	12.37	49.4	39.0	55.2	56.8	42.1	48.8
2	4.78	62.9	53.6		68.6	66.0	63.1
Thuja occidentalis							
1	2.16	4.6ab[5]	1.6b	11.4a	8.3ab	3.6ab	5.9
2	6.54	13.4	14.2		18.6	13.4	15.0
Pinus spp.							
1	5.84	4.2	6.3	11.6	4.8	0.0	5.2
2	2.96	6.0	5.9		4.0	1.9	4.4
Total gymnosperms							
1	11.53	82.8	70.4	90.0	82.2	70.2	79.2
2	3.24	92.0	86.9		92.1	94.6	91.5
Acer rubrum							
1	5.34	46.8	49.8	31.6	51.2	44.0	45.0
2	6.34	57.8	57.1		60.3	62.6	59.5
Betula papyrifera							
1	10.07	31.0ab	42.2ab	6.6b	17.1b	56.7a	30.6
2	10.03	43.4ab	48.5ab		11.9b	62.2a	40.5
Betula populifolia							
1	4.12	11.4ab	10.4ab	0.0b	5.2b	23.0a	10.0
2	5.25	16.0	10.4		5.6	24.4	14.1
Populus spp.							
1	9.23	2.5	2.5	0.8	3.2	20.2	5.8
2	7.45	1.6	3.0		2.8	16.2	5.8
Fagus grandifolia							
1	3.92	6.4	5.2	3.0	0.0	8.8	4.6
2	4.69	8.6	5.2		0.0	8.1	5.4
Prunus serotina							
1	1.71	0.8	2.5	0.0	2.4	5.7	2.3
2	1.99	2.2	8.9		2.0	1.9	3.6
Total angiosperms							
1	6.10	66.9a	63.2a	33.8b	56.0ab	76.2a	59.6
2	4.91	77.2ab	72.6ab		61.9b	83.6a	73.6
Total regeneration							
1	3.76	91.5	84.8	90.0	90.4	92.6	90.0
2	0.80	98.7ab	92.8c		96.0b	100.0a	97.0

[1] Treatments: FDL = fixed diameter limit; MDL = modified diameter limit; S05 = selection, 5-year harvest interval; S10 = selection, 10-year harvest interval; S20 = selection, 20-year harvest interval.
[2] Pooled standard error from analysis of variance.
[3] Weighted by area in each treatment.
[4] In this treatment, only one inventory is taken between harvest intervals.
[5] Within species and inventory, values with different letters are significantly different ($p \leq 0.05$); if there are no letters, differences are not significant at that level.

Table 5. Regeneration abundance following partial harvests repeated at about 5-year intervals at the Penobscot Experimental Forest, east-central Maine, USA.

Species	SE[2]	Harvest[1] 4	5	6	7	Mean	Trend[3]
		Trees ha^{-1}					
Tsuga canadensis	6542	11458	15636	19901	13608	15151	
Abies balsamea	609	9981	10130	10612	7294	9504	Quadratic
Picea spp.	774	2800	4267	6767	5582	4854	Linear
Thuja occidentalis	245	601	1041	1313	1465	1105	
Pinus spp.	595	664	792	476	348	570	
Total gymnosperms	6465	25505	31867	39068	28296	31184	
Acer rubrum	670	2690	2544	2228	2617	2520	
Betula papyrifera	536	1030	535	499	388	613	
Fraxinus americana	267	443	95	158	274	243	
Fagus grandifolia	26	251	73	73	115	128	Quadratic
Quercus spp.	21	21	21	21	21	21	
Total angiosperms	736	4497	3352	3031	3519	3599	
Total regeneration	6458	30002	35218	42099	31815	34783	

[1] Data following earlier harvests are not available.
[2] Pooled standard error from analysis of variance.
[3] When analysis of variance indicated significant ($p \leq 0.05$) differences among harvests, the relationship was determined by partitioning harvest sums of squares by orthogonal polynomials.

the greatest stocking (Table 4). *B. papyrifera* produces abundant, wind-disseminated seed (Safford et al. 1990). Therefore, it is well adapted to become established in any openings created by harvesting. *A. rubrum* probably grows on a wider range of site conditions than any other forest species in North America; furthermore, even small trees produce abundant seed and it sprouts vigorously from stumps (Walters and Yawney 1990). Thus, it is not surprising that it was so common in this study, or that there were no treatment effects on either abundance or stocking.

4.2 Repeated Harvesting Effects on Regeneration

Among the four harvests in S05 for which there were comparable regeneration inventories (Fig. 1), repeated harvesting resulted in few trends in abundance (Table 5), and even fewer in stocking (Table 6). Compared to after Harvest 4, abundance of *Abies balsamea* increased following Harvests 5 and 6, then declined sharply after Harvest 7. The trend for *Tsuga canadensis* was similar but not significant. Although the number of *Picea* seedlings also declined somewhat after Harvest 7, the overall trend was significantly positive. Among angiosperms, the abundance of *Fagus grandifolia* dropped to its lowest level after Harvests 5 and 6, then rebounded following Harvest 7. Nevertheless, stocking of *F. grandifolia* followed a declining trend across the four harvests.

Compared to their abundance after Harvest 6, the number of gymnosperm seedlings fell by over 10 000 ha^{-1} following Harvest 7. The reason for the decline is not clear. Since the harvests and inventories are staggered in time, it is not likely that either logging practices or climatic conditions affected the two replicate compartments the same. Some indication may be found by examining the inventory following Harvest 8 in Compartment 9 (Fig. 1). Except for *Pinus* spp., all other species or groups declined in abun-

Table 6. Regeneration stocking following partial harvests repeated at about 5-year intervals at the Penobscot Experimental Forest, east-central Maine, USA.

Species	SE[2]	Harvest[1] 4	5	6	7	Mean	Trend[3]
		percent stocking					
Abies balsamea	2.77	70.9	77.2	79.8	73.0	75.2	
Tsuga canadensis	8.64	59.0	75.6	76.2	74.2	71.3	
Picea spp.	10.22	43.8	55.2	62.8	58.1	55.0	
Thuja occidentalis	2.82	13.9	11.4	13.0	11.0	12.3	
Pinus spp.	9.98	10.2	11.5	9.0	9.0	9.9	
Total gymnosperms	3.23	83.1	90.0	90.3	87.8	87.8	
Acer rubrum	8.23	29.4	31.6	29.9	39.4	32.6	
Betula papyrifera	6.26	12.2	6.6	11.8	11.0	10.4	
Fagus grandifolia	0.52	5.9	3.0	3.0	2.2	3.5	Linear
Fraxinus americana	1.41	1.3	1.3	1.3	3.4	1.8	
Quercus spp.	0.8	0.8	0.8	0.8	0.8	0.8	
Total angiosperms	9.36	39.2	33.8	35.4	47.0	38.8	
Total regeneration	3.56	84.4	90.0	92.0	92.8	89.8	

[1] Data following earlier harvests are not available.
[2] Pooled standard error from analysis of variance.
[3] When analysis of variance indicated significant ($p \leq 0.05$) differences among harvests, the relationship was determined by partitioning harvest sums of squares by orthogonal polynomials.

dance after Harvest 8. Gymnosperm abundance fell by 17 percent while the total number of angiosperms was 50 percent less than after Harvest 7. Total regeneration stocking also declined somewhat, but still exceeded 92 percent and total stocking of conifers did not change from the previous inventory. Thus, the continued high level of regeneration stocking suggests that no serious problem has yet developed with regeneration in Compartment 9. Furthermore, until a comparable inventory is made in Compartment 16 following its eighth harvest, it is not possible to infer whether the decline in regeneration is a treatment or a site effect.

5 Summary and Conclusions

There were few statistically significant differences among the silvicultural treatments or among repeated harvests in this study. A number of explanations can be considered: with only two replicates the power of the experiment to detect differences between treatments is low; there is considerable site heterogeneity within each treated compartment; the species which occupy this forest type are prolific, robust and adapted to a broad range of site conditions; or, neither the abundance nor stocking of natural regeneration was impacted by the range of partial harvest treatments applied in this study. All these reasons are contributing factors.

Although power in this experiment was low making it difficult to detect differences, there are no trends among the five treatments to suggest that greater statistical power would make the results more clear. For example, prior to the mid-1970s harvest, S20 did not have a lot of overstory angiosperms. Nonetheless, following harvest it had the most regenerating angiosperms, suggesting that relatively heavy overstory removal opened up the stand and favored angiosperm seedlings and sprouts. However, even more open conditions existed in FDL following the harvest but angiosperm regeneration was not

nearly as prolific. Furthermore, the experiment did detect rather subtle differences in stocking of total regeneration; a 3.2 percent difference was significant.

The magnitudes of standard errors compared with their respective means attest to the within-treatment heterogeneity in this study. Thus, although a diligent attempt was made to apply treatments uniformly to the replicates, the sites themselves were not uniform. Sites varied not only in drainage and soils but also in initial stand structure and composition. Repeated harvest entries should eventually result in more uniform structure and composition between treatment replicates. However, site will remain a major determinant of presence and abundance of a particular species. Even in S05 where there has been repeated harvests, the replicates differ; seedlings of *Pinus* spp. have, to this point in time, been found only in Compartment 9 while regenerating *Quercus* spp. are only in Compartment 16. Nevertheless, the overall high levels of stocking indicate that the principal regenerating species have broad site requirements for establishment.

The abundance of the major regenerating species in this study was far in excess of the numbers needed to ensure their presence in the future stands. As a management tool, stocking is a measure of how much regeneration is required. Each regeneration plot was 0.000405 ha. Consequently, to be fully stocked with a particular species, or in total regeneration, only 2469 uniformly distributed seedlings or sprouts were required per hectare. A number of both gymnosperm and angiosperm species or species groups far exceeded the numerical requirement. That stocking was not 100 percent for those abundant species or groups suggests some areas of unfavorable site or overstory conditions within the stands. However, 100 percent regeneration stocking is not necessary for managing a stand for forest products. Frank and Bjorkbom (1973) recommend just that stocking of *Picea* spp. and *Abies balsamea* seedlings combined be greater than 50 percent. All of the treatments in this study exceeded that goal.

These results demonstrate that, under the site conditions in this boreal ecotone forest, natural regeneration of trees is prolific across a broad range of intensities and frequencies of partial harvests. Most of the regeneration is from three taxa of understory tolerant conifers and two species of angiosperms. A number of other gymnosperms and angiosperms are also found, but in fewer numbers and at lower levels of stocking. Thus, for a range of partial harvest strategies in the Acadian Forest, tree regeneration will be sufficiently abundant and diverse to sustain a stand capable of meeting a variety of future management objectives.

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Statistical Opportunities for Comparing Stand Structural Heterogeneity in Managed and Primeval Forests: An Example from Boreal Spruce Forest in Southern Finland

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The horizontal and vertical stand structure of living trees was examined in a managed and in a primeval spruce-dominated forest in southern Finland. Tree size distributions (DBHs, tree heights) were compared using frequency histograms. The vertical distribution of tree heights was illustrated as tree height plots and quantified as the tree height diversity (THD) using the Shannon-Weaver formula. The horizontal spatial pattern of trees was described with stem maps and quantified with Ripley's K-function. The spatial autocorrelation of tree sizes was examined with semivariogram analysis. In the managed forest the DBH and height distributions of trees were bimodal, indicating a two-layered vertical structure with a single dominant tree layer and abundant regeneration in the understory. The primeval forest had a much higher total number of trees which were rather evenly distributed in different diameter and tree height classes. The K-function summaries for trees taller than 15 m indicated that the primeval stand was close to complete random pattern. The managed stand was regular at small distances (up to 4 m). The semivariograms of tree sizes (DBH, tree height) showed that the managed forest had a clear spatial dependence in tree sizes up to inter-tree distances of about 12 meters. In contrast, the primeval spruce forest had a variance peak at very short inter-tree distances (< 1 m) and only weak spatial autocorrelation at short inter-tree distances (1–5 m). Excluding the understory trees (h < 15 m) from the analysis drastically changed the spatial structure of the forest as revealed by semivariograms. In general, the structure of the primeval forest was both horizontally and vertically more variable and heterogeneous compared to the managed forest. The applicability of the used methods in describing fine-scale forest structure is discussed.

Keywords boreal forests, Norway spruce, spatial analysis, K-function, semivariance, structural variation, biodiversity

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1 Introduction

Heterogeneity of forest structure can be viewed at different hierarchical scales (Wiens 1989, Kotliar and Wiens 1990). From an eagle's perspective forest characteristics at the landscape scale are apparently most important, while for microlichens living on needle surfaces the structure and microclimate of individual branches or shoots are crucial. However, perhaps for most forest organisms an intermediate scale of perception, that defined by the structure of the forest at the patch or tree stand level (within meters to tens of meters), is most important. This is because the horizontal and vertical arrangement of foliage and woody biomass defines the spatial distribution of microclimatic conditions within the canopy space and in the forest understory (Pukkala et al. 1991, 1993, Canham et al. 1994). In addition, the spatial arrangement of trees defines the three dimensional geometry of habitat characteristics for birds, insects, tree epiphytes, understory plants and soil micro-organisms (Morse et al. 1985, Lesica et al. 1991, Barik et al. 1992, Gunnarsson 1992, Niemelä et al. 1992).

The structure of a tree stand is a reflection of both autogenic developmental processes, like regeneration pattern, competition and the consequent self-thinning, and past and present disturbance events. In managed forests, the most obvious disturbance factor affecting stand structure is silvicultural treatments like thinnings, which often aim at fully utilizing the site's capacity of quality wood production by homogenizing within-stand variation in tree characteristics. Accordingly, it has generally been concluded that natural tree stands are structurally more complex and diverse than managed stands (e.g. Hansen et al. 1991, Swanson and Franklin 1992).

Much of the recent ecological research of fine-scale forest structures is motivated by the idea that spatially heterogeneous forests may accommodate more species and particularly specific species requiring specialized microhabitats (e.g. Hansen et al. 1991, McComb et al. 1993). This is because structurally complex forests provide a greater variety of microclimates, hiding and nesting sites etc., compared to more homogeneous forests. For example, the complexity of vertical vegetation structure has been found to be related to the number of insect and bird species occupying a given forest area (e.g. McArthur and McArthur 1961, Murdoch et al. 1972, Cody 1975). Thus, the structural complexity of forest often seems to be a good predictor of overall species diversity (Begon et al. 1986). Accordingly, ecological inventories could use analyses of forest structure to assess the conservation or biodiversity value of forest stands (Hansen et al. 1991, Lindholm and Tuominen 1993, McComb et al. 1993).

Although forest ecosystems have a multitude of characteristics which can be used for descriptive purposes, the structure of the tree stratum obviously has a central role in determining the ecological processes and habitat characteristics in the forest. The structure of a tree stand can be defined in terms of tree size distribution and the spatial arrangement of trees. In this study we examine and discuss some statistical methods to quantify the structural heterogeneity of the forest in terms of size and spatial distribution of trees. These methods are of general nature, developed for georeferenced data in spatial statistics and geostatistics. We use these methods to compare the structure of a primeval and managed spruce dominated forest stand in southern Finland.

2 Material and Methods

2.1 Sample Stands: Their History and Measurement

The material consisted of two forest sample plots, one representing a managed forest in Vuorijärvi and the other a primeval forest in Susimäki. The examined forests are located in southern Finland, close to the Hyytiälä Forestry Field Station of the University of Helsinki (61°50' N, 24°17' E, alt. 150 m a.s.l.). The area belongs to the south-boreal vegetation zone (Ahti et al. 1968) and the effective temperature sum (5° C threshold) of the location is approximately 1150 d.d. Both forest plots were growing on *Myrtillus* site type, which is a medium fertile type according to the Finnish site classification system.

The Susimäki forest preserve was officially

established in 1955, because of its distinct old-growth forest characteristics. However, the Susimäki forest has developed largely without human influence for a long time, since there were no distinctive signs of human disturbance on the study plot. For the Vuorijärvi stand there are no exact historical records on the management history of the forest. However, growth release analysis based on the widths of annual rings from tree borings (n = 5, data not shown), suggests that timber was extracted from the stand approximately 35 years ago. The area of the sample plots in both forests was 0.25 hectares (50 m × 50 m). On both plots trees taller than 1.3 m were measured for location, height, DBH and species (Table 1).

The forest of the Susimäki plot (Grid 27°E: 6864:354) was approximately 150 years old. There were 1756 trees per hectare of which 6.4 % were dead standing trees. Dead trees were most frequent in small diameter classes (Fig. 1). The total standing wood volume of the trees was 427 m^3 ha^{-1} of which dead standing trees comprised 5 m^3 ha^{-1} (1.2 % of volume). There were no recent treefalls or other natural disturbances on the plot (Table 1).

The age of the managed stand of Vuorijärvi (Grid 27°E: 6860:358) was approximately 105 years. There were 1360 standing trees per hectare, of which 0.6 % were dead. The total standing wood volume was 335 m^3 ha^{-1}, of which 6 m^3 ha^{-1} (1.8 % of volume) was dead trees. Thus, the Vuorijärvi stand had fewer but larger dead standing trees than the primeval Susimäki stand.

Both plots had Norway spruce (*Picea abies* L. Karst.) as the dominant tree species and Scots pine (*Pinus sylvestris* L.) and birch (*Betula pendula* Roth. and *B. pubescens* Ehrh.) as co-occurring species. In addition, the Vuorijärvi stand had rowan (*Sorbus aucuparia* L.) in the understory and the Susimäki plot had one aspen (*Populus tremula* L.) in the upper story (see Table 1).

In the upper story (h ≥ 15 m) the primeval Susimäki stand had a more even species distribution, due to the more abundant occurrence of birch (18.4 %), when compared to the managed Vuorijärvi stand. In the lower story (h < 15 m) the

Table 1. Structural characteristics and tree species composition of the managed Vuorijärvi and the primeval Susimäki spruce-dominated forest sample plots.

Property	Vuorijärvi	Susimäki
Number of trees, ha^{-1}		
Total	1360	1756
Living	1352	1644
H ≥ 15 m	400	664
H < 15 m	952	980
Tree species proportions, %		
H ≥ 15 m		
Picea abies L. Karst.	92.0	76.3
Pinus sylvestris L.	4.0	4.7
Betula pendula Roth., *Betula pubescens* Ehrh.	4.0	18.4
Populus tremula L.	-	0.6
H < 15 m		
Picea abies L. Karst.	52.7	94.8
Pinus sylvestris L.	0.8	1.1
Betula pendula Roth., *Betula pubescens* Ehrh.	32.7	4.1
Sorbus aucuparia L.	13.8	-
Stem volume of standing trees, m^3 ha^{-1}		
Total	335	427
Living trees	329	422
Dead trees	6	5

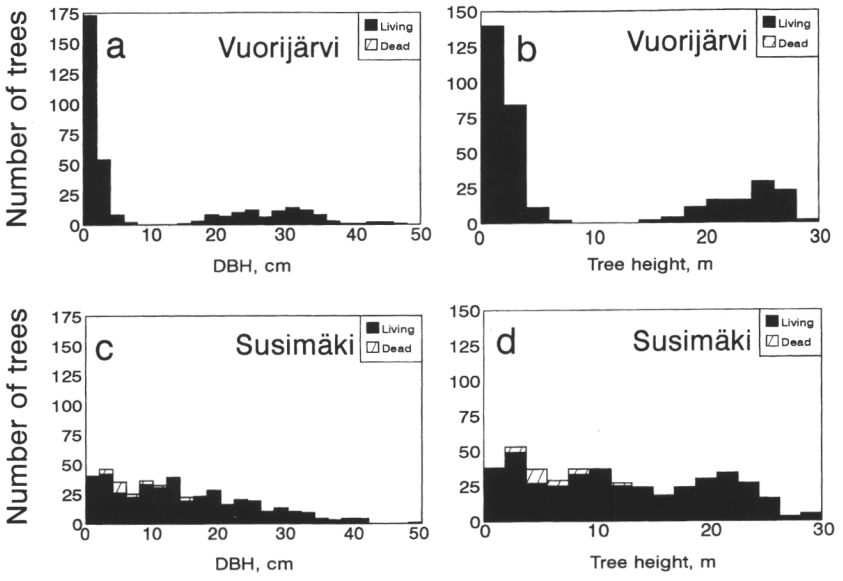


Fig. 1. Frequency distributions of DBH and tree height in the managed Vuorijärvi (a and b) and in the primeval Susimäki (c and d) forest plots.

reverse was true, the managed Vuorijärvi stand had more species (due to the occurrence of rowan) with greater evenness than the primeval Susimäki stand (Table 1).

2.2 Methods

An intuitive method for comparing stand structures is to compare frequency histograms of tree sizes and to draw horizontal stem or crown maps and vertical profile diagrams (e.g. Hallé et al. 1978, Koop 1991). These methods were also used in this study. Graphical illustration was complemented with quantitative techniques to assess tree stand structure in order to facilitate rigorous comparisons between the different aspects of forest structure.

Vertical Distribution

The complexity of the vertical distribution of foliage weight or surface area is probably most important in creating the vertical modulation of microclimatic conditions and available feeding, mating and nesting sites for canopy-dwelling organisms. Since vertical foliage amounts are tedious to measure, we confined ourselves with the tree height distribution to characterize the vertical structure of the forest. First, we examined the downward cumulative percentage of the number of trees by 2 meter deep horizontal layers. This approach resembles the Kaplan-Meier curve used in survival analysis (Kaplan and Meier 1958). Second, the tree height diversity (THD) was quantified with the Shannon-Weaver formula (e.g. MacArthur and MacArthur 1961, Murdoch et al. 1972) using 2 meter deep horizontal layers (0–2 m, 2–4 m ...). This measure of diversity is defined as

$$THD = H' = \sum_{i=1}^{n} p_i \log_e p_i \qquad (1)$$

where p_i is the proportion of trees in the *i*th height layer. The difference in THD between the two stands was tested using t-statistic as described by Hutcheson (1970), see also Magurran (1988).

Horizontal Distribution

The horizontal pattern of tree locations in a forest can be viewed as a two-dimensional point process. Three traditional distribution types are, *regular* pattern, *completely random* or Poisson pattern and *clustered* pattern. Three broad categories of methods to characterize spatial distributions of trees can be considered: quadrat methods, distance methods and second-order methods, which require stem-mapped data. Early studies of spatial point patterns were mainly concerned in comparing area (or quadrat) counts to Poisson distribution. In addition, among the most commonly used approaches are the so-called nearest-neighbor methods. Distances may be measured between trees and nearest neighboring trees or between sample points and nearest trees. The advantage of nearest-neighbor methods in applied purposes is that they were intended to be used in the field (Cressie 1991), but they are hampered by the restriction to small-scale pattern separation only and by the difficulty to obtain a random sample of trees in the field. Nearest neighbor methods have been further developed to account for scale effects and spatial location of quadrats (e.g. Moeur 1993).

For stem-mapped data the Ripley's K-function analysis is more powerful than nearest neighbor methods (e.g. Moeur 1993). Unlike nearest neighbor analysis, which considers only distances from a given point to its nearest neighbor, Ripley's K-function considers the distances between all pairs of points in the study area (Ripley 1981). For applications related to trees see e.g. Sterner et al. (1986), Tomppo (1986), Getis and Franklin (1987), Kenkel (1988), Penttinen et al. (1992) and Moeur (1993).

Ripley's K can be defined as follows. If λ is the density of trees (mean number per unit area), then $\lambda K(d)$ is the expected number of further trees within the distance d from a randomly chosen tree. The boundary-corrected estimator $\hat{K}(d)$ can be computed for n trees on an area A, as follows:

$$\hat{K}(d) = A \sum_{\substack{i,j=1 \\ i \neq j}}^{n} \sum^{n} \left[\sigma_{ij}(d) / n^2 \right] \qquad (2)$$

where $1 / \sigma_{ij}$ is defined as the proportion within A of the circumference of a circle centered at tree i with boundary passing through tree j (Ripley 1981, p. 159). For a completely random pattern $E\hat{K}(d) = \pi r^2$. Therefore, instead of $\hat{K}(d)$ a transformed version $\hat{L}(t)$ is used:

$$\hat{L}(t) = \sqrt{\left[K(d) / \pi \right]} \qquad (3)$$

For determining the statistical significance of departures from random patterns, the 95 % confidence envelope has been done using simulations of the Poisson process. Another method is based on the approximation leading to the confidence bounds $\pm\ 1.45\sqrt{(A / N)}$, where A is the area of the plot and N is the number of trees on the plot (Ripley 1988). Crossing of the upper or lower limit of the confidence envelope can thus be considered as a significant departure from randomness.

Spatial Autocorrelation of Tree Sizes

The shortcoming of spatial point pattern analysis is that they only account for the locations of trees but not for their size variation in space, which is an essential characteristic of forest structure (Matérn 1960) and important from the ecological point of view (Rossi et al. 1992). Here we use the semivariogram to examine the spatial autocorrelation in tree sizes. In particular, the semivariogram can suggest the scales of patchiness of the forest structural mosaic (Palmer 1988, Biondi et al. 1994).

Semivariogram is a measure of the degree of spatial dependence between samples, which summarizes the variance as a function of scale. More specifically, the semivariance is the sum of squared differences between all possible pairs of points separated by a given distance (often given as a distance class). The semivariance is defined as:

$$\gamma(h) = \frac{1}{2} E\left[z(i) - z(i+1) \right]^2 \qquad (4)$$

and its estimator is:

$$\gamma(h) = 1 / 2N(h) \sum_{i=1}^{n} \left[(z(i) - z(i+1) \right]^2 \qquad (5)$$

where z(i) and z(i + 1) respectively are the values of a variable measured at locations separated

by distance h, and N(h) is the number of pairs of points separated by distance h. Other estimators can be found in Cressie (1991).

The summary is a plot of $\gamma(h)$ as a function of h. As the distance between points increases the values of the measured variables usually become increasingly dissimilar, and the semivariance increases. The increase continues until the points are so far apart that they are not related to each other and their squared difference becomes equal to the average variance of the samples. This flat region of the graph is called the sill. The maximum distance within which the samples are still autocorrelated is called the range. If the semivariogram is a straight horizontal line ("pure sill"), the variable is not spatially correlated.

The advantage of the semivariogram approach is that different data forms, i.e. transect, quadrat and point data, can be readily utilized (Burrough 1987, Turner et al. 1991). In this study the semivariogram is applied to individual mapped trees (their sizes and locations, assuming the locations of the trees to be fixed). Although trees are discrete objects their sizes can be thought to be realizations of the effects of spatially continuous variables, like radiation and soil nutrients, thus motivating their autocorrelation analysis. However, for inventory purposes it would probably be more convenient to use transect or quadrat methods instead of mapping individual trees.

3 Results

3.1 Size Distribution of Trees

Frequency Histograms of DBH and Height

In the managed Vuorijärvi forest the DBH distribution of trees exhibit a distinct bimodal pattern, so that most of the trees are smaller or equal than 5 cm at DBH and a second broad peak in the distribution is in the 18–36 cm DBH-classes (Fig. 1). When compared to the managed forest, the primeval Susimäki forest has a much higher total number of trees which are more evenly distributed in different diameter classes. Also in this case small trees are most abundant but the frequency of trees decline more or less continuously with increasing diameter.

The tree height distributions of the two forest plots naturally resemble those of BHD (Fig. 1). The managed Vuorijärvi forest has a two-peaked height distribution of trees, while the primeval Susimäki forest has trees in all of the defined 2-m-wide height classes up to 32 m. The difference in tree height distributions is further illustrated in Fig. 2, showing the downward cumulative percentage of the number of trees in 2 meter deep layers. The greater frequency of smaller trees in the managed Vuorijärvi forest is clearly seen when compared to the Susimäki plot.

3.2 Spatial Description

Horizontal and Vertical Patterns

The horizontal stem maps of the two forest plots reveal the greater density and size variation of trees in the primeval Susimäki plot as compared to the managed Vuorijärvi forest plot (Fig. 3). In Vuorijärvi there is more understory regeneration and a distinct dense regeneration group in a gap in the north-eastern corner of the area. This regeneration may have been enhanced by the last logging operation, allowing more light to penetrate the stand and providing favourable regener-

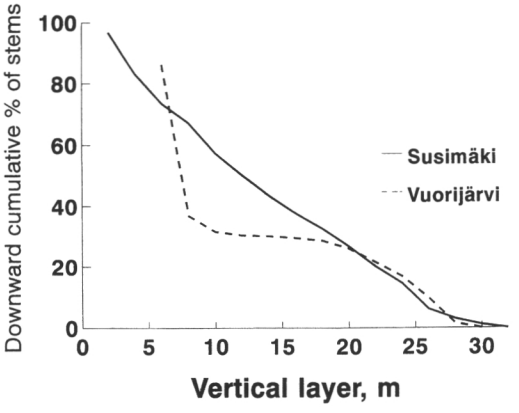


Fig. 2. The downward cumulative percentage of tree numbers in 2 meter deep layers in the managed Vuorijärvi and in the primeval Susimäki forest plots.

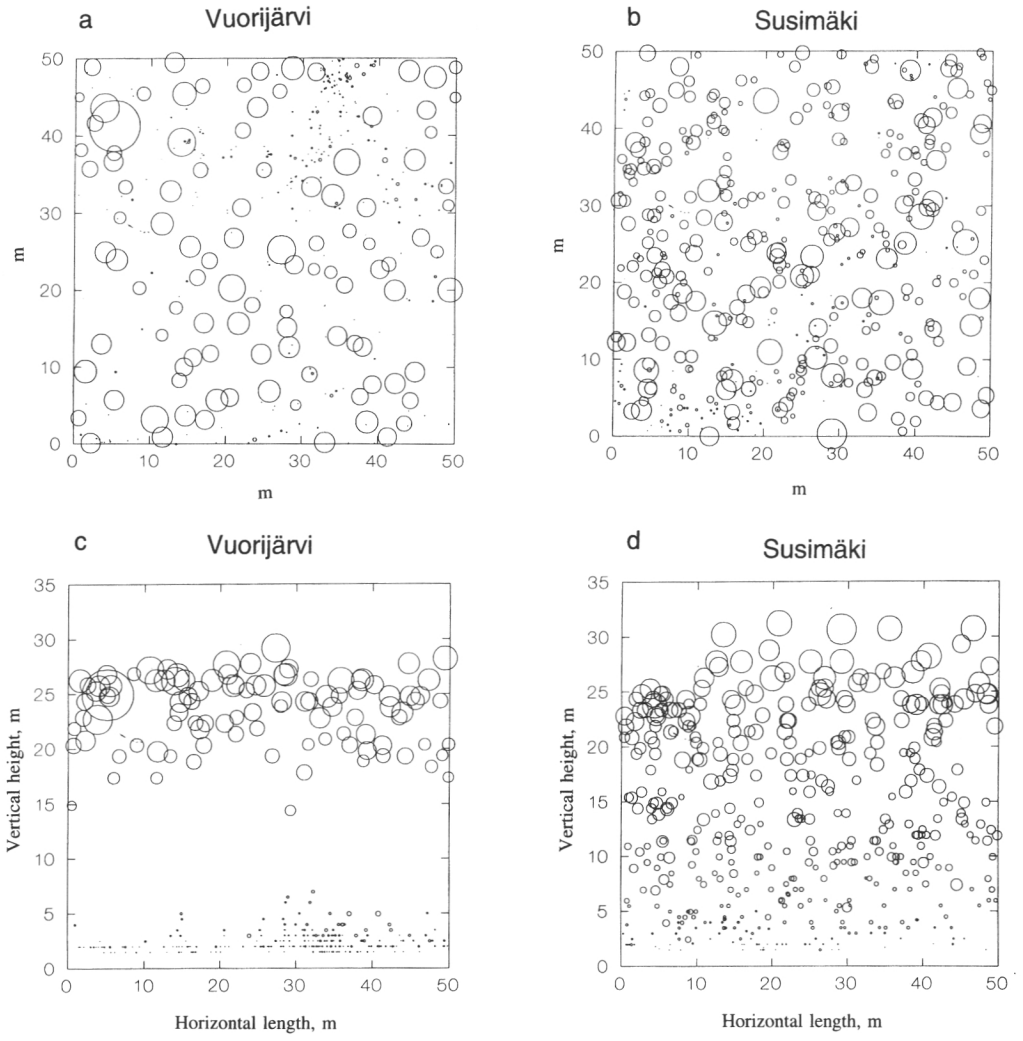


Fig. 3. Stem maps of (a) the managed Vuorijärvi and (b) the primeval Susimäki forest plots, and tree height distribution diagrams of (c) the managed Vuorijärvi and (d) the primeval Susimäki spruce forests. The size of the circle is proportional to the DBH in all figures; in the tree height diagrams tree heights are indicated by circle midpoints.

ation microhabitats due to soil disturbance.

The illustration of the vertical distribution of tree heights shows the distinctive two-layered structure of the managed forest, consisting of a dominant tree layer of trees taller than 15 m and abundant regeneration in the understory. On the other hand, the primeval Susimäki forest has an all-size structure, without any distinct vertical layering (Fig. 3).

The Shannon-Weaver index (H') for tree height diversity (THD) was considerably higher in the unmanaged Susimäki forest (2.71), when compared to the managed forest of Vuorijärvi (1.66) (Table 2). An attempt was also made to assess the significance of this difference in tree height distributions. The method of Hutcheson (1970) gave the t-value of 15.71 on 380 degrees of freedom, indicating that the tree height diversity,

Table 2. The Shannon-Weaver index (H') for tree height diversity (THD) and its variance for the tree height diversity in the two sample plots.

	Vuorijärvi	Susimäki
Shannon index (H')	1.656	2.707
Variance of H'	0.00422	0.00225

as quantified with the Shannon-Weaver formula, is significantly different ($p < 0.001$) between the two forest plots. However, the test assumes independency of tree heights which is not necessarily fulfilled. Hence the p-value obtained can only be regarded as a crude approximation.

Ripley's K-function was used to compare the spatial pattern of the locations of the trees in the two plots. Because large trees comprise most of the forest biomass and thus contribute significantly to the overall structure and microclimatic conditions of the forest, we first chose trees taller than 15 m for the analysis. Ripley's K-function indicated that the managed Vuorijärvi forest is regular up about 4 m distances (Fig. 4). However, in the primeval Susimäki forest the deviation from random pattern is not significant. The more regular spatial pattern in the managed Vuorijärvi forest is possibly caused by thinnings that have homogenized the spatial pattern of trees.

The K-function analysis was also done for trees smaller than 15 m. The results (not shown) indicated that in Vuorijärvi the spatial pattern of understory trees show strong heterogeneity. The same was true for Susimäki, but to a lesser extent.

Semivariograms of Tree Size

The omnidirectional semivariograms of DBH and tree height, computed for all trees taller than 1.3 m, indicate that in the managed Vuorijärvi forest plot there exists clear spatial autocorrelation in both the DBHs and heights of trees up to tree distances of about 12 m (Fig. 5). This means that especially trees closer than 12 meter apart are in general more of the same size while trees farther apart are not. The Vuorijärvi semivariograms also show a nested-like pattern, since there is strong autocorrelation up to inter-tree distances of about 10 m, then a levelling off up to approximately 20 m and then again a rise in semivariance up to 25–30 m.

In contrast to the managed forest, the semivariograms of the primeval Susimäki forest come close to a horizontal pattern ("pure sill"), indicating only weak spatial autocorrelation in tree size. However, an interesting feature is the local high semivariance value within very small inter-

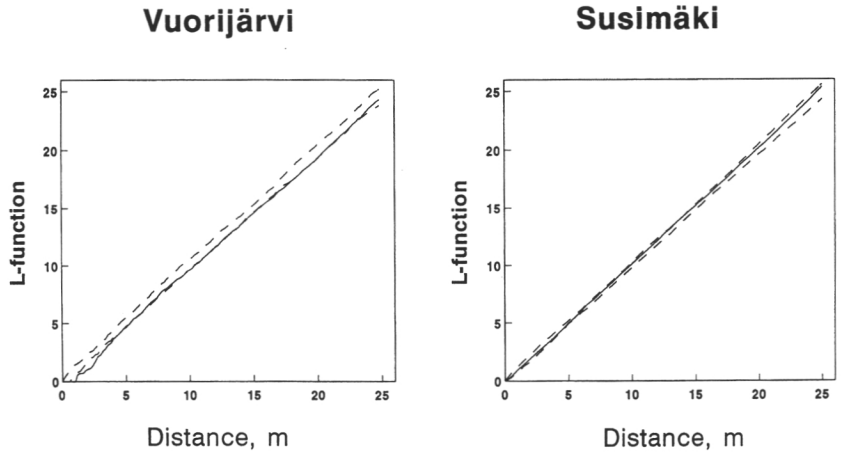


Fig. 4. Ripley's K-function analyses of the spatial pattern of tree locations for trees taller than 15 m in the managed Vuorijärvi forest and in the primeval Susimäki forest.

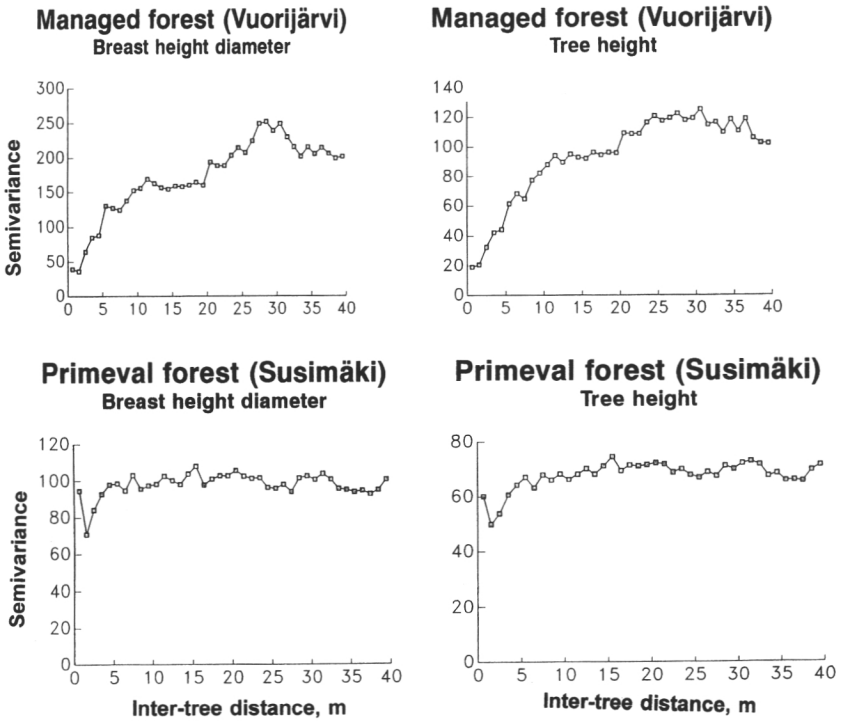


Fig. 5. Omnidirectional semivariograms (showing the semivariance $\gamma(h)$ (= gamma) as a function of lag distance h) for DBH and height of trees in the managed Vuorijärvi and in the primeval Susimäki forest plots. The first lag distance class shown includes 130 and 240 pairs of trees in Vuorijärvi and Susimäki, respectively; further points represent over 400 pairs of trees.

tree distances (< 1 m), and positive autocorrelation at inter-tree distances 1–5 m.

To examine the importance of different canopy layers for the autocorrelation patterns detected, the semivariograms were also calculated only for trees taller than 15 m, which form the dominant tree layer (Fig. 6). In the Vuorijärvi plot the clear autocorrelation structure seen in Fig. 5 for all trees disappears, and, although there is much variation in semivariance, the overall variogram is "pure sill", i.e. no autocorrelation. In the Susimäki stand the most notably change in the variograms compared to Fig. 5 is the disappearance of the variance peak at small distances. This is a logical result of the exclusion of small suppressed trees from the analysis. The positive autocorrelation at distances 1–5 m, shown in Fig. 5, remains for DBH, but disappears for tree height.

In conclusion, the semivariograms show that the spatial size-structure pattern of the primeval Susimäki forest is clearly different from the managed Vuorijärvi forest, and that this difference is largely due to the structure of the understory. The primeval Susimäki forest is spatially more "unpredictable", i.e. more heterogeneous and complex when compared to the managed Vuorijärvi forest.

4 Discussion

To evaluate the potential contribution of different forest stand structures to species conservation or ecological diversity, we should ideally know the habitat requirements of all the differ-

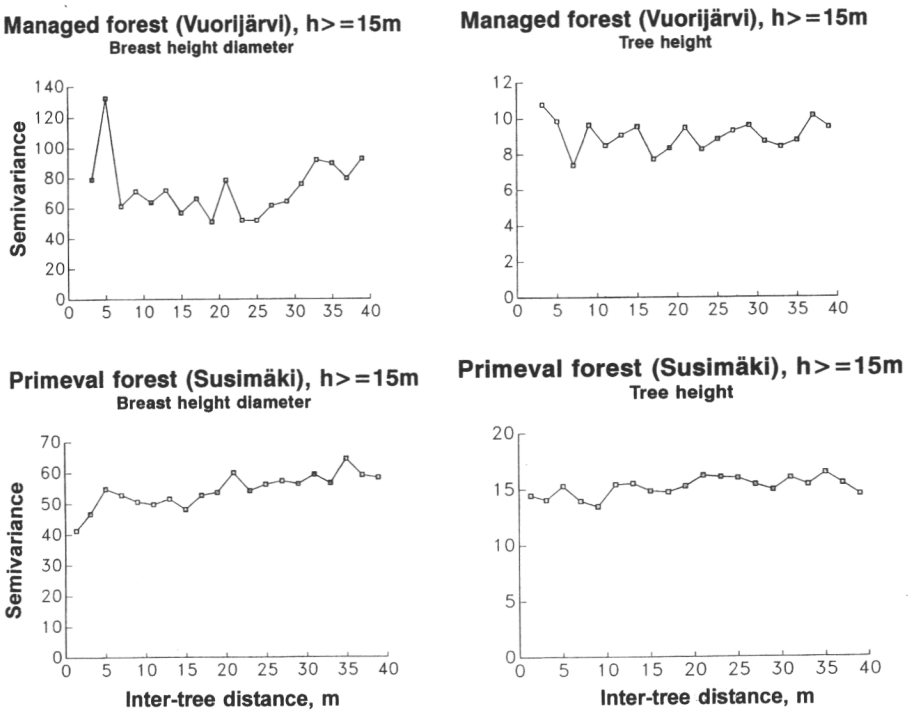


Fig. 6. Omnidirectional semivariograms of trees taller than 15 m for DBH and tree height in the managed Vuorijärvi and in the primeval Susimäki stands. The first lag distance class respesents 65 and 70 pairs of trees in Vuorijärvi and Susimäki, respectively.

ent forest-dwelling organisms. To approach this goal in boreal forests, significant research has been carried out recently (e.g. Kouki 1994). At the moment, however, our understanding of the habitat preferences of many forest organisms or groups of organisms is very limited. On the other hand, it is often impossible to inventory taxonomic groups like arthropods and soil invertebrates, because of practical problems related to sampling and availability of taxonomic expertise. In this situation a conservative strategy would be to use forest structure as a surrogate for other organisms and to try to maintain and enhance such structural properties of the forest that seem to accommodate diversity in general (Hansen et al. 1991, Pielou 1992, McComb et al. 1993, Kuuluvainen 1994, Mladenoff and Pastor 1994). When considering the ecological significance of forest structure at the within-patch or within-stand scale, the leading principle appears to be that structural complexity of vegetation enhances species diversity. Accordingly, analyses of forest stand structures and dynamics show promise in predicting and evaluating the conservation or diversity values of forests. Forest structural analyses are also needed for developing alternative silvicultural practices (e.g. Hansen et al. 1991, McComb et al. 1993, Haila et al. 1994).

Quantitative assessments of conservation and biodiversity values in forests are needed to include these assessments in forest management planning procedures and to develop practices of sustainable ecosystem management (Hansen et al. 1991, Pielou 1992, Swanson and Franklin 1992, Kangas and Kuusipalo 1993, Mladenoff and Pastor 1994). However, tree stands are highly complex in their three-dimensional structure and one problem is to find quantitative measures of forest structure, which are ecologically relevant and facilitate rigorous structural comparisons among stands.

The variation in tree sizes is a fundamental

characteristic of forest structure, that reflects both previous disturbance events and autogenic developmental processes of the forest. The coefficient of variation and the gini coefficient have been used for the quantification of the variation in tree sizes (e.g. Weiner 1990). In fact these two indices, when applied to tree size distributions, have been shown to correlate closely (Knox et al. 1989). However, the problem with these two common indices is, when applied to heterogeneous forests, that it is statistically senseless to compare forests of bimodal (or multimodal) and unimodal size distributions. Therefore, we used the Shannon-Weaver formula, which is derived from information theory, to calculate tree height diversity index (THD). The computed THD's indicated that the vertical complexity of the primeval forest was considerably greater compared to the managed forest. This is also in accordance with the visual impression obtained from the histograms of tree height distributions (Fig. 1) and from the graphs showing the vertical distribution of tree heights on the plots (Fig. 3). Ideally the THD index should be computed based on the vertical stratification of foliage area or mass (FHD, foliage height diversity) (MacArthur and MacArthur 1961). Although this may be possible for research purposes, it may be too laborious for inventory purposes, for which the measurement of tree height distributions may suffice. The THD (or FHD) index has been used successfully in a number of ecological studies (e.g. MacArthur and MacArthur 1961, Murdoch et al. 1972), and it seems to provide a robust measure of the vertical complexity of the forest. In general, in the description and comparison of tree size distributions, distribution-free methods are preferable, because tree size distributions, being frequently bi- or multimodal, often fail to conform any conventional distribution model.

The horizontal pattern of locations of trees taller than 15 m was examined with Ripley's K-function analysis. In the primeval Susimäki stand the deviation from random pattern was not statistically significant. In the managed Vuorijärvi stand the analysis indicated a regular pattern of tree distribution within distances up to about 4 m. This difference compared to the primeval stand may be caused by thinnings (from below) in the managed forest, which usually aim at making the spatial distribution of trees more even. The spatial pattern of understory trees showed strong heterogeneity in both plots.

The computed semivariograms of tree sizes (DBH, tree height) for all measured trees ($h \geq 1.3$ m) revealed clear differences in stand structures between the managed Vuorijärvi forest and the primeval Susimäki forest. In the managed Vuorijärvi plot there was a clear spatial dependence in tree sizes up to distances of about 12 meters, while in the primeval spruce forest of Susimäki only weak spatial autocorrelation was detected (Fig. 5). The semivariograms of the Vuorijärvi plot also showed a nested pattern with two steep rises in semivariance as a function of distance (0–10 m and 18–25 m). This pattern suggests that the forest structure is regulated by two factors operating at different spatial scales. The first factor could be small scale regeneration and/or competition interactions, while the larger scale structural variation could be caused e.g. by variation in soil properties.

In the primeval Susimäki forest the semivariograms suggested only weak spatial dependence in tree sizes at inter-tree distances of 1–5 m. An interesting feature of the semivariogram was the variance peak in tree sizes in trees very close (< 1 m) to each other. This is apparently mostly because in natural stands even severely suppressed spruce trees (which there were many) are able to survive for prolonged periods of time beneath taller trees (asymmetric competition). In general, the semivariograms indicated that trees of different sizes occur throughout the forest largely independent of each other. Thus, a high fine-scale variation in tree sizes characterized the studied primeval spruce stand.

To examine the importance of the understory for the detected autocorrelation patterns of tree size, the semivariograms were also calculated solely for trees taller than 15 m, which form the dominant tree layer (see Figs. 3 and 6). The analysis indicates that the detected differences in the variograms in the spatial structure between the two stands were mainly due to the lower story ($h < 15$ m). This result suggests that the structure of the lower storey (dominated trees) may be of fundamental importance to the habitat characteristics of the forest.

This paper has explored some quantitative

methods to characterize the structural properties of tree stands that could be used in evaluating the biodiversity-related non-timber values of the forest. These methods were used to characterize forest structure of two contrasting stands, a managed and a primeval spruce-dominated stand. Because these two forests are similar in site type and age, and grow close to each other, their comparison has potential to illustrate the effects of human intervention on stand structure in this forest type. The analysis suggests that from the point of view of an organism living in the environmental space defined by a tree stand, the examined managed and primeval spruce-dominated forest plots differ considerably from each other as spatial environments.

We emphasize that, in addition to commonly applied measures of forest structure like tree species composition and size variation, especially small-scale spatial analyses, utilizing methods from spatial statistics and geostatistics, are useful for detecting and quantifying differences in the structure of the forest.

Acknowledgements

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Species Richness and Structure Variations of Scots Pine Forest Communities during the Period from 5 to 210 Years after Fire

Vadim V. Gorshkov and Irene J. Bakkal

Postfire recovery of species diversity (including a number of species, entropy of species relative coverage (Shannon index of species diversity) was studied in lichen and green moss site types of Scots pine forests in the central part of the Kola Peninsula. The results obtained indicate the difference in the dynamics of characteristics of biodiversity of forest components during postfire recovery. The stabilization of separate components of forest community varies in time from 5–15 to 120–140 years after the fire. Characteristics of the dwarf shrub and herb stratum recovered and stabilized 5–15 years after fire, while the complete stabilization of characteristics of moss-lichen cover is observed in community with fire ages of 90–140 years. Species richness of tree stratum recovered 120–140 years after fire. Time of complete stabilization of species richness of the community was estimated 120–140 years after fire. The size of the area over which characteristics of the biodiversity were estimated effected the mean values and, in most cases, the character of variation of studied characteristics. Over an area of 1 ¥ 1 m dynamics of characteristics of species diversity coincide in forests of the studied types. Regardless of forest type within the area of 100 m^2 species richness recovered 30 years after the fire (i.e 3–5 times earlier than the establishment of the complete stabilization of the forest structure). That means that floristic composition of the forest remained unchanged from 30 to 210 years after the fire.

Keywords postfire recovery, biodiversity, pine forest
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List of Symbols

N Number of species
H' Shannon index of species diversity
S_i The cover proportion of species i in comparison with the total coverage of the N species

1 Introduction

The process of recovery of vegetation cover after sudden external force is, by all appearances, the only mechanism available for the efficient retrieval of the stability of the biosphere.

Recovery time (i.e. the time period after whose expiration the community could be treated as stationary, climax one) is fundamental characteristic of vegetation. Studying the process of recovery makes it possible to determine both the character and rate at which the vegetation cover reacts to various disturbances.

In boreal forest ecosystem fires are very common; their recurrence is in the average of 40–100 years (Zakrisson 1977, Foster 1983, Engelmark 1987, Gromtsev 1993). The recovery time for the most of characteristics (excluding the tree age structure and the store of biomass) spans approximately 100–150 years (Siren 1958, Morneau and Payette 1989, Gorshkov 1995, Gorshkov et al. 1995). At the same time studies in recovery of vegetational cover, based on strict quantitative analysis are concentrated predominantly at the initial stages of succession (Shafi and Yarrangton 1973, Lindholm and Vasander 1987, Anderson and Romme 1991). In all except a few of works describing postfire plant chronosequence during the period of more than 200 years (Siren 1958, Zakrisson 1977, Black and Bliss 1978, Zjabchenko 1984, Sannikov and Sannikova 1985, Payette et al. 1985, Morneau and Payette 1989, Sannikov 1992, Engelmark et al. 1993) the questions of dynamics of characteristics of biodiversity are not given attention.

As noted by Tilman and Downing (1994), the majority of researches on problems of biodiversity is devoted to the theory and modeling. Only the small part (20–30 %) is submitted by experimental work and studies of natural objects.

Thus, dynamics of biodiversity of communities during their recovery after fires belongs to a problem, which so far remains opened. The necessity of empirical studies in this field is emphasized by many researchers (Payette et al. 1989, Drake 1990, Vanha-Majamaa and Lähde 1991, Parviainen et al. 1994, Parviainen 1995).

The purpose of the work – is to characterize dynamics of species density (i.e. number of species per the unit area) and the species structure of various forest components (tree stratum and the regrowth of tree species, dwarf-shrub and herb stratum and moss-lichen cover) in the process of 210-year postfire recovery.

As far as the characteristics of diversity essentially depend on the size of area over which they were estimated (Hopkins 1957, Kyrbi et al. 1986, Magurran 1992, Barkman 1993) in the work me analyzed characteristics, determined at the area of 1 m^2 and 100 m^2.

2 Material and Methods

2.1 Study Area

Investigations were carried out in the central and western parts of the Kola Peninsula (67°40'–68°00'N; 30°50'–34°50'E), predominantly at the territory of the Lapland Biospheric Reserve. The study area presents an elevated plain covered by deep sand deposits laid down by till and glacial meltwater during Pleistocene (Armand and Kudlayeva 1975). Mean elevation ranges between 400–500 m above sea level. Soils within the study area are of podzolic type with a low pH and contain low levels of inorganic nutrients and organic matter (Nikonov 1987). The average annual temperature is 0.5°C; the average July temperature, 14°C, and the average January temperature, –13°C (meteostation in the town of Monchegorsk). The annual precipitation is about 500 mm, with 30 % as snow. The average frost-free period is 104 days. (Scientific and applied reference book... 1988). The regional vegetation corresponds to the northern part of the Boreal Forest.

The level of air pollution determined by sulphur dioxide and heavy metals dust not exceeds that of the background (Barkan et al. 1990; Barkan 1993).

All studied forests are situated in the regions avoid from reindeer grazing (Bobok 1971, Semenov-Tjan-Shansky 1977), felling and other types of anthropogenic activity.

2.2 Objects

Studied pine forests correspond to three groups of types: I lichen (the share of lichens in the moss-lichen cover exceeds 70 %); II green moss–lichen (the respective share of lichens remains within 30–70 %); III green moss type (lichen share is below 30 % and that of moss exceeds 70 %).

Performed analysis of data collected has emerged a similar character of recovery process in forests from groups II and III; in this connection they were pooled to form one sample under the title "green moss type".

All studied pine forests are characterized by low productivity and poor species richness. The woodstand is either purely pine (*Pinus sylvestris* L.), or, has a sprinkling of spruce (*Picea abies* (L.) Karst., *Picea obovata* Ledeb.) or birch (*Betula subarctica* Orlova). Crown density of trees reaches 20–40 %. The average trunk diameter (of trees 120–150 years of age) is 15–30 cm at 1.3 m of height. Average tree height is 10–15 m. The undergrowth is usually absent, or remains within 1 %, if found. It may include *Populus tremula* L., *Salix caprea* L. and *Juniperus communis* L.

Regardless of the forest type, the main dominants of the dwarf shrub and herb stratum are species of two families: *Ericaceae* Juss. and *Empetraceae* S.F.Gray: *Empetrum hermaphroditum* Hagerup, *Vaccinium vitis-idaea* (L.), *V. myrtillus* (L.), *Arctostaphylos uva-ursi* (L.) Spreng. and *Calluna vulgaris* L.) Hull. The total projected coverage of the stratum amounts to 13 % in lichen type and 28 % in green moss type. Herbs present only 1 % and 3 % in the cover, respectively. The total number of species registered in all sites is 18 (9 species of dwarf shrubs and 9 species of herbs).

The total projected coverage by the moss-lichen cover in forests affected by fire more than 30 years ago reaches 70–90 %. The total number of lichen species amounts to 45, that of mosses – 34. In pine forests of lichen site type 40 years after the fire the ground cover is dominated by *Cladonia deformis* Hoffm., *C. cornuta* (L.). Hoffm., *C. crispata* (Ach.) Flotov and *C. gracilis* (L.) Willd. Within the time span from 60 to 100 years after the fire it is dominated by *C. mitis* (Sarnst.) Hale et W.Culb., *C. rangiferina* (L.) Nyl. and *C. uncialis* (L.) Wigg. *Cladina stellaris* (Opiz.) Brodo is the main dominant in the moss–lichen cover in forests when fire occurred over 120 years ago. The ground cover in pine forests of green moss site type up to 40 years after the fire is dominated by *Polytrichum* spp. and *Pohlia nutans* (Hedw.) Lindb.; the main dominants in forests with fire aged more than 60 years are *Pleurozium schreberi* (Brid.) Mitt. and *Dicranum* spp.

2.3 Sampling Methods

Vegetation analysis was performed at 50 permanent sampling sites 0.1–1.0 ha of size. From twenty to one hundred 1×1 m plots, organized into blocks of four (so that 2×2 m squares were formed) were established in each sampling site along 2–4 parallel transect lines. The distance between blocks was constant for each given site and was equal to 7 or 10 meters. The projected coverage (in percentage) of each species was estimated at each plot using the frame divided into 100 squares of 10×10 cm. The smallest surface area registered for tree species approximated ~1 dm^2, that for species of the dwarf shrub and herb stratum, moss–lichen cover and the regrowth was 1 cm^2.

The postfire ages of the selected sites were 5, 30–40, 60, 90, 150 and 210 years. Fire dating was based on the tree ring chronology, using living trees with fire scars at the radial distance of 50–100 m from sampling site. The age of the last fire was taken to be equal to the difference between the current age of a tree and that at the moment of injuring. In each case being analyzed the age of the last fire, determined in at least 5 of the trees, was one and the same.

For quantitative characteristic of species di-

versity two indicators were used: the total number of species, and the Shannon index of species diversity in a community, that is the entropy of species relative coverage.

The Shannon index was defined as:

$$H' = -\sum S_i \ln S_i \quad (1)$$

where S_i corresponds to the cover proportion of species i in comparison with the total coverage of the N species (Odum 1971, Magurran 1988).

The number of species and the Shannon index were calculated over the area of 1 m^2 and 100 m^2. The area of 100 m^2 was made up by one hundred of 1 m^2 plots. The area characterized in that case averaged 0.1–0.2 ha.

2.4 Statistical Analysis

To process the data collecting principles of the single factor gradient analysis was used (Whittaker 1973 a, b). Correlation analysis (Zachs 1976) was performed to examine relationships between the values of characteristics involved and the fire age.

To avoid erroneous interpretation of the results due to uneven distribution of sites along the fire gradient (the number of sites for the particular fire age ranges from n = 2 to n = 12), two statistical criteria were simultaneously used: non-parametric technique of sample comparison after Tukey (quick Tukey test) and the one-way analysis of variance (ANOVA) (Fisher 1955, Tukey 1959, Afifi and Azen 1982). Differences between samples were assumed to be valid when they were significant according to both criteria.

Lines in figures link the average meanings for significantly different samples. When the differences between samples were not significant the lines illustrate the average meaning for polled sample.

2.5 Nomenclature

The nomenclature used follows Cherepanov (1995) for the vascular plants, Santesson (1993) for lichens and Ignatov and Afonina (1992) for mosses.

3 Results

3.1 Moss–Lichen Cover

3.1.1. Number of Species

In lichen pine forests maximal values of the average species number ($N = 16$) over the area 1 m^2 were found 10–40 years after fire (Fig. 1a). By 90 years after fire average species number reduced 2-fold and did not change any more. Significant differences were recorded between samples of averages for forests burned 7–40, 60 and 90–210 years ago (Table 1). Samples of averages for forests with fire ages of 90 and 210 years were not statistically different (Table 2).

In green moss type of pine forests (as well as in lichen site type) maximal values of average number of species ($N = 15$) over the area of 1 m^2 were recorded in forests burned 30 years ago (Fig. 1b). Further the values reduced 2–3-fold and stabilized 90 years after fire.

At the total area of 100 m^2 30 years after fire species number averaged 38 in pine forests of lichen site type and 31 in green moss site type (Fig. 2a, b) and stabilized afterwards. No significant changes in the number of species at the total area of 100 sq.m were detected between samples for forests of both types burned from 30–210 years ago (Table 2).

3.1.2. Shannon Index of Species Diversity

In lichen pine forests maximal average meanings of the Shannon index ($H' = 2.0$) for the samples of 1 m^2 were found in forests with fire age of 30 years. Later, values gradually decreased and stabilized 120–140 years after fire at $H' = 0.5$.

In pine forests of green moss site type over the area of 1 m^2 Shannon index has reached a maximum ($H' = 2.0$) about 30 years after fire, then dropped and stabilized 90 years after fire (Fig. 1d).

In pine forests of lichen site type over the area of 100 m^2 the character of variation of the Shannon index coincided with the post-fire dynamics of that index over the area of 1 m^2: maximal

Table 1. Summary table of non-parametric comparison of samples of averages of characteristics involved for forests with differing fire ages (Quick Tukey test).

n	Figure	Characte-ristics	Forest type	Periods compared i	ii	Test statistics T_1	T_2	$T_{corr.}$	T	Signi-ficance
1	1a	*N*	l	7–40	60	6	12	1	17	***
2	1a	*N*	l	60	90–210	12	11	–	23	***
3	1b	*N*	m	30–60	90–210	7	11	1	17	***
4	1c	*H'*	l	30–40	60–90	4	8	2	10	*
5	1c	*H'*	l	60–90	150–210	14	8	1	21	***
6	1d	*H'*	m	30–60	90–210	6	4	1	9	*
7	2c	*H'*	l	40	60–90	3	8	2	9	*
8	2c	*H'*	l	60–90	150–210	8	4	1	11	**
9	3a	*N*	l	60–90	150	14	2	6	10	*
10	3a	*N*	l	5–90	150	16	1	9	8	*
11	3a	*N*	l	5–90, 210	150	20	1	11	10	*
12	3c	*H'*	l	60–90	150	13	1	6	8	*
13	3c	*H'*	l	5–90	150	15.5	1	9	7.5	*
14	3c	*H'*	l	5–90, 210	150	19.5	1	11	9.5	*
15	5a	*N*	l	40–90	150–210	14	4	2	16	***
16	5b	*N*	m	40–90	150–210	4.5	4	1	6.5	**

Abbreviations: *N* – number of species; *H'* – the Shannon index of species diversity; l – pine forests of lichen site type; m – pine forests of green moss site type.
*, **, *** – asterisks denote significant differences between two samples compared at $\alpha = 0.05$, $\alpha = 0.01$, $\alpha = 0.001$ respectively.
Statistics: T_1 – number of values in the second sample (involving the highest value for two samples compared) which are in excess of all values in the first one. T_2 – number of values in the first sample (involving the smallest value for two samples compared) being under all values in the second one. $T_{corr.}$ – correcting value at substantial [significant] ($n_2 > 3 + 4n_1 / 3$) differeces of samples compared (see Zachs 1976, Tukey 1958). *T* – Tukey test statistics.

index value was observed 30–40 years after fire, then it decreased and stabilized about 120 years after fire (Fig. 2c; Tables 1 and 2).

In pine forests of green moss site type Shannon index shifted to a value $H' = 1.5$ 40 years after fire and stabilized afterwards (Fig. 2d; Table 2).

3.2 Dwarf Shrub and Herb Stratum

3.2.1. Species Number

Over the area of 1 m^2 species number stabilized 5–10 years after fire in both lichen and green moss site types of pine forests, averaging 3 and 4 respectively (Figs. 3a, b; Tables 1 and 2).

In all the studied forests the number of species at the total area of 100 m^2 reached a certain value as soon as 5–10 years after the fire ($N = 7$ in lichen pine forests and $N = 9$ in green moss ones) and did not change further on (Figs. 4a, b; Table 2).

3.2.2. Shannon Index of Species Diversity

The species structure of the dwarf shrub and herb stratum levelled down during the first 5–10 years after fire. The Shannon index was rather stable in both measured forest types as well in plots and in total areas (Figs. 3c, 3d, 4c and 4d).

The average meaning of the Shannon index per 1 m^2 plots approximated 0.6 in lichen and 0.8 in green moss site type of pine forests.

Over the total area of 100 m^2 index values stabilized at a level of about 1.3 in both forest types.

3.3 Tree Stratum and the Regrowth

3.3.1. Species Number

Maximal average number of tree species and regrowth (N~1) was observed in lichen pine forests burned 60–90 years ago (Fig. 5a) and 30–90 years ago – in pine forests of green moss site

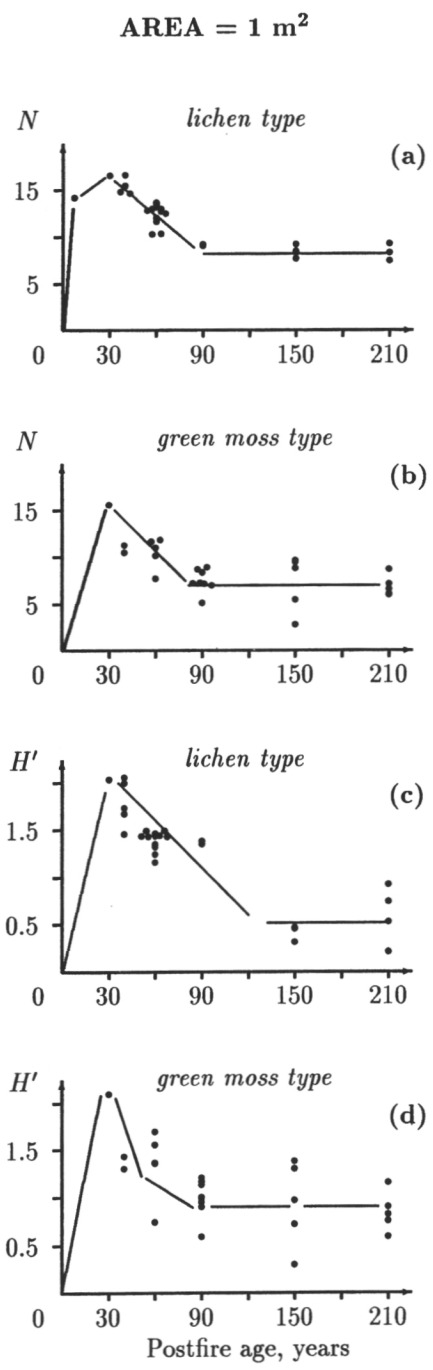


Fig. 1. Mean values of species number (N) and Shannon index of species diversity (H) of lichen cover in Scots pine forests of (a, c) – lichen site type and (b, d) – green moss site type in the Kola peninsula with differing postfire ages (estimated over an area of 1 × 1 m).

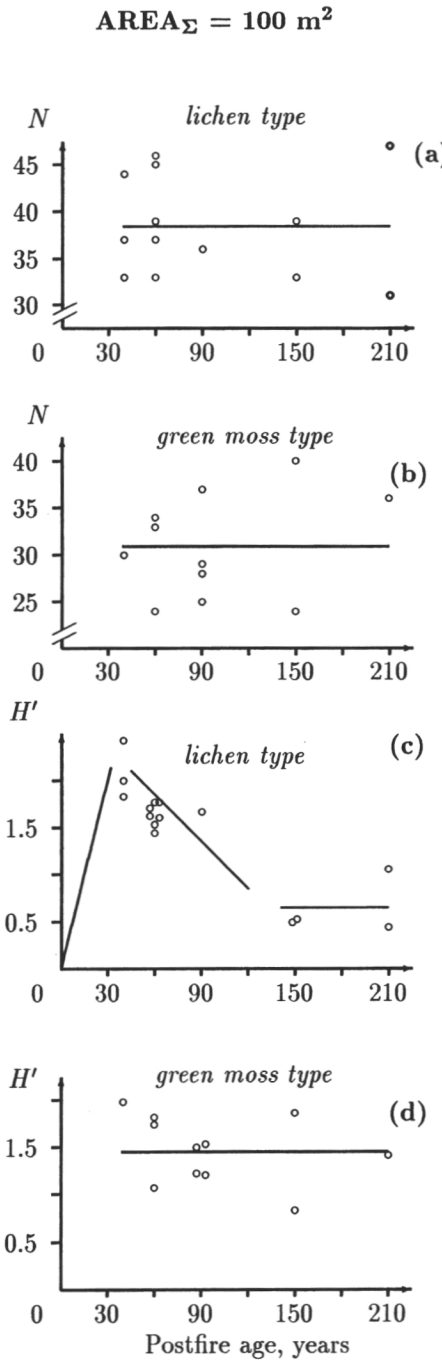


Fig. 2. Values of species number (N) and Shannon index of species diversity (H) of lichen cover in Scots pine forests of (a, c) – lichen site type and (b, d) – green moss site type in the Kola peninsula with differing postfire ages (at the cumulative area of 100 m^2).

Table 2. Summary tables of ANOVA.

n	Figure	Characte-ristics	Forest type	Postfire time span	Unit area	Statistics v_1	Statistics v_2	F-ratio	Signi-ficance
Lichen cover									
1	1a	*N*	l	90–210	1	2	7	0.58	
2	1b	*N*	m	90–210	1	2	17	1.00	
3	1c	*H'*	l	150–210	1	1	7	1.43	
4	1d	*H'*	m	90–210	1	2	17	0.96	
5	2a	*N*	l	40–210	100	4	11	0.66	
6	2b	*N*	m	40–210	100	4	4	0.24	
7	2c	*H'*	l	150–210	100	1	4	0.69	
8	2d	*H'*	m	40–210	100	4	4	2.90	
Dwarf-shrub and herb stratum									
9	3a	*N*	l	5–210	1	6	19	1.60	
10	3b	*N*	m	30–210	1	5	26	3.90	**
11	3b	*N*	m	30–210	1	1	30	0.39	
12	3ß	*H'*	l	5–210	1	6	19	1.86	
13	3d	*H'*	m	30–210	1	5	26	4.58	**
14	3d	*H'*	m	30–210	1	1	30	3.70	
15	4a	*N*	l	5–210	100	6	11	2.80	
16	4b	*N*	m	40–210	100	4	7	0.40	
17	4c	*H'*	l	5–210	100	6	11	0.80	
18	4d	*H'*	m	40–210	100	4	7	0.93	
Tree stratum and undergrowth									
19	5a	*N*	l	5–210	1	5	18	10.50	***
20	5a	*N*	l	150–210	1	1	4	0.61	
21	5b	*N*	m	40–210	1	4	15	3.14	*
22	5b	*N*	m	40–210	1	1	18	7.95	*
23	5b	*N*	m	150–210	1	1	5	0.33	
24	6a	*N*	l	5–210	100	5	11	0.95	
25	6b	*N*	m	40–210	100	4	3	0.03	
26	6c	*H'*	m	5–210	100	5	11	1.16	
27	6c	*H'*	m	5–210	100	1	15	0.65	
28	6d	*H'*	m	40–210	100	4	3	0.44	

Abbreviations: *N* – number of species; *H'* – the Shannon index of species diversity; l – pine forests of lichen site type; m – pine forests of green moss site type.

* – significant at $\alpha = 0.05$; ** – significant at $\alpha = 0.01$; *** – significant at $\alpha = 0.001$. Absence of asterisk denotes the lack of significant differences at $\alpha = 0.05$ (according to Fisher's test). Statistics: v_1 – degrees of freedom between groups; v_2 – degrees of freedom within group.

type (Fig. 5b). In both forest types the recovery of species number was detected 120–140 years after fire, approximating 0.6 in lichen type and 0.8 in green moss type.

At the total area of 100 ^{2} the average number of tree species and regrowth was 3 in lichen forest type and 4 in green moss forest type (Figs. 6a, b).

3.3.2. Shannon Index of Species Diversity

The average species density of trees and regrowth within the area of 1 m^2 is less than 1. It means that they were not present at each sampling plot. In those occasions the values of Shannon index for the area of 1 m^2 were not defined.

Recovery of the Shannon index over the total area of 100 m^2 coincided in time with the recovery of species density over that area (Figs. 6c, d) and was detected 5–15 years after fire. Mean

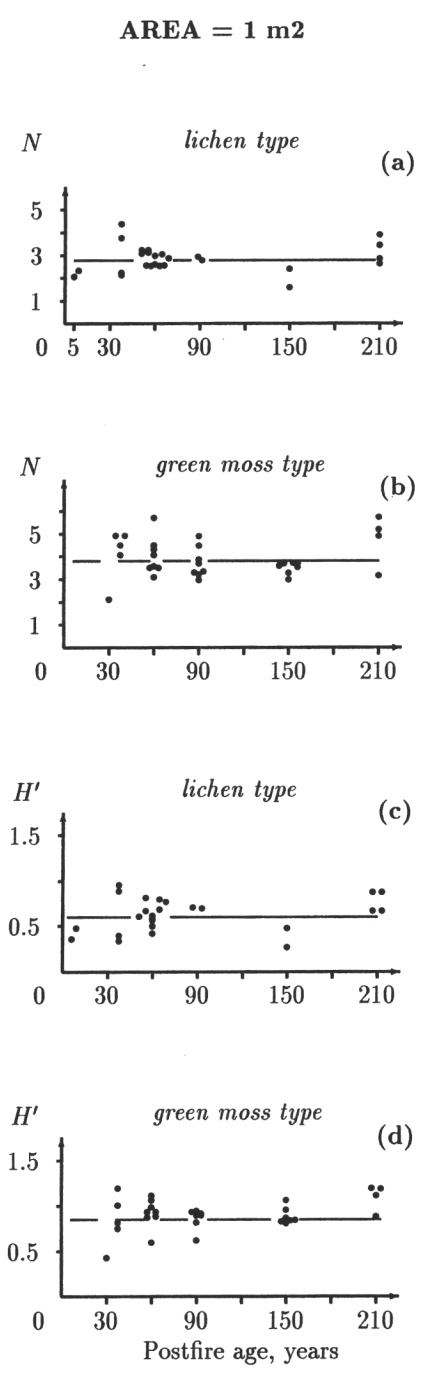


Fig. 3. Mean values of species number (N) and Shannon index of species diversity (H) of dwarf shrub and grass layer in Scots pine forests of (a, c) – lichen site type and (b, d) – green moss site type in the Kola peninsula with differing postfire ages (estimated over an area of 1 × 1 m).

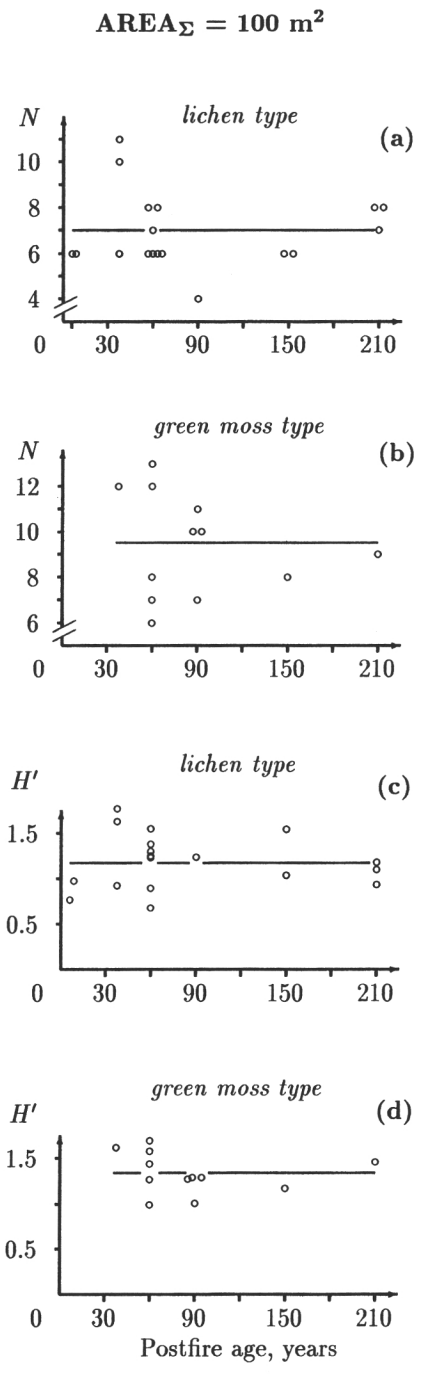


Fig. 4. Values of species number (N) and Shannon index of species diversity (H) of dwarf shrub and grass layer in Scots pine forests of (a, c) – lichen site type and (b, d) – green moss site type in the Kola peninsula with differing postfire ages (at the cumulative area of 100 m^2).

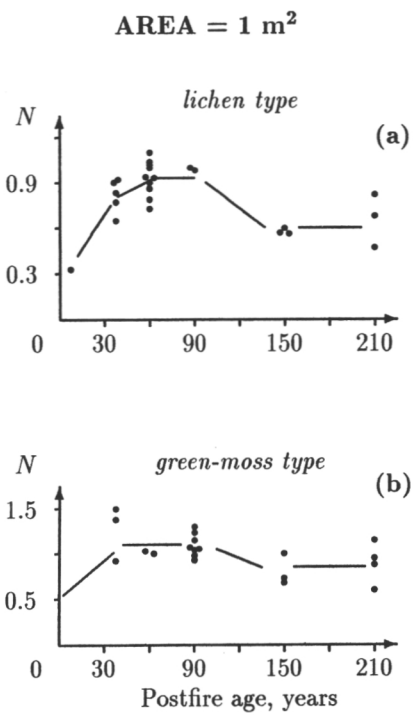


Fig. 5. Changes in mean values of number of tree species during postfire recovery in Scots pine forests of (a) – lichen site type and (b) – green moss site type in the Kola peninsula (estimated over an area of 1 × 1 m).

values of index averaged (H~0.2) in lichen and 0.5 in green moss forest type. No significant differences were evident between plots within the whole studied period.

4 Discussion

The results obtained indicate the difference in the dynamics of characteristics of biodiversity of separate forest components during postfire vegetative development (Table 3).

Characteristics of the dwarf shrub and herb stratum recovered and stabilized 5–15 years after fire, while the complete stabilization (restoration to its stationary non-perturbed state) of characteristics of the tree layer, regrowth and moss–lichen cover is observed in communities affected by fire

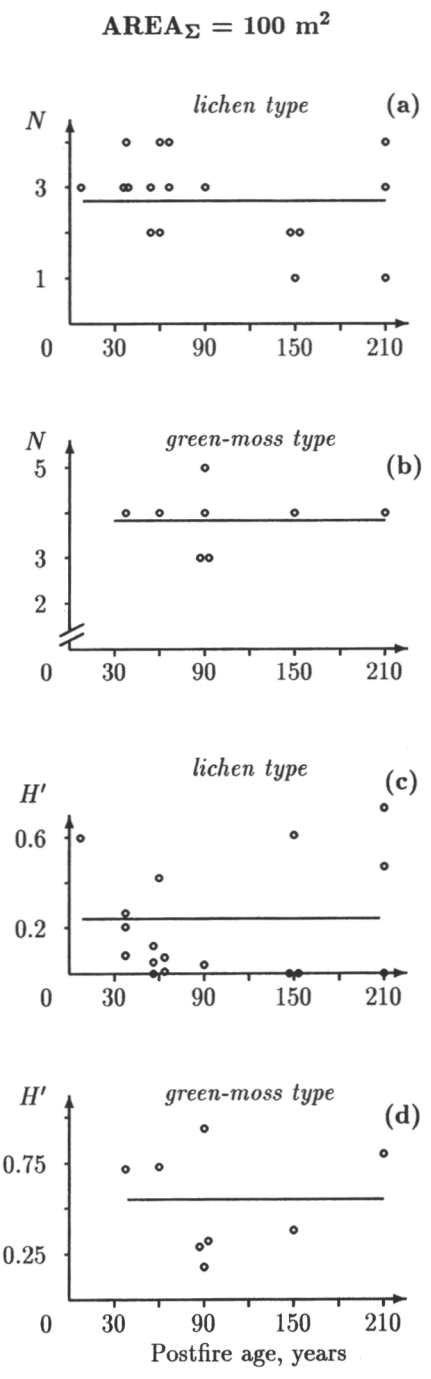


Fig. 6. Changes in values of species number (N) and Shannon index of species diversity (H) of tree species during the postfire recovery in Scots pine forests of (a, c) – lichen site type and (b, d) – green moss site type in the Kola peninsula (at the cumulative area of 100 m²).

Table 3. Recovery time of characteristics of biodiversity in lichen and green moss types of Scots pine forests in the Kola peninsula. (Abbreviations – see Table 2)

Forest component	Characteristics Characte-ristics	Forest type	Recovery time On area: 1¥1m	$A\Sigma = 100\ m^2$	Complete
Moss-lichen cover	*N*	l	90	30	90
	N	m	90	30	90
	H'	l	120–140	120–140	120–140
	H'	m	90	30	90
Dwarf shrub & herb stratum	*N*	l	5–15	5–15	5–15
	N	m	5–15	5–15	5–15
	H'	l	5–15	5–15	5–15
	H'	m	5–15	5–15	5–15
Tree stratum & regrowth	*N*	l	120–140	5–15	120–140
	N	m	120–140	5–15	120–140
	H'	l	–	5–15	5–15
	H'	m	–	5–15	5–15
Complete	*N*	l	120–140	30	120–140
	N	m	120–140	30	120–140
	H'	l	120–140	120–140	120–140
	H'	m	90	30	90

90–140 years ago. Therefore, time of complete stabilization of species richness of the community is approximated 120–140 years after fire.

Presented regularity of postfire restoration of characteristics of biodiversity is in general agreement with the process observed during post-fire succession elsewhere in Boreal Forest (Shafi and Yarranton 1973, Bazzaz 1975, Black and Bliss 1978, Southwood et al. 1979, Morneau and Payette 1989, Payette et al. 1995). Coincidence of the stabilization time of characteristics of biodiversity in different forest types and geographically isolated parts of boreal forest can not be accidental. It proofs that the recovery time of characteristics of biodiversity, approximating to 120–140 years, – is one of the fundamental characteristics of boreal forest communities.

The character of response (i.e type of relationship, mean value, location of maximum and the relaxation time) produced in species diversity significantly depends on the surface area from which such characteristics are retrieved.

The time of complete stabilization of characteristics of species diversity of communities is determined by the time of their restoration in the 1 m^2 sampling plots. On the total area of 100 m^2 stabilization of characteristics appears earlier or at the same time as in the 1 m^2 sampling plots.

Species density on the total area of 100 m^2 recovers quickly after fire, taking 30 years only, and then remains unchanged up to 210 years after fire (this is 3–5 times earlier than establishment of the complete stabilization of species density in the community as a whole). That means that floristic composition (the overall set of species of separate forest components) remains unchangeable from 30 to 210 years after fire.

Essential differences in the dynamics of species density and the entropy of relative coverage of species during post-fire regeneration, found at different area analyzed, indicates the existence of 2 levels of organization of the community: the interior, corresponded to the area of 1 m^2, the exterior, corresponded to the area of 100–400 m^2.

Structural replacement in vegetational cover is realized at the interior level. Period of complete stabilization of diversity characteristics at that level was found to be equal to 120–140 years after fire.

On the exterior level sustains the basic species set, necessary for the community functioning in recovery and stationary (climax) regimes. The period of recovery and stabilization of species richness at that level is not more than 30 years.

Acknowledgments

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Total of 46 references

North European Platyphyllous Forests: Biodiversity Dynamics and Climate Changes in Northwest European Russia

Anton K. Chtchoukine

Distribution, biodiversity and reforestation dynamics of the platyphyllous forests in the Northwest European Russia were investigated. Data assembled from 21 landscape regions (250–350 sq. km each) show special features of small-leaved lime, Norway maple, mountain elm and English oak reforestation during the last two decades.

New tendencies were found for the taiga areas with natural Norway spruce and Scots pine vegetation. Natural platyphyllous reforestation in cut spruce areas poses as supposed a special question for forest management policy in the relationship to global climate changes. Feasible unsustainability of the common types of succession (Norway spruce – European birch; Norway spruce – European aspen) is discussed.

Biodiversity of herbs, shrubs and tree species of platyphyllous forests is high and complex and is situated in 4–15 oldgrowth relics in each landscape region. Low level genotype heterogeneity of nemoral flora species of such isolated populations is presumed. Special biodiversity conservation regulations are proposed.

Keywords European platyphyllous forests, biodiversity, climate and reforestation
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1 North European Platyphyllous Forests

Platyphyllous, or nemoral broad-leaved, forests form an extensive band in temperate Europe between Atlantic Ocean and Ural Mountains. Moreover, mountain elm *(Ulmus glabra* Huds.*)*, English oak *(Quercus robur* L.*)* and some other platyphyllous tree species dominate or codominate in plant communities in the boreal North and Northeast Europe (Kurnaev 1968, 1980, Popadjuk et al. 1994).

Floristic composition of the platyphyllous vegetation includes a number of species which are known by a particular origin as a nemoral floris-

tic element (or the tertiary flora of the South East Asia). Relic nemoral flora communities with their structure and biodiversity richness are opposing to taiga forests monodominancy in the boreal regions of Europe and Asia (Sochava 1946, Tolmachev 1954).

Such platyphyllous forest communities in the boreal areas of Europe will be named below as North European platyphyllous forests in a contraposition to temperate regions broad-leaved arboreal vegetation. Some ecological reasons on this opportunity were demonstrated by some authors, for example, when the "dark platyphyllous forests" type was singled out (Kurnaev 1980).

Meanwhile platyphyllous forest communities are sufficiently investigated in temperate regions of Russia, there are no complete data for boreal (or taiga) regions (climatic and vegetation zoning according to: Aleksandrova et al. 1989). The aim of this work is to summarize extensive field research results and some odd data on holocene history of and human impact on, structure and dynamics of platyphyllous forest vegetation in Northwest Russia.

Biodiversity dynamics in connections with forest structure succession is a special interest of this paper. Natural climatic changes were the main factor of biodiversity changes during the Holocene. Composition of the nemoral and the boreal floristic elements (including trees, shrubs and herbs species) was a product of successions related with long-term distribution areas increasing process.

Both climatic affect of the Little Ice period and extensive human activity forced out the nemoral flora from plains to river valleys and calciferous areas (Zinzerling 1932). Platyphyllous forests were subplanted by Norway spruce and preserved only in some localities. Present situation demonstrates a reverse process when the nemoral flora species become the important part of forest composition.

2 Platyphyllous Forests in Northwest European Russia

The Northwest European Russia region is a Baltic Sea basin territory between Ladoga Lake and Finland in the north and Daugava River (Belorussia) valley in the south. Land square of the region is more than 150 thousand sq. km around Saint-Petersburg city. Plain country with some moraine hills (not over 300 m above sea level) is covered by boreal taiga forests: with Scots pine *(Pinus sylvestris* L.*)* on sand soils and Norway spruce *(Picea abies* (L.) Karst.*)* on clay soils. Anthropogenous vegetation on cut areas is represented by self-sown European birch *(Betula pubescens* Ehrh., or widely distributed hybrid races *B. pubescens x B. pendula* Roth*)* and European aspen *(Populus tremula* L.*)* (Nitzenko 1958).

Fig. 1 presents boreal (taiga) vegetation zoning for Northwest Russia (Aleksandrova et al. 1989) where north (1), middle (2), south (3) and subtaiga (4) subzones are shaped. Some authors (Kurnaev 1968) name subtaiga subzone as mixed coniferous-platyphyllous forests and suppose that it is not boreal, but temperate climate vegetation. The boundary between the middle and the south taiga subzones in Northwest Russia is in compliance with the limit between the south boreal and hemiboreal subzones according to Hamet-Ahti (1976). Typical landscape areas investigated in this research are marked (black areas) in Fig. 1 too.

Platyphyllous forests distribute sporadically in Northwest European Russia now, where they were cut extensively during years 1700–1950, especially for small-leaved lime *(Tilia cordata* Mill.*)* wood products. Therefore, in South Sweden platyphyllous forests are more typical vegetation and some points for South Finland are checked (Kalela 1961, Bjornstad 1971, Kielland-Lund 1981, Korotkov 1991).

2.1 Holocene Vegetation History

Holocene vegetation history of Northwest European Russia includes a warm, temperate and moist period between 6.5–5.5 thousand years ago (Neishtadt 1957). During this time the most part

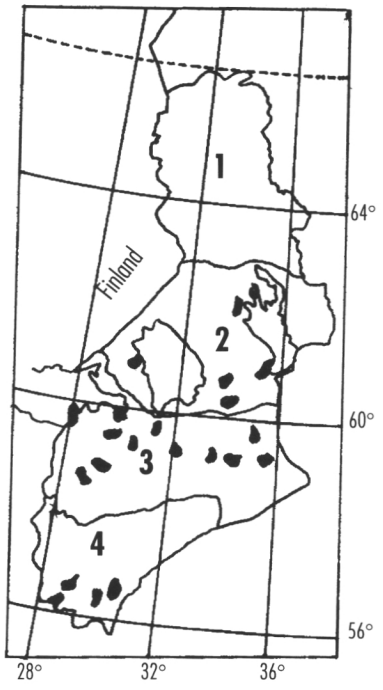


Fig. 1. Northwest Russia vegetation zoning (Aleksandrova et al. 1989) and landscape areas investigated. (Zones: north (1), middle (2), south (3) and subtaiga (4), typical landscape areas investigated in this research (black areas)).

of the region was covered by English oak, small-leaved lime and mixed European birch – small-leaved lime forests on clay soils as well as Scots pine and mixed pine-platyphyllous communities occupied sandy habitats (Nitzenko 1955).

Near 6.0 thousand years ago the northern boundary of English oak distribution area was limited by the south shoreline of White Sea (latitude 65) that is more than 500 km north from present habitats. Similar distribution was peculiar characteristic to small-leaved lime, mountain elm, European elm *(Ulmus laevis* Pall.*)*, European ash *(Fraxinus excelsior* L.*)* and Norway maple *(Acer platanoides* L.*)*. Even European beech *(Fagus sylvatica* L.*)* is known from pollen deposits of Northwest European Russia (Neishtadt 1957).

Middle Holocene was continued by a period with humid climate and unstable temperature conditions when Norway spruce area was increasing. Norway spruce became to the Northwest European Russia near 5.0–4.5 thousand years ago as second layer tree in platyphyllous forests (Nitzenko 1955, Minyaev 1966). Pollen data on Norway spruce distribution have some contradictions. The natural areal increasing process was very gradual and only almost 2.0 thousand years ago this tree species was spread to the northwestern part of the region – to Karelian Isthmus (Malyasova et al. 1965). Other point of view show not "south-to-north" but "east-to-west" Norway spruce coming (Tallantire 1972, Elina 1981). Last authors mark distribution boundaries near Petrozavodsk (Karelia) 7.5 thousand years ago and near Helsinki 3.5 thousand years ago.

In other way, unstable temperature conditions were provoking platyphyllous forests depression during the last few thousand years. Cold winter temperatures of boreal climate were marked with English oak, European ash and mountain elm areals decreasing. Norway spruce succession in platyphyllous forests changed soil acidity and light conditions and flora of the nemoral shrubs and grasses was migrating into intrazonal habitats. As a result the dark coniferous taiga with Norway spruce became dominance type of vegetation in the region of Northwest European Russia.

2.2 Human Impact

The present distribution of platyphyllous tree species and forests in the Northwest European Russia is connected with two main factors: (1) the past climate changes described above and (2) the human activity.

The density of human population passed two maximums in the rural areas in the regions similar to the Northwest European Russia. First maximum was checked between 11th and 14th centuries when traditional slush and burn agriculture was effective on the basic of climatic conditions. Then The Little Ice Period began and both the cold climate and historic tendencies induced immigration to towns and to the Central European Russia. Second maximum was embracing 18th–19th centuries and strengthened by the construction of St.Petersburg city and the redevelopment of neighboring areas.

The human impact had relations to the existence of platyphyllous forests. Historically English oak and small-leaved lime vegetation had occupied the most fertile soils in Northwest European Russia. Such areas were first involved in agricultural development, and the land annals demonstrate that in 19th century the agriculture regions were took place on special "poddubitsy" (i.e. "oak forest soils") soil type (Zinzerling 1932).

Mature oldgrowth English oak forests were cut extensively for construction and shipbuilding purposes and young small-leaved lime forests – for footwear handicrafts. Footwear handicraft alone was consuming more than 2 thousand sq. km of lime forests per year in the European part of Russia during the 19th century (Kurnaev 1980).

In the 20th century, active migration processes followed by industrial development and organization centers in connection with railroad network became the main cause of the changes in rural regions. Old, 19th century agricultural regions were neglected, and at the same time some of the 19th century forest regions were turned into account of agriculture and cutting areas. So, in 20th century the most important human impact to platyphyllous forests is ordinary forest management with extensive cutting processes.

2.3 Present Distribution

Traditionally, Russian geobotany and forestry interpret platyphyllous forests in the taiga zone as intrazonal habitats vegetation type (Zinzerling 1932, Porfiriev 1970, Lavrenko 1980, Korotkov 1991). Calcareous and alluvial valley soils and river valley microclimate conditions are named as a leading factor of modern platyphyllous forests distribution. Such an approach also includes an idea of English oak monodominant position in East European platyphyllous forests (Nitzenko 1958, Popadjuk et al. 1994).

Some authors (Kurnaev 1968, 1973, 1980) suppose that in the natural platyphyllous forests English oak grew as monodominant tree species in steppe and forest-steppe vegetation of temperate zone, but small-leaved lime and mountain elm codominance in boreal taiga regions. In this way, English oak boreal taiga forests have an anthropogenous nature of origin caused by pasture and cutting. Mixed lime – elm – European maple – European ash vegetation named as "dark platyphyllous forest" in opportunity to "light platyphyllous forest" with monodominant English oak.

The most recent areal maps (Hulten and Fries 1986, Bubyreva 1992) show northern limit of modern distribution for small-leaved lime and European maple near the south coast of the White Sea; for both, mountain and European, ash near the north coast of Onega Lake (Central Karelia); for English oak and European ash the south shoreline of Ladoga Lake (and South Finland for English oak too). So, all East European tree species have distribution inside the whole territory or main part of the Northwest European Russia.

3 Materials and Methods

The Northwest European Russia is divided into 70–80 landscape areas with special climatic and geomorphologic features. Previous data consider that only near 15–35 points of each platyphyllous tree species were known for near 150 thousand sq. km. And in most cases platyphyllous trees were found only as shrub form or second layer stand.

Special investigation was begun in 1991 and as a result 21 landscape regions of the Northwest European Russia (see Fig. 1) were inspected (250–350 sq. km each) in different climatic subzones (from middle taiga in Karelia to mixed coniferous-platyphyllous forests subzone in the south, near the Belorussian border).

Primary landscape analysis based on detail map and description data was given for every landscape region to indicate 'hot spots' points before field research. Also, herbarium samples data were taken into account for preliminary delimitation of concrete area of investigation.

Field research included two stages: (1) preliminary route inspection of the area, and (2) detailed investigation of platyphyllous and related forest communities.

The preliminary inspection of the area supposed common vegetation cover description, human impact analysis for forest areas (forestry activity evaluation, main sources of air pollution

determination, analysis of the past and the present agricultural influence to forests, *etc.*), detailed geomorphological analysis. Concrete localisations of platyphyllous and related forest communities could be given only during the preliminary inspection too, in causes that this type of vegetation is not marked on the forest maps for Northwest Russia.

The detailed investigation stage is based on forest analysis made in accordance to Sukachev approach of dominance-oriented classification of vegetation cover (Ipatov et al. 1995) with some additional components from landscape and biodiversity analysis. Vegetation is described on 400 sq. m samples in large forest areas or in the limits of concrete small homogenous contour (200–800 sq. m).

Description includes trees height (average and maximal for every canopy level and every species), stand volume (could be transferred into biomass) measurement, underwood or shrub evaluation, age analysis and taxation. Moss, herbs and semishrubs abundance and coverage (average for every spot of mosaic and for the whole contour) are estimated. Total square of each type of moss, lichens and herbs cover patch is measured and complete species composition is determinated. Soil typification is given for every type of cover patches. Special geomorphological description is accomplised for the landscape element where the interesting community is situated.

Completely, more than 240 communities were described and were involved into further analysis. Common classification scheme are based on dominant approach, but also communities were subdivided into groups related for the specific landscape elements (river valleys, plains or hills slopes vegetation, vegetation on calciferous and non-calciferous rocks, on sand, clay or semiclay soils, on moraine, abrasive, accumulative or maritime sediments, *etc.*). Detailed distribution maps for the every nemoral species which was found in the communities and for the every type (dominant association) of communities were given.

As it was ascertained the biodiversity of platyphyllous forests herbs, shrubs and trees species is high and complex and situated in 4–15 oldgrowth relics subregions in each landscape region between Norway spruce, Scots pine and anthropogenous European aspen or European birch vegetation. There are no strong interrelations between calcareous soils and platyphyllous forests habitats. Plain habitats frequency is similar or equal to frequency of river valley forests. There are no differences in square frequency of platyphyllous trees species between middle taiga, south taiga and mixed coniferous-platyphyllous forests subzones, but anthropogenous influence and agriculture history are playing an important role.

4 Structure and Dynamics

Both in plain and valley sites small-leaved lime and mountain elm are forming nearly 20 m high first storey in oldgrowth forests. In some points middle-aged English oak, European elm and European ash cover were found. There are no European maple upper layer stands. In common case, 2–3 platyphyllous tree species are participating in community cover as well as 1–2–3 another tree species. Also mixed coniferous-platyphyllous stands are represented, especially with Norway spruce, and with Scots pine in rare cases. Anthropogenous mixed European aspen – English oak (or small-leaved lime) vegetation is common case than pure platyphyllous vegetation.

The variety in structure is caused by the dynamics variety and represents a row degree of platyphyllous forests succession from communities dominanted by Norway spruce to platyphyllous communities. Local distribution anomalies of some species caused mostly by human impact and geochemical heterogeneity of the area have significance too. Three examples of the forest structure demonstrated below are grouped in order of supposed succession direction.

4.1 Mixed Coniferous-Platyphyllous Forests

Mixed coniferous-platyphyllous stands represent Norway spruce formation in the majority of cases, but Scots pine formation exists sometimes. Ordinary community is dominated by Norway spruce dominance with 20–25 m high and 80–150 years old trees. In many habitats Norway

spruce is forming pure upper storey, but one part of the points shows mixed Norway spruce – European aspen stands as a result of small-area selective cutting of the beginning of the 20th century. In fact both species could be predominant, but the biomass of European aspen is lower usually.

Platyphyllous tree species are situated at lower layer in communities described above. Small-leaved lime and mountain ash live successfully under the cover of the upper level of Norway spruce branches. Broad-leaved trees have a wide amplitude of age and biomass in stands between 12 and 19–20 m high. The age of some trees is very difficult to estimate because of different productivity (high – in most cases and very low – in others) and of the possible continuos prefertile period. Shrubs forms of *Tilia cordata* were registered in some landscape regions and in addition coppice shoots trees (even 120–150 years old shoot groups).

Communities which were investigated show a variety of seminatural self-sown secondary coniferous-platyphyllous forests distributed on areas which were cut in 1850–1940 years. Norway spruce vegetation is primary in the Northwest European Russia excluding some taiga green-moss habitats. Semi-natural forests successions are near primary successions in some landscape regions and habitats with low post-cutting anthropogenous influence. A great number of coniferous-platyphyllous forests were found in areas where direct human pressure was discontinued after the cutting.

4.2 Mixed Aspen-Platyphyllous Forests

The second stage of succession is affected by clearcutting of coniferous-platyphyllous forests. Clearcutting was followed with an agricultural development in cutting areas and did not occupy large area before 1910. After that, in 1920–1970, clearcutting was the main path of forest harvesting and most part of the area in the process became self-sown semi-natural communities.

In most cases the European aspen became the first after-cutting dominant tree species. Somewhere (more often – in peat-forests and on low productivity soils) European birch formed first layer woodstands too. Really, in both situations platyphyllous trees species are playing a similar role, but aspen-platyphyllous forests have a spreading in all landscape regions.

At the age of 40–60 (70) years the aspen-platyphyllous forests should be divided into two groups. Group 1 includes communities with first storey of aspen (monodominancy, 18–23 m high) and low second layer of seed or(and) coppice shoots trees of small-leaved lime or seed European maple stands (11–12 m high). In such communities platyphyllous thicket is changing light and soil conditions in a wide scale, but only broad-leaved trees wood will be including the only 15–30 per cents of whole biomass. And only after new clearcutting a possibility of platyphyllous dominance will be a question of the day.

More rare and more interest picture is shown for Group 2, where platyphyllous and aspen stands have equal age. European aspen is growing better and more quickly in the first period of reforestation and is forming an upper layer. After age 20–30 English oak and small-leaved lime have more preferable conditions for growth under the aspen cover (in reasons on winter minimum temperature adaptation in undergrowth microclimate conditions). Moreover, after age 40 platyphyllous second layer stands begin to consolidate into the upper, aspen storey. This process of platyphyllous tree penetration into the upper layer is a probable way of final stage succession.

4.3 Platyphyllous Forests

The third and the final type of communities have two sources of origin. First, some oldgrowth relic platyphyllous forests are locating in a number of landscape regions. These primary, wild forests were found on both clay and sand planes and valley terraces. Primary forests are populated by mountain elm, English oak, small-leaved lime everywhere and by European ash in only 1 location. Monodominant stands are more typical for European ash and English oak communities. Mountain elm is growing in some cases as codominant with small-leaved lime and in other locations as monodominant.

Relic oldgrowth communities are represented not only by primary forests, but also by platyphyllous forests gap-mosaic successions stages. Primary forests with stands of one age group have the upper layer 14–17 m high in middle taiga subzone landscape regions and 18–21 m high in south taiga subzone. Similar data were obtained for gap-mosaic succession stages, but the first storey is lower in some points. In some places original lime-tree stands were cut more than a century ago, but trees of coppice shoot origin form the upper storey 20 m high now.

Platyphyllous vegetation with another source of origin is more significant for dynamics investigation. Some communities were observed where the dominance of platyphyllous tree species is a result of aspen-platyphyllous forests succession. There is only probable succession in common case, but some examples of the habitats demonstrate a real row of variants of communities in which aspen dominance decrease gradually as well as small-leaved lime, mountain elm or English oak biomass and importance grow up.

Similar secondary platyphyllous forests are represented by mixed *Ulmus glabra – Tilia cordata* communities in valley habitats and *Quercus robur – Tilia cordata* stands on plains. Average age of dominant tree species is near 40–60 years and the upper layer resulted is near 18–22 m high. Some exclusions were shown for the middle taiga regions in which small-leaved lime or European maples occupy clear-cut areas of Norway spruce areas as monodominant tree species. But succession history was limited by 10–15 years in all such cases.

5 Climate Changes Impact

Climate dynamics and human activity were the main factors in spreading of platyphyllous species and forests in past. Although its climate changes impact is well known, but was described only as long-term influence affect. Mainly macroclimatic changes with 100–1000 duration cycles were investigated and the species composition of communities only was shown as a result of interrelations between climate conditions, their changes and vegetation history.

Present and future climatic changes are supposedly occurring more quickly and their results should be more intensive. Especially short-term vegetation structure and composition changes are playing significant role for the forestry and the biodiversity preservation. In this matter 10–100 years forest succession cycles stability under the climate changes influence become a most important part of the boreal taiga sustainability. And specific changes in the modern short-term successions effected both by continuous climate changes and catastrophically fluctuations could be demonstrate probable future forest succession paths.

5.1 Succession Type Unsustainability

Climate dynamics is a leading factor of small-leaved lime and mountain elm reforestation now, as were shown during investigations in 21 landscape regions of the Northwest European Russia (Chtchoukine 1995). Average year temperature is growing in some parts of the territory during the last two decades. A great number of new young platyphyllous growth was found (between 8–45 examples per landscape region). Data show that only last 10–15 years give a new basic tendency – platyphyllous (not aspen and birch) reforestation in cut spruce areas. This type of succession is common now not only in the mixed platyphyllous-coniferous forests climatic zone, but also in the south and the middle taiga subzones (even in Central Karelia).

In favorable climatic conditions similar type of vegetation succession could be common in extensive areas of the Northwest European Russia and, probably, in the southern Scandinavia. Warmer climate also gives more possibilities for aspen-platyphyllous communities succession into pure platyphyllous forests. Potential vegetation of the region (or for a part of its, especially for plain habitats on clay soils) should be platyphyllous forests with 2 or 3 broad-leaved species codominance.

Two kinds of unsustainability may be possible due to climatic changes in the future in the connections with platyphyllous vegetation existence in the boreal zone of the North Europe. Both will be affected by modern biodiversity unsustainability and the structure of succession cycles re-

development caused by warmer climate.

At first, coniferous (mainly, Norway spruce) self-sown on cut areas will be suppressed under more competitive platyphyllous forests succession type. There is a question which type of succession (through aspen to Norway spruce or through aspen to broad-leaved wood species) is more competitive in natural, gap-mosaic successions, but clear-cut territories give more chances for small-leaved lime and mountain elm in the Northwest European Russia. Concrete way of the processes of climatic changes could be resulted in more fast or slow Norway spruce type of succession depression. In these reasons, detailed mosaic of microclimates and habitats should be a main factor of succession type differences.

Another succession unsustainability source is placed in the population structure of platyphyllous tree species in the North Europe. Small-leaved lime, English oak, mountain elm and other nemoral tree species were growing in Northwest European Russia and neighbored countries in isolated populations during some decades or, may be, centuries. Moreover, previous data give an information that small-leaved lime had not have seed reproduction during the first half of 20th century and only vegetative, coppice shoots trees populations are presented now.

In this matter, modern situation suggests a low level genotype heterogeneity in each landscape region or habitat and high level heterogeneity of populations from different landscape regions. Main problem in this case is a great unsustainability of such isolated populations and their posterity during climate changes and fluctuations. Platyphyllous stands followed from new types of succession cannot be more stable than primary Norway spruce vegetation. More detailed modelling for this purposes is needed, but first suggestions conclude that special genotype management for platyphyllous forests sylvicultures and wild genotypes resources investigation and attraction are requested. In this way Ural Mountains platyphyllous tree species populations which are existing in more continental conditions could be used as genotype source, for example.

5.2 Dark Coniferous Taiga Biodiversity

Probable process of Norway spruce type of succession depression which will be subject of few next decades according to modern climate change effect and clear-cut forestry technique if forests are left to regenerate naturally provokes new biodiversity threat for some boreal regions.

Dark coniferous forests species include a natural group of grasses and semi-shrubs adapted to cold climate, acid soils and low light density conditions of boreal vegetation. Part of such species has not have chances for an adaptation to more warm climate, to high light density and sand, poor water soils of Scots pine forests or to more neutral and alkaline leaf fall of platyphyllous trees.

In the new situation some species will be suppressed and become extinct in the most part of their European areals after the platyphyllous type of succession establishment caused by climate changes. Three ways of suppression are supposed:

- *particular* – when species has more wide habitats distribution and will be preserved in another, non Norway spruce communities *(Vaccinium myrtillus* L., *Neottia nidus-avis* (L.) L.C.Rich, *Solidago virgaurea* L., *etc..);*
- *direct* – when species will be depressed by only climatic conditions changes *(Aconitum septentrionale* Koelle, *Rubus arcticus* L., *etc..);*
- indirect – when species will be avoided by the platyphyllous type of succession influence not by direct climatic conditions effects *(Pyrola media* Sw., *P. rotundifolia* L., *Epipogium aphyllum* (F.W.Schmidt) Sw., *etc..).*

Afterwards, dark coniferous forests biodiversity preservation is needed in connections of future climate and vegetation changes in regions with modern south and middle taiga climatic subzones. Mainly whole habitats of Norway spruce oldgrowth forests with complex boreal biodiversity should be preserved and habitats of dark taiga herbs and semi-shrubs threatened by indirect suppression should be retained too.

5.3 Nemoral Flora Biodiversity

It could be strange, but nemoral flora biodiversity will be under the threat particularly too. A leading factor of such phenomenon is not future climate changes itself, but modern status of nemoral flora species populations and local biodiversity.

The biodiversity of the nemoral flora (i.e. flora of platyphyllous forests) in the Northwest European Russia is like giant broken mirror pieces dispersed between boreal taiga foreground. Only 2 cases from 21 landscape regions show a complete nemoral flora list with near 50 species of trees, shrubs and grasses. In other cases only part of species is presented, near 20–30 nemoral flora species in a common case.

Situation described before calls a necessity to make special preservation measures for each old-growth or significant biodiversity level platyphyllous forests communities and for post-platyphyllous nemoral flora (where broad-leaved trees stands were cut, but nemoral herbs and shrubs biodiversity is presented) forests too. Some grass species which have a modern spreading only in limited number of locations should have special regulations (for example, *Sanicula europaea* L., *Mycelis muralis* (L.) Dumort., *Mercurialis perennis* L., *etc*..).

Such measures are necessary, because a modern low genotype heterogeneity of nemoral flora of each landscape region (not only for trees as was shown above) can be a main part of future platyphyllous forests unsustainability when climatic conditions oscillations will be revealing.

5.4 Forest Management

Two basic problems are connected within forest management and afforestation in relations with platyphyllous type forest succession in the south and middle taiga subzones of the Northwest European Russia.

Warmer climatic conditions will give most productive broad-leaved trees sylviculture in the region. Some experiments (Timofeev 1966, Kurnaev 1980) demonstrated that lower, second storey of small-leaved lime in Norway spruce forests increase timber production on 40 per cents in comparing with ordinary monodominancy Norway spruce forest, both in sylviculture and in natural communities. Tendencies of climatic changes should give a possibility of extensive small-leaved lime sylviculture development in existing Norway spruce forest areas.

Another question is given by modern technique of plantation and self-sown forestry. Main modern sylviculture strategy in the Northwest European Russia and some neighbored countries is a Norway spruce plantation production and self-sown Norway spruce forests regeneration through semi-natural successions. It is especially important that ordinary reforestation practice uses for recovery genotypes of Norway spruce (and Scots pine too) from the modern most productive populations.

There is no any guarantee that the modern most productive populations will be most productive in the future, in other climatic conditions. Moreover, it is possible that after 40–50 years from reforestation Norway spruce as a boreal species will be suppressed in the North Europe. The present south limit of Norway spruce spreading is placed near 800 km to south from Finland, and only 450 km to south from modern taiga zone board. Where will be southern limit of Norway spruce area when the global climate changes? There is a question which was not analyzed with any simulation model. In these reasons, some improvements of reforestation policy should be given in the interrelations with climate changes processes.

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Impact of Fire on Finnish Forests in the Past and Today

Jari Parviainen

Nearly every forest stand in Finland has been burnt down by a wildfire at least once during the past 400–500 years. Slash and burn cultivation (1700–1920) was practised on 50–75 percent of Finland's forests, while prescribed burning (1920–1990) has been applied to 2–3 percent of the country's forests. Because of land-use changes and efficient fire prevention and control systems, the occurrence of wildfires in Finland has decreased considerably during the past few decades. Owing to the biodiversity and ecologically favourable influence of fire, the current tendency is to revive the use of controlled fire in forestry in Finland. Prescribed burning is used in forest regeneration and endeavours are being made to revert old conservation forests to the starting point of succession through forest fires.

Keywords forest biodiversity, wildfires, slash and burn cultivation, prescribed burning
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1 Introduction

Biodiversity is presently the leading concept in forestry by developing forest silvicultural practices in boreal zones. This includes the dual objectives of protecting the rare and vulnerable forest ecosystems and practising the silviculture with more nature oriented principles. Silviculture is expected to follow methods that mimic natural events. Stand structures of production forests should manifest specific features of natural forests like the quantity of standing or fallen dead trees and the presence of broad-leaved species and charred wood.

In the case of Finland, for example, the way in which silvicultural measures are applied is steered by historical developments and human impact on forests (e.g. slash and burn cultivation and diameter based selection cuttings) and from the viewpoint of natural forests, by forest fires and other natural catastrophes. Wildfires have been a fundamental element of the natural development of Finnish forests, but the most important impact that fire has had on forests involved the partnership of man. This review summarizes the impact of fire on Finnish forests and evaluates the possibilities and needs for reviving fire management in silvicultural practices.

2 Wildfires

Hundreds of years ago, the forests of Finland were untouched wilderness areas. In addition to fires lit by lightning, fires were also lit by hunters. However, hunters would roam hundreds of kilometres beyond the outermost settlements. Occasionally they would start off forest fires deliberately, but mostly by accident. Negligence in putting out campfires was probably the main cause behind fires.

At times forest would be burnt purposely to attract moose into the smoke away from the insect pests. Hunters were then in a good position to slay them. Forests were also burnt with the purpose of providing better feeding grounds for moose (Kardell 1984).

The oldest statistics in Finland on the numbers of forest fires and on the areas swept over by them go back some 130 years (Saari 1923). While wildfires were very common on crown land in the 19th century, the areas affected were relatively small. Some 50 000–70 000 hectares were burnt down in the worst years 1868, 1888 and 1894. A hundred years ago, there were 150–200 forest fires each summer (Table 1, Fig 1).

The small area burnt in individual fires is explained by the weather conditions and the mosaic-like structure of Finnish woodlands, the alternation of dry heathland forests and wetland sites. One third of Finnish forests grow on peatland sites. Although hundreds of thousands of hectares of forest may have been burnt by fire during hot and dry summers, with suitable assistance from wind, Finland has not been afflicted by fire catastrophes to the extent of more continental boreal regions like Siberia or China.

Research results obtained in northern Sweden indicate that wildfires on dry sand and gravel soils ignited in natural conditions by lightning have reoccurred at an average interval of 50 years (Zackrisson 1977). On moist moraine soils this interval has been 120 years. South-facing

Table 1. Occurrence of wildfires on crown land in Finland during the period 1865–1920.

Period	Annually burnt Total, hectares	Number of fires in average/year	Average size hectares
1865–1870	13764	105	131
1871–1880	8507	134	63
1881–1890	8707	127	69
1891–1900	9335	121	77
1901–1910	3407	87	39
1911–1920	3560	127	28

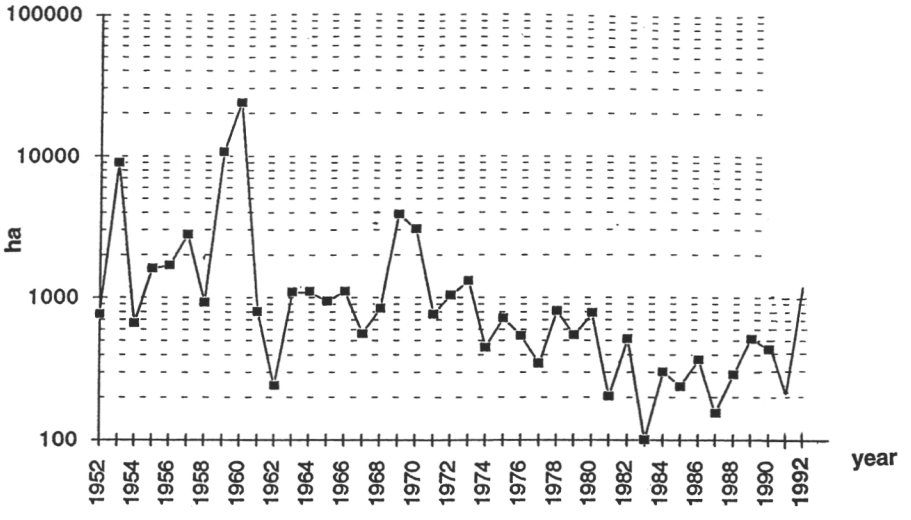


Fig. 1. The annual forest area burnt by wildfires in Finland during the period 1952–1992.

slopes have been more prone to wildfires than north-facing slopes; similarly, hill tops were sensitive to fire damage whereas valleys were not. Similar figures for fire intervals has been obtained troughout lake sediment analyses also in Southern Finland (Tolonen 1983). The interval between wildfires has shortened towards our time from 4000–3000 years b. Ch. With forest fire statistics and the average interval between fires as the basis, it can be estimated that Finnish forest land has been burnt down at least once during the past 400–500 years.

The annual number of fires, several hundred (400–500), has remained constant during the last decades because of efficient fire prevention. Today, the average area afflicted is a mere 0.5 hectares (Fig. 1) whereas a hundred years ago it was between 60–80 hectares. The total area burnt during the past 40 years amounts to approx. 80 000 hectares (Metsätilastollinen Vuosikirja 1993–94).

Spruce *(Picea abies)* is usually killed by fires. While old, thick-barked pine *(Pinus silvestris)* will usually survive, the butt will often become scarred in places where the cambium under the bark is killed by the fire. Silver birch *(Betula pendula)* is another species that has developed a degree of fire resistibility. Pioneer tree species (birch, aspen, alder and pine) are the first to reclaim burnt, treeless sites. The young forest is dominated by broadleaves of both coppice and seed origin. Gradually, the short-lived light-demanding pioneer species begin to give up and pine begins to take over. Later on, the sites begin to have an increasing proportion of spruce and in the climax stage stands will be composed almost entirely of spruce. The species composition in the climax stand depends on site quality. On dry sites, pine will be the dominant species, but as the site becomes more moist, spruce takes over (Kalela 1945, 1948, Kuusela 1990, Schmidt-Vogt 1991).

The fire has a vital importance in maintaining the nutrient cycle, biological productivity, and biodiversity. In a climax stage forest the nutrients are bound up in the growing stock and in the underlying raw-humus layer. Only a few percent of the total nutrients are actually involved in the cycle between the trees and the soil. The raw-humus layer of an old stand of spruce, for example, will contain 1500 kg/ha of nitrogen in an unavailable form. At the same time, a mere 20 kg/ha of nitrogen is actually cycling between the trees and the soil (Kellomäki 1987).

3 Slash and Burn Cultivation

Although wildfires belong to the natural succession of boreal forests, the most important impact that fire had on forests in the 18th and 19th centuries in Finland involved the partnership of man. The rural populations of those times relied on the practice of slash and burn cultivation for their livelihood.

The two principal forms of slash and burn cultivation were practised (Vilkuna and Mäkinen 1988):

1) The first phase was to burn down the more fertile forests dominated by broadleaves nearby the villages. This technique was called "lehtipuukaski". The swidden areas close to settlements were subjected to turnip, barley and rye shifting cultivation. The fallowing period between the crops in turnip, barley and rye cultivation was 8–30 years depending on the development of the secondary forest.

   A fresh opening would be made in a grey alder wood or a mixed wood that had established by natural regeneration in the area. Fast-growing tree species did not take long to build up a sufficient amount of combustible woody material. Plots would be cropped for 1–2 years and then they would be left fallow and allowed to revert to forest.

2) In the 16th century, slash and burn cultivation began to be practised in middle and eastern Finland with a technique to cut down and burn mature stand of spruce sometimes very far from the settlements. This technique was called "huuhtakaski". The new technique led to the spreading out of human settlement throughout the country.

   The basic idea for this technique was the killing of standing trees by ring-barking. (pykälikkömenetelmä). The ring-barking of old, mature trees – perhaps as many as 300 trees per hectare, was a preparatory stage. The drying-up of the trees and

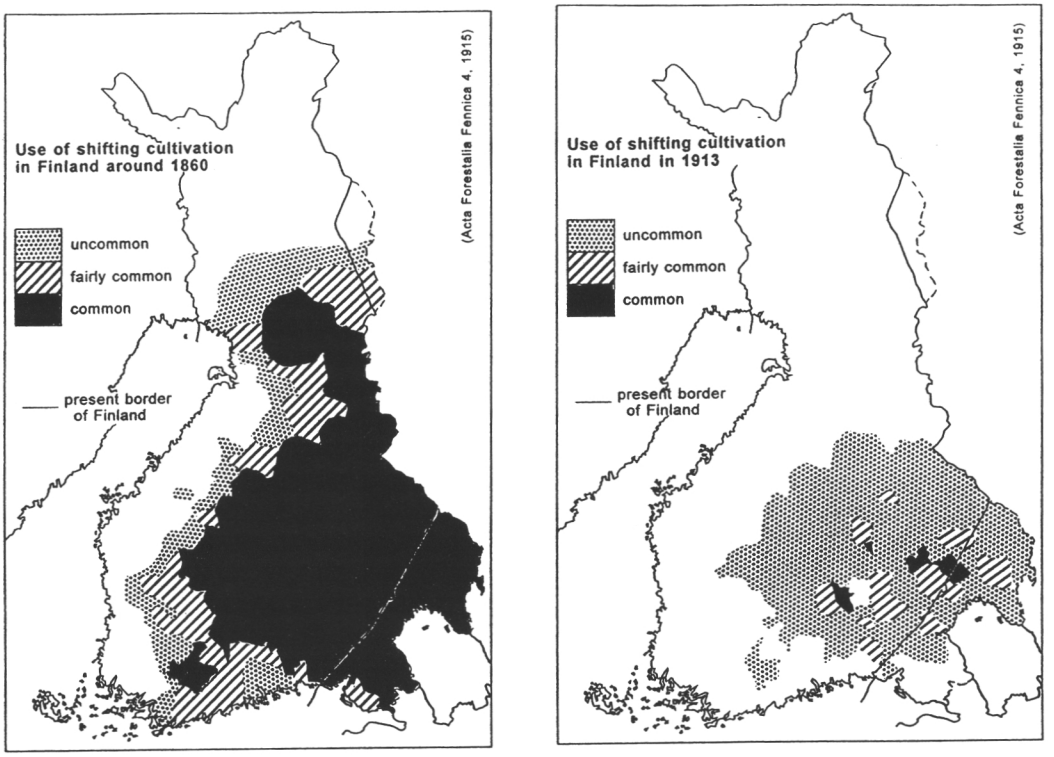


Fig. 2. The relative application of slash and burn cultivation in different localities of Finland during the years 1860 (3a) and 1913 (3b).

their roots made the raw-humus layer more porous, which in turn improved the burning. A drying period of 10–15 years was followed by the burning. Not all of the ring-barked trees were necessarily cut down. Rye was sown in the ash.

During the intervals between consecutive swidden operations, the plots of land would often serve as forest pastures. Grazing of farm animals hindered the forestation as mere grass was not adequate to satisfy the nutritional requirements of the farm stock. The cows and horses would eat tree seedlings and lower branches and consequently swidden areas would develop into patchy forests (Heikinheimo 1915). These areas would also be accessed for winter fodder for the cattle and horses and conifer branches as bedding. Collecting of conifer branches tended to reduce the survival of spruce. Fields and meadows had to be fenced and this consumed a lot of sapling and thus influenced the species composition of swidden areas (Helander 1949, Linkola 1987).

Heikinheimo's studies (1915) revealed that slash and burn cultivation in Finland was practised over more than 4 million hectares per year (Fig. 2). By the beginning of this century, some 50–75 percent of Finland's forest area had been exploited in this manner. In the eastern part of Finland shifting cultivation was practised longer and more intensively than anywhere else in the country.

Slash and burn cultivation gave rise to conflicting opinions. It was necessity for the livelihood of the rural population. Nevertheless, the government authorities were worried because of it. On the other hand, already in the 19th century it was feared that loss of forest cover because of shifting cultivation would lead to a cooling of the climate and to Finland becoming unsuitable for human settlement (Leikola 1988). Another, more urgent cause for concern involved the rising economic significance of the forests. Sawtimber and timber for mining were becoming

increasingly important. Concern over the loss of the country's forest resources culminated in the inviting of a German forestry expert, E. von Berg, in 1858 to come and report on the state of Finland's forests. The report gave a very gloomy view of the forests in areas of intensive shifting cultivation. Moreover, tar distillation, a practice that destroyed the best trees, had created large areas of dismal landscape, especially in western Finland. The forests in the vicinity of villages were all-aged woods of pine, hardwoods and mixed species. Slash and burn cultivation had already made it difficult to find firewood or timber for building and construction near villages (von Berg 1859).

Legislation was passed in an endeavour to safeguard timber for industrial needs. A bill passed in 1734 made it compulsory for farmers to have a licence before they could burn over forest. But it was not until the end of the century that this regulation began to have a real effect in heartland of shifting cultivation. The Private Forest Act of 1929 still permitted the practice of slash and burn, but only in places where it could be defended as being a sensible practice.

In addition to influencing the availability of timber, slash and burn cultivation had a major influence on the landscape, the cycling of soil nutrients and regional biodiversity (Linkola 1987). It also influenced the nutritional status of inland waters and the species composition of the forests.

The results of the first national forest inventory, conducted in 1921–1923, showed that 50–60 per cent of the forest land in south-eastern Finland was covered by woodlands less than 40 years of age (Ilvessalo 1927). Broad-leaved species accounted for nearly half of the forest area with the share of spruce being only 12–15 per cent. The most recent inventory conducted in the same part of the country, and completed in 1988, revealed that spruce and pine amount to 40 percent each with broadleaves making up the remaining 20 per cent (Metsätilastollinen vuosikirja 1993–94).

4 Prescribed Burning

With the ending of the era of slash and burn cultivation in the early part of this century, methods derived from this practice began to find use in the regeneration of under-productive forests. Burning of logging waste and raw humus layer was recommended as a means of promoting the natural regeneration. Broadcast-seeding-on-snow in spring, with prescribed burning preceding it, found widespread use in the 1920s. Prescribed burning in those times amounted to approx. 8000 hectares per year (Fig. 3). With time, however, this method's popularity declined; in the 1930s, the annual area burnt over in this manner was only a few hundred hectares a year (Kulotus-

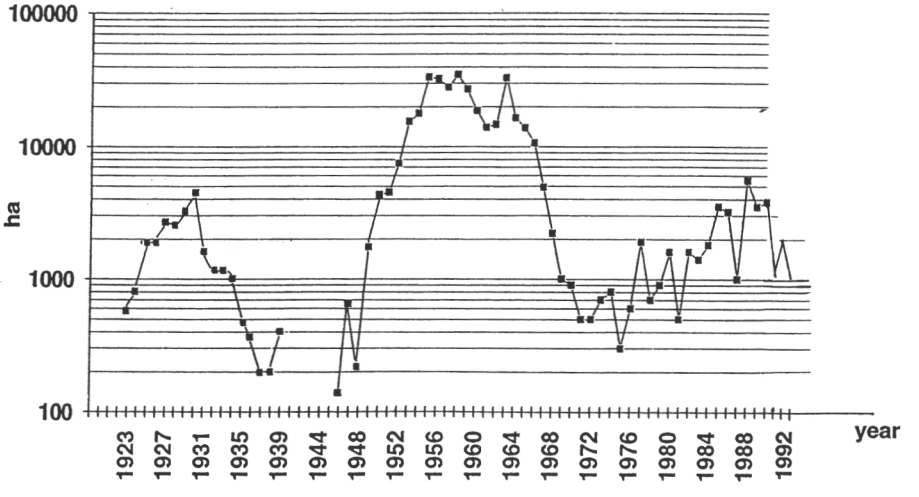


Fig. 3. Annual areas treated with prescribed burning in Finland during the period 1920–1992.

toimikunnan mietintö 1980).

Prescribed burning enjoyed a comeback after World War II and the peak of over 30 000 hectares was reached in the mid-1950s. This method was used especially for the regeneration of northern Finland's spruce stands characterised by thick raw humus layer. However, this prescribed burning's second coming came to an end in the latter half of the 1960s when it was replaced by mechanized site preparation. The annual area of prescribed burning stayed at 500–1000 hectares a year up to the recent past.

The reasons for the decline in prescribed burning are technical. The burning depends on weather conditions and this leads to difficulties in organising the operation. The risk of fire getting out of control, the risk of nutrients being leached from the soil, and the increased risk for fungal or insect epidemics in the dense young pine stands are the most common forest regeneration problems associated with prescribed burning.

Prescribed burning has many advantageous influences on the physical, chemical and biological properties of the soil. These effects depend on site fertility and the intensity of the fire (Mälkönen 1993). Prescribed burning is recommended on moist and dryish mineral soils with sufficient stores of soil water. On more fertile sites, prescribed burning can reduce the availability of phosphorus. The nitrogen released from burning organic matter is lost entirely into the atmosphere and consequently the stores of nitrogen in the forest are reduced. This loss of nitrogen is not, however, fatal for the development of new forest growth, because only a small proportion of the nitrogen stored in forest soils is in a mineralised form. Prescribed may rise by 1–2 units of the pH of the humus layer and stay there for several decades. The rise in pH in the uppermost mineral soil layer has been modest.

Artificially regenerated forests by planting or seeding in Finland currently amount to slightly more than 5 million hectares. Since the total productive forest area is approx. 20 million hectares, artificially regenerated forests represent 25 percent of the whole (Parviainen 1994). Following soil scarification, regeneration sites produce an abundance of naturally arisen conifer and hardwood seedlings, and these develop into mixed woods (Parviainen 1988). Over a period of 80–90 years, prescribed burning has been applied on a total of 0.5 million hectares. This corresponds to 12 percent of Finland's artificially regenerated forests and 2–3 percent of the total forest area.

5 Conclusions

Nearly every forest stand in Finland has been burnt down by wildfires at least once during the past 400–500 years. Slash and burn cultivation (1700–1920) was practised in 50–75 percent of Finland's forests while prescribed burning (1920–1990) has been applied to 2–3 percent of the country's forests.

Since wildfires, a fundamental element of the natural development of boreal forests, have been subdued, forest structure and biological diversity in production forest will change unless fire or its substitutes are implemented as silvicultural measures. The only way to ensure the existence of organisms reliant on charred wood is to increase the use of prescribed burning in forest regeneration (Annila 1993). The long-term maintaining of forest biodiversity, productivity and the nutrient cycle inevitably mean that the natural cycle should be simulated by creating an open stage with a proportion of decaying woody material. This can be simulated through small-scale regeneration cutting areas, untouched small keybiotopes, by favouring broadleaves, and by speeding up the soil's nutrient cycle through light site preparation techniques or prescribed burning (Parviainen and Seppänen 1994).

One element of the variation in the biodiversity of Finnish forests lies in the country's remaining natural forests (approx. 10 percent of the area of forest land). Untouched forests are needed to be set aside as national parks and nature reserves representing different site types and regions. In order that forest environment might be enriched with the various successional stages, conservation areas should be extended to include pristine forests of all ages. In fact, there is a need to burn areas of standing forest here and there, and thus create natural forests in their early stages of development.

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Development and Utilization of Russian Forest Resources

Valentin Strakhov and Anatoly Pisarenko

A presentation based on the historical development of Russia is given in the form of an overview of the development of Russian forest resources, of the wood, non-wood, and biological aspects of the forest ecosystem. The list of non-wood forest resources includes resin, saps, oils, berries, wild nuts, mushrooms, hay harvesting, game animals, etc. The dynamics of the system are presented in the light of the data of the Forest State Account (FSA) of Russia for the period 1956–1993. The most significant changes in the dynamics of Russia's forest resources are related to concentrated, large-scale wood harvesting operations. The dynamics of non-wood resources follow the process of the economic recession in all parts of the forest sector of Russia, the said recession having begun in the mid-1980s. The forests of Russia are considered to be of immense social and cultural value and a globally significant factor contributing to the sustainable development of forest resources.

Keywords Russian forest resources, forest uses, minor forest products, forest dynamics
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1 Introduction

Dynamic changes taking place in Russian forests determine the levels of biological diversity and sustainability of the biosphere in Russia. In many respects such situation is considered to be of vital importance owing to its scale: forest lands make up ca. 69 % of Russia's territory (including inland waterways), 78.5 % of the closed-canopy forests being situated in the Russian Federation's Asian region and 21.5 % in the European and Urals regions (EUPR). The closed-canopy forest lands account, on an average, for 45 % of the forest cover (38 % within the EUPR).

The Forest State Account (FSA) is based on periodic generalization of data obtained through management inventories and in the course of planning work. In the case of forests not under management the corresponding data are obtained in the form of material from aerial evaluation of forests and by interpreting satellite imagery. The

records in the FSA are linked to the administrative units in charge of the forest lands at different levels. On average, the FSA data are updated every five years throughout all the forest management levels. The data of FSAs are available relating to January 1 for the years 1956, 1961, 1966, 1973, 1978, 1983, 1988, and 1993 (Reference book ... 1995).

The accounts' categories used in FSA were established in Russia two hundred years ago for describing the mosaic of plant life, waters, roads, land use, settlement, and so on as the result of economic and natural processes. The study and analysis of dynamics of the forest resources in Russia should be of assistance in the practical implementation of the strategy of sustainable forest management, a strategy that could lead to reduced accumulation of atmospheric emissions of carbon dioxide. The following analytical information concerning the forest resources of Russia may be useful in the endeavour to achieve balanced development of the different regions of Russia. This approach is based on investigations carried out at the ARICFR.

2 A Brief Ecological History of the Russian Forests

Annalists bear witness to vast forests and woods around the settlements of the ancient inhabitants of Russia along the Dnieper river and in the city of Kiev, the ancient capital of Russia (currently the capital of the independent Republic of Ukraine). However, there are no records of these forests following the 11th century: by that time they had disappeared. Reports do exist on the past existence of dense forest cover in the extreme north-east of the European Urals region of Russia (EUPR). By exploiting arable land already established instead felling forests along the rivers, ancient Russians felled trees close to their homes to satisfy their need for wood raw material and when necessary they also cleared land for agricultural purposes. Such a way of making one's home and selecting places for felling trees was retained throughout the following centuries. From 14th to 16th century, there was a special routine for carrying out felling in the forests of the central regions of the EUPR which were of great strategic value (e.g. the Tula abatis) and played a significant role in defending the country against the forays of ancient Turkish tribes, who called these forests "great fortresses".

Since the 17th century factories consuming timber and charcoal have been set up. From the 18th to the end of 19th century, high-quality shipbuilding timber was consumed by the navy and the merchant fleet, while large-sized timber (in second place as regards wood consumption) was mainly demanded by artillery forces. Since the 19th century the railway network developed within the EUPR, and this meant demand for sleepers, firewood, telegraph poles, as well as for structural and carpentry timber.

For a long time, the buildings of settlements, including cities, in Russia was mainly based on wood. Numerous forest products (masts, shipbuilding timber, resin, etc.) were exported to European countries on a large scale. As compared to other regions, the forests of the central regions of the EUPR were cleared to make arable land much earlier. In the 17th century it was observed that there was a relatively auspicious age structure in these forests. However, young-growth stands and clearings turned out to be nearer to waterways and cities, whereas mature forests grew in the more remote areas. The steady population increase between the 18th and 19th centuries made it necessary to clear more arable land, but no reserves of land were available in the EUPR. The intensive wood harvesting which took place in private forests in 19th century was a natural course of events in the endeavour to meet the economic development, at first, with the birth and then with the further development of a capitalist economic system in Russia (Arnold 1884).

The increase in population was accompanied by an increase in area of arable land, hayfields, and pastures, and a decrease in the area of forest (Bobrov 1990). According to annalists and the data compiled by the Ministry of State Property of Russia (the body that produced periodically the economic and statistical atlas of European Russia), the forests covered 44 % to 95 % of the total land area. For a period of 219 years (1696–

1914), there was a steady decrease in the percentage of forest land in European Russia: 52.68 % in 1696, 51.16 % in 1725, 42.27 % in 1861, and, finally, 35.16 % in 1914. However, that percentage decreased unevenly in different regions. The well-forested regions were affected least of all. So, for instance, by 1915 about 91.8 % of the initial forest area was still retained in the northern parts of European Russia (Arkhangelsk, Vologda and Olonetsk Regions), 80.6 % in the Perm Region, and 77.4 % in Novgorod, Pskov and St Petersburg Regions. The most drastic reductions in forest land were observed in the regions of central and forest-steppe zones.

The average rate of forest clearing in the European Russia amounted to 203 000 to 233 000 ha per annum in the 17th century; in the first half of the 19th century the figure was 164 000 ha. Between 1862 and 1888 (i.e. after the abolition of serfdom and up to the adoption of the "Regulations on Forest Conservation") ca. 900 000 ha of forests were cleared every year (Belin 1962). At the end of the 19th century and at the beginning of the 20th century, the rate of forest clearing was somewhat reduced to what it had been earlier. Within a period of 200 years, about 67 million ha of forests had been cleared in European Russia and converted into arable land, household gardens, and to provide land for housing. At the same time, reforestation was carried out on only 1.26 million ha (2 % of original forest area), including 0.7 million ha of forest planting within the bounds of forest districts (as a result of reforestation of harvested sites in forestry), and only 0.6 million ha consisted of afforestation of new sites (Arnold 1884, Bobrov 1990). Hence, strictly speaking, restoration amounted to only 1 %. During the period 1695–1914, the forest area within the EUPR was reduced by one third, i.e. the percentage of forest land decreased from 52.7 % to 35.2 %, mainly as a result of clearing forests for the purpose of expanding arable land. Unrestricted felling of forests took place during the period of the Civil War (1917–1920).

The documented history of developing the Asian part of Russia goes back to the era of Czar Peter the Great and his contemporaries, i.e. to the end of the 17th century, despite the fact that the first settlers from European Russia reached Siberia and the Far East as early as in the 16th century (Bobrov 1990, Pisarenko et al. 1995) . In view of the extremely long distances, the impact of the development of the thinly populated Asian Russia on the region's forest resources gained in importance since the second half of the 19th century. The intensive process of settling and developing the forests of Siberia and the Far East began at that time, and it has been accompanied by the study and detailed description of the forests of the region, including the botanical characteristics of the timber species, the discovering of the northern boundaries of the forests, and the various ways of forest exploitation practised by local people.

By 1925–1928 Russia had regained the level attained in 1893 concerning industrial wood harvesting, manufacturing of sawn goods and plywood (manufacturing of pulp and paper proved to exceed the level achieved in 1893). However, the demand for timber (in particular, as a source of hard currency) increased more and more (History of ... 1960, Koldanov 1992). With this end in view, work was commenced on establishing mechanised wood industry. Between 1926 and 1937, extensive industrialisation of the country took place. Principles of forest management such as sustainability of forest use hindered the turning out of unlimited quantities of wood of varying quality.

By 1975 the scale of forest use and forest conversion reached the mark of 366 million cubic metres of harvested timber. This was a period of economic development when the nation's forest resources were severely damaged, especially those in the north (taiga). The volume of forest use was controlled by "planned needs for timber" (Koldanov 1992). Actual wood harvesting sites were chosen mainly with the aim of procuring timber of high quality closest to major transportation routes, and without concern over issues of ensuring even-paced and sustainable forest use. The felling outturn pattern had nothing to do with the tasks of reasonable forest management, and all forest issues were, as a rule, subordinated to the interests of wood procurement.

3 Dynamics of Russia's Wood Resources

According to the FSA data, there was between 1966 and 1992 a rise in the average annual loss of stocked forest area as regards the main timber species, including conifers. This process took place over the whole of the Soviet Union, both in the EUPR and in the Asian parts (Fig. 1). As regards hardleaved broadleaves, a similar rise took place only within the EUPR. At the same time, there was a tendency towards an increase in the average annual growth of softleaved broadleaves stands (Fig. 2), especially within well-forested regions (such as the Northern and the Urals regions).

The age structure of Russian forests is characterised by a predominance of mature and overmature stands (47 %), including ca. 50 % for conifers, despite the decrease in the area covered by such stands during the period 1988–1993. This was due to felling and reduction in the area of coniferous stands by almost 39 million ha. Simultaneously, there was an increase in the proportion of young increment stand and middle-aged stands. Between 1966 and 1992, the proportion of forest covered by mature and overmature stands was reduced by an average of 0.58 % per annum (including reduction by 3.7 % between 1988 and 1992, corresponding to a decrease of 0.74 % per annum). As regards the EUPR, the corresponding figures were 13.0 % and 0.48 %, and during the period 1988–1992 the figures were 0.6 % and 0.12 %, respectively.

As regards conifers, the proportion of forest area covered by mature and overmature stands was somewhat reduced during the aforementioned period: on the national scale by 17.9 % (on average by 0.66 % per annum) and by 4.8 % between 1988 and 1992 (on average by 0.96 % per annum). As regards the EUPR, the said indices amounted to 17.1 % (on average to 0.63 % per annum) and for the period 1988–1992 by 0.6 % and 0.12 %, respectively). By the year 2000, the age structure of all species groups is expected to be characterised (on the national level) by the predominance of the proportion of stocked forest area covered by mature and overmature stands (45.3 %), including 47.6 % of coniferous

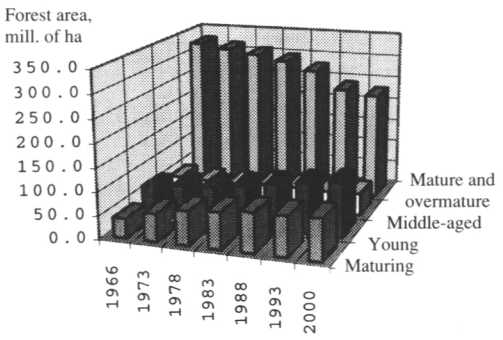


Fig. 1. Russian coniferous forests.

stands. However, the area covered by mature and overmature stands is expected to decrease, on the national level, by 1.7 % between 1993 and 2000, including by 2.3 % for coniferous stands. As regards the EUPR, the said indices are expected to amount to 1.4 % and 2.4 % (for conifers), while in the Asian part of Russia the corresponding values are expected to be 1.8 % and 2.2 % (for conifers). There will take place a subsequent redistribution of the forest area among age groups resulting in a smoothing of the age structure (Strakhov et al. 1995).

In Siberia and the Far East, as well as in the well-forested regions of the EUPR, natural regeneration is of great importance owing to young growth, understorey trees, and second growth being retained when felling timber, and also due to assistance given to subsequent regeneration. For instance, provided the regulations of felling and harvesting technologies are observed, the natural peculiarities of the forests in the Krasnoyarsk Territory provide grounds for expecting successful natural regeneration with commercially valuable species on up to 90 % of the harvested areas within the Angara-Yenisey taiga forest industries region, and on up to 60 % within the southern mountainous taiga forest industries region.

Over the last two FSA periods, a considerable decrease has taken place in the total volume of standing forest in Russia: between 1982 and 1987 there was a fall of 0.78 billion cubic metres, and between 1988 and 1992 the loss was 1.67 billion cubic metres, including 1.15 and 2.48 billion cubic metres of coniferous wood. As regards

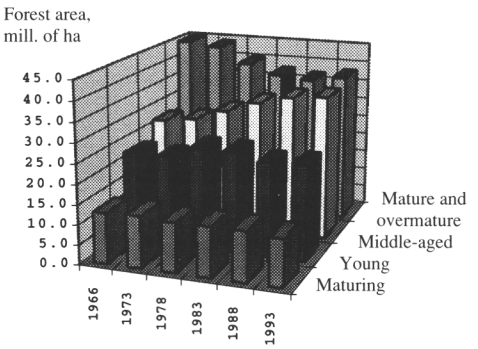


Fig. 2. Russian broadleaved forests.

softleaved broadleaves, the corresponding standing volume increased: by 0.35 billion cubic metres between 1982 and 1987, and by 0.78 billion cubic metres between 1988 and 1992. The decrease in standing volume occurred at the expense of the Asian part of Russia (Tiumen Region, Krasnoyarsk and Khabarovsk Territories, Sakhalin Region, and the Republic of Sakha-Yakutia). As regards the EUPR, it has been observed since 1966 that there is a shift towards an increase in the total standing volume (and in the standing volume of coniferous forests) owing to the increase in the total average increment and the steady smoothing of the age structure in the region. During the past forest account period, the total standing volume in the EUPR increased by 0.53 billion cubic metres, including 0.09 billion cubic metres of coniferous forests (Strakhov et al. 1995).

The gross average increment of the standwise standing stock of the main timber species increased between 1988 and 1992 by 14 billion cubic metres, including 6 billion cubic metres within the EUPR. The average timber volume per hectare of all tree species amounted to 112 cubic metres on the national level according to FSA 5, including 114 cubic metres (permanently) for coniferous species. The average annual increment per hectare of stocked forest land (main timber species) on the national level amounted to 1.29 cubic metres (data for 1.1.1993), including 1.07 cubic metres for coniferous species (1.09 cubic metres in 1988). As regards the EUPR, the aforementioned index amounted to 2.04 cubic metres for the main timber species (2.01 cubic metres in 1988), including 1.60 cubic metres for coniferous species. This index turned out to be considerably lower when compared to the values for average increment in the forests of some other boreal countries. In addition to the concept of increment having a different meaning in Russian statistics, this can be accounted for by unfavourable climatic conditions, the presence of vast permafrost lands and peatland areas in the Russian North, Siberia, and in the Far East (i.e. in the regions containing the major timber resources). This is further supported by existence of large areas covered with stands of site class IV.1 (i.e. below-average site class), the average site class being 4.3 for coniferous species. On the national level, the stocked forest lands characterised by site class V or less for the main timber species amount to 46.3 % of the total stocked area, with only 10.3 % falling into the categories of site classes I or II. Within the EUPR, the average site class is 3.5 for all species, and 3.9 for coniferous species. There the proportion of forests growing on poorer site classes (V–Vb) is especially high, especially in the North Economic Area (59.8 % of the total stocked area and 67.2 % of the area covered by conifers).

According to our estimates, it is most likely that the stocked forest area comprising the main timber species will increase, on the national level, by 5.1 million ha during the period 1993–2000 (mainly because of young increment stands), including 3.7 million ha of coniferous forests and 1.8 million ha of softleaved broadleaves forests. A similar shift is believed to take place within the EUPRR and in the Asian parts of Russia. The proportion of conifers within the stocked forest area comprised of the main timber species over the country as a whole is expected to stabilise; within the EUPR, there is expected to occur a decrease of 0.2 %, whereas softleaved broadleaves are expected to increase their share by 0.1 %).

4 Dynamics of Russia's Non-Wood Resources

According to Russian forest legislation, the following forest uses, in addition to wood harvesting, are permitted: a) gum tapping; b) harvesting of secondary by-products (stumps, bast, rind, birch bark, twigs of fir, spruce and pine); c) concurrent forest exploitation (haymaking, grazing, beekeeping, sap extraction, collecting of wild fruits, mushrooms, berries, nuts, medicinal plants, industrial raw materials, moss, litter, etc.). Natural non-wood, plant-based foodstuffs, together with forest game, are integral parts of forest ecosystem production. They have an essential additional function in satisfying the multiple needs of local people as regards food. Wild fruits, berries, nuts, and mushrooms are foremost among these. Nearly 200 species of fruit trees, shrubs, dwarf shrubs, and climbing plants bearing edible fruits grow in Russian boreal forests. The directive "Instructions for carrying out forest inventory and planning " now in force (Instruction for ... 1995) requires that an account be made of the food resource, medicinal plants, and technical raw material when evaluating forest resources.

Tapping and Resin-Tapping

Mature and overmature stands of pine, spruce, Siberian stone pine and larch are considered to be assigned for final (2nd and 3rd group forests) or regeneration felling (1st group forests) as resources for tapping,. The gum obtained when tapping coniferous trees (mainly pine) is used to make important products such as resin and turpentine. Resin is used in the manufacturing of paper, lacquers, dyestuffs, soap, as well as by chemical, petrochemical, metallurgical, food industries, etc. Before 1917, tapping was conducted on an experimental basis in Russia. It is since the 1920s that it has attained an industrial scale. On the national level, the gum yield per hectare (kg) averaged as follows:

Year:	1973	1974	1975	1976	1977
Gum, kg/ha/year:	71.4	65.9	71.6	72.0	73.6

According to the data provided by the latest forest account (1.1.1993), the total area of pine stands that can annually be exploited for tapping purposes amounts to 1 712 200 ha (with 766 500 ha within the EUPRR and 945 700 ha in the Asian parts of Russia) (Reference book ... 1995). The total area of pine stands exploitable for resin tapping amounts to 413 100 ha (with 243 900 ha within the EUPRR and 169 200 ha in the Asian parts of Russia) (Strakhov et al. 1995).

Production of Tree Saps

Mature stands of birch are the foremost source of tree saps. The diameter of tapped trees must be in excess of 20 cm. Sap yields in suitable stands of birch can be as high as 20–30 t/ha during one season. Tapping is carried out 5–10 years prior to felling. Less than one third of birch stands suitable for sap are actually tapped. The leading source of birch sap in Russia was the Central Economic Region providing more that 40 % of all sap produced, followed by the West Siberian Region (18 %) and the Volzhski Region (16 %). The actual average annual production volume during the period 1970–1978 was 4300 tons, in 1976–1983 it increased to 11 000 tons (in the European-Urals part to 8600 tons). These were more than enough to meet the demand (Strakhov et al. 1995). Now, due to lack of markets, the production of birch sap has almost disappeared, and sap has become a rarity.

Medicinal Material

Over 2000 species of vascular plants with medicinal properties grow in the forests of Russia. Over 600 of them can be used by the pharmaceutical industry. Of the 200 species of used by the medicinal industry in 1987, 150 were purely forest species. Up to 70 % of the medicinal material purchased each year is based on wild forest plants. The resources of medicinal plants are far from having been fully explored, and more or less comprehensive data are available only for some species in some of the regions (Strakhov et al. 1995). As the enumeration and description of all the medicinal species of forest plants are not the

goals of this paper, the main attention is paid to the most common of such species.

Purchasing and processing medicinal raw material are highly profitable for forest management units. In 1986 there were nearly 80 specialised forest reserves in Russia. In many regions, as a result of an unsystematic and non-regulated exploitation, dramatic changes occurred in the proportions of biological and commercial stocks of sea buckthorn, dog rose, *Schisandra chinensis,* ginseng, snowdon rose, sand immortelle, etc.

The past years' average annual purchases of forest commodities by Russian forestry enterprises were as follows: "chaga" 25–27 tons, birch buds 10–12 tons, oak bark 7–9 tons, hawthorn 7.5 tons, buckthorn 4.5 tons, dog rose 2000–2500 tons, *Leuzea carthamoides* ca. 2 tons, Eleutherococcus over 23 tons, *Oplopanax* 3 tons, Saint-John's-wort over 2 tons (dried), Immortelle over 2.5 tons, bearberry ca. 3 tons, sea buckthorn 400–450 tons. The statistics of the Federal Forest Service of Russia report volumes of purchases of medicinal and technical raw material in combination. In all the regions the purchase volumes varied depending on the actual crops.

Honey Collecting

The collecting of honey differs from the collecting of other forest-based foodstuffs. The forest vegetation (several species of trees, shrubs, and herbs) constitutes a real source of honey in Russian. To collect it, one has to establish apiaries in forests and entrust their care to skilled personnel, beekeepers who keep an eye on the state of the beehives and attend to the timely extraction of honey. According to the Forest Account for 1.1.1993, the area of forest stands dominated by lime (when in flower, lime is a very important nectar source) exceeded 3 million ha, and 73 % of such forests (2.2 million ha) were in the European-Urals part of Russia, mainly in the Urals (48.7 %) and Volga-Vyatka (6.7 %) economic regions (Reference book ... 1995). During one season a hectare of a lime forest can yield up to 50 kg of honey. Another 'honey tree' is the locust (60 % of the honey-bearing capacity of lime) and willow (30 %). Many forestry enterprises are familiar with beekeeping; the apiaries maintained by forest management units (*leskhozes*) are only a little smaller than those of collective farms (Strakhov et al. 1995). The honey from Bashkortostan, North Caucasus, and Primorye enjoys the highest demand both on the domestic and foreign markets. The honey yield (as well as harvest of other non-wood forest products) directly depends upon weather conditions, especially when nectar-bearing plants are in blossom.

As honey is supplied not only from forest lands, but also from the fields of collective farms and from other "green belts", we consider it appropriate to take into account only products supplied by forestry enterprises. During the period 1970–1977, the average annual volume of the honey supply was 762.6 tons for Russia as a whole (Strakhov et al. 1995).

Research into the resources of such plants in all regions is an important challenge from the viewpoint of the wise use of forest foodstuffs. The area under wild fruit trees and shrubs (excluding nut trees and chestnut), as accounted on 1.1.1993, amounted to 42 100 ha for Russia as a whole, including 35 700 ha within the EUPR (Reference book ... 1995). In actual fact, the area is much larger: forest accounts often fail to mention areas of berry and fruit plants growing under the forest canopy and cases where they form less than 10 % of the forest stand.

A summary survey of the wild fruit and berry resources of Russian forests was compiled by ARICFR experts on the basis of information provided by the most recent State Forest Account (Reference book ... 1995, Strakhov et al. 1995), reports by inventory and planning enterprises, public literature sources (references), and data obtained by regional forest experimental stations. The computed biological stock was "shared among users". Birds and mammals usually consume 20–70 % of the biological crop (depending on the year's yield and animal population density in the given region). The computations applied 50 % of the biological crop as the average index of consumption by animals in all the economic regions, except for the eastern regions where the corresponding figure was 70 %. The remaining part of the biological stock was deemed to be the commodity resource. Then,

and bearing in mind the coefficient of accessibility (estimated by the experts for each region), computations were made as to the share of the commercial resources in the commodity resources. The commercial resources provide the commercial supply and domestic consumption by local people. The losses during harvest (trampling) amount to nearly 40 %. Thus, only 60–40 % of commodity resources, or 10–30 % of the biological crop can actually be used by local people for household consuming.

Wild fruits and berry resources are the most important. The annual biological crops of the major berry species are as follows: cowberry 3 260 000 tons, bilberry 1 800 000 tons, blueberry 640 000 tons, cranberry 1 100 000 tons. According to calculations, their mean biological yields exceeds 5 million tons throughout the country, and the accessible commercial resources approach 600 000 tons. Currently, less than 30 % of the commercial resources are exploited, but in several regions the figure is over 60 %, and 90 % in the Central regions.

Wild Nuts

Forest tree and shrub species producing nuts are valuable resource components and they add to forest biodiversity.

Pine Nuts

Pine nuts produced by *Pinus sibirica, P. koraiensis, P. pumila*. The forests of *P. sibirica* and *P. koraiensis* are spread over 39.8 million ha, and those of fruiting age cover 27.2 million ha. Besides these, special commercial nut zones have been set aside on forest lands covering 10.9 million ha with these pine stands occupying 6.8 million ha. The total area of *P. pumila* in the mountain regions of East Siberia and the Far East (including Kamchatka, Sakhalin and the Kuril Islands) is 37.6 million ha, with those of fruiting age covering 35.9 million ha. High nut crop seasons occur every four or five years in the case of *P. sibirica* and every three or four years in the case of *P. pumila*. The average yield per hectare depends on stand age, stand density, and the proportion of pine in the stand. Pine nuts are a foodstuff of high value. They contain – on average – 60 % vegetable fats, up to 16 % of proteins, and up to 12 % of carbohydrates. In terms of its oil content, they excel almost all oil plants, including sunflower. The oil produced from pine nuts excels – in terms of its taste qualities – many vegetable oils, and it could be a fairly good export product of high value. The value of pine nuts gathered during one felling period exceeds the value of timber that could be taken from the same hectare of forest land.

Hazel

Hazel occurs on large areas in the forests of Russia, mainly as undergrowth. Only according to forest account as for January 1, 1993, the area of fruiting hazel stands is 10 200 ha, calculated area of hazel under forest canopy adds nearly 1.8 million ha (Reference book ... 1995). The core of hazel nut contains up to 22 % of proteins, 77 % of fats, 13 % of sugar and many vitamins. It is also rich in cobalt that stimulate producing blood corpuscles and hemoglobin. Now hazel resources are being depleted, its thickets are not managed. Therefore it yields little (20–30 kg) ha in stands under forest canopy).

European Walnut

European walnut *(Juglans regia):* occurs as natural stands mainly in the North Caucasus region. The European walnut is a valuable foodstuff, contains up to 65 % of fats, up to 17 % of proteins, up to 16 % of carbohydrates, and many vitamins. The oil produced from it is equal to olive oil. Walnut oil cake is a very nutritive feed. According to the last forest account, the area of European walnut stands amounts to 9600 ha, and those of fruiting age cover 4900 ha. Average yields vary from 120 to 300 kg/ha. When applying an average yield of 200 kg/ha, its average biological resources (bearing in mind that the stands are mixed) are estimated to be amount to 720 tons per annum, and the commercial resources are estimated to be 320 tons.

Manchurian Walnut

Manchurian walnut *(Juglans mandschurica):* occurs only in the Territories of Primorye and Khabarovsk. It covers 6600 ha (of fruiting age, beginning at age of 6–7 years). It grows mainly as an admixture with other species that make up 50–60 % of the stand composition. Therefore, the productive area is actually half of the above, i.e. 3300 ha. Taking into account its yield per hectare and its age, the crops of Manchurian walnut are estimated to average at 500 kg/ha. It fruits every year, but abundant crops occur every second or third year. Thus, its biological crop averages 1650 tons per year, and the commercially accessible resource is estimated to be 800 tons per year. The Manchurian walnut's nuts are mainly gathered by local people for household consumption, and commercial purchases are minor.

European Chestnut

European chestnut occurs predominantly in the forests of the southern regions of Russia. Its fruits are used fresh, fried, roasted, and boiled, and they are in great demand for confectionery purposes. Pure stands are rare, usually up to 30 % of stands containing chestnut are of oak, beech, hornbeam, and other species. Chestnut stands yield well and regularly from age 10–15 years onwards. Their total area in Russia is 48 900 ha and their productive area is 34 300 ha. The average yield capacity of chestnut is 200–250 kg/ha, while the total biological crop may amount to 4300 tons. These resources are exploited to the degree of 25–30 %, including no more than 10 % by commercial organisations.

Edible Mushrooms

Mushroom collecting is the most profitable and lasting of all the forest uses. *Pileus* (cap) mushrooms occur throughout Russia, from the very limit of vegetation in Arctic Ocean's islands to the steppe zone, and in all the forest types. They are at their most abundant in boreal forests, in the middle and southern taiga zones. Only 5–7 % of all known mushroom species are well-known and eaten. The yield capacity of the major species of edible mushrooms – per unit area – in different types of forest lands and different habitats rises to close to 70 kg per annum, including worm-infested mushrooms. Damage by insect larvae can amount to ca. 30 % depending on weather conditions and the mushroom crop. For purposes of computing the biological resources, the figure of 50 kg/ha is taken as being the average yield. This results in the figure of 4.1 million tons per year as the biological mushroom resource of the country as a whole. The figure includes 656 900 tons for the European-Urals part and 340 660 tons for the Asian part (Strakhov et al. 1995). The corresponding commercially accessible resource figures are 439 800, 171 500, and 268 300 tons.

Forest-based foodstuffs have always enjoyed great demand among Russians. Russia has exported them since long ago. According to sectorial statistics, the average annual exports of forest wild products in 1965–1976 were as follows: cranberry 1345 tons, cowberry 430 tons, dried bilberry 89 tons, wild nuts 1759 tons, honey 4574 tons, mushrooms 587 tons, plus the value of medicinal plants and vegetable raw materials for technical uses.

Cattle Grazing and Haymaking in Forests

Forest hayfields and meadows provide pastures for cattle (more than 30 % of the hayfields) and for domesticated reindeer (more than 50 % of the pastures). At present, the area of hayfields is ca. 2 million ha, and 52.4 % (1.04 million ha) of these hayfields lies within the EUPR. The average annual yield of hayfields in Russia is about 750 kg/ha. According to the FSA data for 1993, forest pastures occupy 17.5 million ha. Since 1956 the area of hayfields has diminished from 8 million ha down to 2.3 million ha (i.e. by 71.4 %), mainly at the expense of the Asian parts of Russia (where the corresponding area diminished by more than 75 %). Contrary to this, the area of pastures increased between 1956 and 1993 by 15 million ha, mainly at the expense of reindeer pastures. Only 2.3 % of the pastures are situated within the EUPR, the rest are in the Asian part,

chiefly in the Kamchatka Region (52.3 %), Yakutia (28.9 %), the Krasnoyarsk Territory (4.4 %), the Tyumen Region within its old borders (4.3 %), and Tuva (3.1 %). Thus, these five regions contribute 93 % of the national pasture area. Grazing is carried out both on dedicated meadows and in some open forests and grassy glades. Despite the distribution of the area of hayfields being more or less equal over the EUPR and the Asian parts of Russia, about 75 % of the total volume of harvested hay is carried out by the FMUs of the EUPR and this is explained by the region's higher population density and better accessibility of forest areas.

5 Hunting and Sporting Facilities Provided by Forests

Russian boreal forests are the chief habitats of the most valuable species of game animals. The boreal forests are home to the majority of professional hunters and trappers. Official statistics of Russia report that the total area of game habitats in the country in 1993 year was 1286 million ha, including 1076.7 million ha allocated to actual users. Of all the game habitats, those in the forests make 48.2 % (619.8 million ha). The share of the Federal Forest Service of Russia hardly exceeds 2 % (13.57 million ha, including 12.82 million ha specially allocated to users). More than 16 % of habitats are not allocated to actual users. This means that game management there lacks rules. In the Asian parts of Russia such lands amount to almost 20 %. The sound commercial development of such lands could improve the use and restocking of game resources.

One important issue needs a special mention. In many eastern regions of Russia, the forest stands are formed mainly of larch on sites of low site index and with a lot (30–40 %) of decaying trees. In these forests the value of secondary, non-wood products, including food and game, are much higher than that of felled timber. Therefore, it would be inappropriate, both economically and ecologically, if not to say detrimental, to allocate such forests for any kind of final felling.

If one compares the current numbers of some game species with the data for the period 1971–1978, one notes an increase in the populations of marten, hare, roe deer and wild boar. On the other hand, muskrat numbers have dropped by more than half. Such data should be taken into account when drawing up plans for game harvesting.

6 Conclusions

According to the data available to us, climatic conditions comparatively favourable for forest growth are to be found on 59 % of Russia's mineral soil lands (70 % within the EUPR). According to our estimates, 78 % of Russian territory may be referred to as being boreal forest land and more 87 % of Russia's stocked forest land is concentrated on this area.

During the period 1995–2005, the positive trends in Russian forest resources dynamics are expected to lead to increases in the area of coniferous young increment stands belonging to the 1st age class, as opposed to the trend of reduction of that area as outlined after 1983. As regards individual regions, such as the Karelian Republic, the North-West and Central Areas (including Kostroma and Yaroslavl Regions), the Kirov Region, the area of coniferous young increment stands belonging the 1st age class is expected to decrease. This trend is a result of the drain of accessible forest plantings, reductions in the area of wood harvesting, and the predomination of areas belonging to the 2nd age class as opposed to the sharp fall in reforestation (this especially applies to the fall in forest planting areas).

About 70 % of the total area covered by coniferous young increment stands belonging to the 1st age class lies in Siberia and the Far East.

It is expected that by the year 2000 the area covered by young increment stands will be transferred to the category of valuable stands and should exceed the clear-cut area provided that the projected silvicultural works are carried out completely. In addition, a considerable proportion of non-stocked forest lands (mainly in Sibe-

ria and the Far East) is situated in regions difficult to access in terms of timber growing, and such areas are actually used only as pastures. Some of the lands on which forests can not be grown should, in fact, be classified as being non-forestry lands, i.e. steep mountain slopes, peatlands with occasional pine, birch and other trees, etc.

It is necessary to ensure further acceleration of forest use by involving soft-leaved stands in the commercial turnover, especially in some of the EUPR regions. As regards hard-leaved tree species, the most probable development would be a slight (0.1 %) decrease in the proportion of the main timber species within the stocked forest area of the Asian part of Russia. Within the EUPR, a corresponding rise is expected.

By the year 2000, the average annual increase (no longer a loss!) of the stocked forest area of the main timber species (including conifers) is expected to amount to 0.14 % (over the whole country, as well as in the EUPR and in the Asian Russia) and respectively 0.73, 0.21 and 0.52 million ha (Strakhov et al. 1995).

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Tasks of Forest Biodiversity Management and Monitoring Deriving from International Agreements

Jari Parviainen

1 Ongoing Processes

Since the Rio 1992 Earth Summit governments, environmental groups, the business community and consumers have agreed, that there is a need to develop a common understanding of the definition and characteristics of sustainable forest management. Four governmental efforts are underway to reach consensus on indicators of sustainable forestry (Harmonization of... 1995.

Through the Helsinki process, European countries have developed and reached a pan-European, binding consensus (Geneva, June 24, 1994 and Antalaya Statement, January 28, 1995) on criteria and indicators. This effort has been designed to identify the important characteristics of sustainable forest management and through these criteria and indicators, provide the ability to measure progress towards that goal. Through assessments of progress, European countries inted to be able to demonstrate that on national level specific countries are sustainable managing their forestlands. The first interim report on the progress has been produced at the end of April 1995 coordinated by Liaison Unit in Helsinki (Interim Report... 1995).

The Montreal process is a parallel effort to Helsinki-process including non-European Temperate and boreal forest countries; Canada, The United States, Russia, Japan, Chile, China, Korea, New Zealand and Australia. In February 1995 an agreement was reached on a number of international level criteria and indicators (Sustaining the World's... 1995, Santiago-Agreement). Their purpose is to provide a method to describe and develop a broader list of criteria and indicators in a national process than those agreed to at the international level.

The International Tropical Timber Organization (ITTO) adapted the year 2000 as its target date for sustainable management of all topical forests. The ITTO have developed guidelines for the sustainable management of natural tropical forests as early as 1990, planted tropical forests, conservation of biodiversity in tropical production forests and tropical forest management, but they are not identical to either the Helsinki or Montreal Process lists.

In the Spring 1995 the countries around the Amazon basis have developed a joint initiative for creating guidelines of sustainable forest management of the Amazonian tropical rain forests (Tradtado de Cooperacion Amazonica, Tarapota, Peru 1995).

It is estimated that as many as 15–20 distinct processes are under way in the private sectors by nonprofit organizations and forprofit companies, some domestic and others international in scope. Through some of them, the goal is to create a certificate for "good" silviculture, an 'eco-label' or equivalent, on the basis of which consumers will be able to sense the presence of an environmentally sound forestry practice.

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Perhaps the most wide-ranging definition work of non-governmental organizations is the undertake by the Forest Stewardship Council, FSC, set up by the WWF (the World Wide Fund for Nature International). The parameters of sustainability adopted by FSC are in agreement with those brought forward in connection with the follow-up work of the European Ministerial Conference. Differences arise from the difference in emphasis given to certain aspects. Conservation bodies attach primary importance to evaluation of the sustainability of forest management from the perspective of conservation and ecology.

2 Criteria and Indicators

The term used in this connection is 'criteria of sustainability' which depict the various dimensions that sustainability has. The purpose is to use indicators in measuring changes in the criteria of sustainability; e.g. in relation to time. In actual fact, the indicators are instruments, parameters compiled from statistics of from data obtained by conducting various measurements in the forest. The information provided by indicators is then evaluated in connection with societal or international debates, and they form the basis for the setting of policies to implement sustainability.

In addition to quantitative indicators, there is a need for descriptive parameters with which to assess the realization of the measures taken (e.g. in legislation). Development work in this area has begun. The need for clarification is particularly needed with respect to the socio-economic aspects of sustainability.

Six criteria have become the characteristic features of sustainability in European forestry (Ministerial Conference... 1994):

- forest resources and the carbon cycle
- the health and vitality of forests
- multiple production functions of the forests
- the biological diversity of forest ecosystems
- maintenance of the protective functions of forests (soil and water system)
- maintenance of socio-economic functions

Each criteria consists of a number of indicators (in the group 'forest resources', for instance, trends in the development of the forested area and the centrally important characteristic stand features of the forest) and their development is monitored in relation to time. In all, at European level there are at the moment 27 agreed indicators. Taken together, the set of criteria and indicators suggests an implicit definition of the conservation and sustainable management of forest ecosystems at the county level. It is recognized that no single criterion or indicator is alone on indication of sustainability.

3 Forest Biodiversity in the Helsinki and Montreal Processes

The greatest number of indicators are been discussed during the Helsinki and Montreal processes in the criteria forest biodiversity. For the present, consensus has been reached only with regard to the factors of most central importance. In the matter of ensuring the preservation of forest biodiversity in production forests, the proportion of mixed woods and genetic biodiversity are the only factors agreed upon. Discussion have been held in issues such as fragmentation of forests, how to define naturalness, age distribution, the proportion of decaying wood in forests, and the methods to be applied in forest regeneration and timber harvesting. A uniform indicator platform, applicable in different forest vegetation zones, is still lacking.

The criteria 4 "Maintenance, conservation and appropriate enhancement of biological diversity in forest ecosystems" of the Helsinki-process contains the following indicators with separate definitions:

4.1 Changes in the area of:
   a. natural and ancient seminatural forest types
   b. strictly protected forest reserves
   c. forests protected by special management regime

4.2 Changes in the number and percentage of threatened species in relation to total number of forest

species (using reference lists e.g. IUCN, Council of Europe or the EU Habitat Directive)

4.3 Changes in the proportions of stands managed for the conservation and utilisation of forest genetic resources (gene reserve forests, seed collection stands, etc.); differentiation between indigenous and introduced species

4.4 Changes in the proportions of mixed stands of 2–3 tree species

4.5 In relation to total area regenerated, proportions of annual area of natural regeneration

For comparison, the Montreal-process biodiversity is defined by indicators as follows:

Criterion 1:
Conservation of biological diversity. Biological diversity includes the elements of the diversity of ecosystems, the diversity between species, and genetic diversity in species.

Indicators:

Ecosystem diversity

a. Extent of area by forest type relative to total forest area (a)1
b. Extent of area by forest type and by age class or successional stage (b)
c. Extent of area by forest type in protected area categories as defined by IUCN2 or other classification systems (a)
d. Extent of areas by forest type in protected areas defined by age class or successional stage (b)
e. Fragmentation of forest types (b)

Species diversity

a. The number of forest-dependent species (b)
b. The status (rare, threatened, endangered, or extinct) of forest-dependent species at risk of not maintaining viable breeding populations, as determined by legislation or scientific assessment (a)

Genetic diversity

a. Number of forest-dependent species that occupy a small portion of their former range (b)
b. Population levels of representative species from diverse habitats monitored across their range (b)

1 Indicators followed by an "a" are those for which most data are available. Indicators followed by a "b" are those which may require the gathering of new or additional data and/or a new program of systematic sampling or basic research. No priority is implied in the "a" and "b" designations.

2 IUCN categories include: (I) Strict protection. (II) Ecosystem conservation and tourism, (III) Conservation of natural features, (IV) Conservation through active management, (V) Landscape/Seascape conservation and recreation, (VI) Sustainable use of natural ecosystems.

4 The Task for Research

The criteria used should be such that they produce objective information for the sustainability. An example of a criterium that works in practice is the assessment of forest health. The measurement methods used are the result of many years of research, discussion and co-operation at international level. The same techniques are applied throughout Europe. Annual assessment provide the basis for indicating general trends in forest health. Weakening in forest health condition is a sign to political decision makers to introduce emission restrictions, for instance. There is need to develop parallel system for monitoring forest biodiversity on a practical scale.

The public discussion demands for wood production oriented forest management to be replaced by a more balanced management of forest environment and the realisation of biodiversity (Oldeman et al. 1994). These goals are being approached through total protection of the foremost regionally representative natural forests and by managing production forests with more nature-oriented principles (Parviainen and Seppänen 1994).

In order that silviculture might be practised on a sufficiently high level of diversity throughout the forest ecosystems, we must learn about the development processes in undisturbed forests. The clarification of these processes require specific research on structure, succession, biodiversity and long term monitoring of natural forest ecosystems (Leibundgut 19978, Schmidt-Vogt 1991a and 1991b, Remmert 1992). Protected for-

est areas or forest reserves are the main, still remaining samples of undisturbed forests, and are therefore the basic experimental forests for research on biodiversity (Schuck et al. 1994).

Due to modern silvicultural practices many important regimes in temperate and boreal forests have disappeared or have become a rare sight (Angelstam and Rosenberg 1993, Kouki 1994): – Burnt areas with large amounts of dead wood – Dying trees, snags and down logs – Deciduous components in forests – Natural development processes: Human intervention in the natural dynamics and development of forests in spatial and temporal respects – Size: Fragmentation of existing natural and semi-natural forests in total.

Trees and stand structure are in close interaction with all other parts of the forest ecosystem e.g. soil, flora and fauna. Therefore studies on stand structure and dynamic development processes on a stand level play a key role in the description of biodiversity indicators in different forest vegetation types. Parameters of structure, giving valuable information on dynamics and development processes, are easy to measure. A large number of permanent sampling plots already exist for long periods of time in many European countries providing useful data (Schuck et al. 1994).

When measuring sustainability, attention is paid to the difference in the development of production forests as compared to that of natural forests. A central point is that of recognising the regular functional features peculiar to individual forest zones; e.g. the clear developmental difference between boreal forests and temperate forests. In the case of Finland, for example, the way in which silvicultural measures are applied is steered by historical cultural developments of forest use (slash-and-burn cultivation, diameter-based selection felling) and, from the viewpoint of natural forests, by forest fires and other natural catastrophes (Parviainen 1993, 1994, Parviainen and Seppänen 1994).

Following key topics for research needs (as practical approach) on biodiversity can be distinguished:

Biodiversity management (stand level):
— key stand indicators (parameters) for biodiversity
— differences in biodiversity indicators between undisturbed and managed forests
— influence of disturbances (fire, storm, insect attacts, avalanches) on biodiversity indicators
— influence of stand structure and successional phases on biodiversity indicators
— guidelines of forest operations for taking into account the maintenance of biodiversity by regeneration and thinnings

Monitoring of biodiversity (landscape level):
— integrating the biodiversity characteristics with the national forest inventories
— representativeness of forest protection areas (aerial distribution, site classes, age structure, geographical location)
— the influence of forest biodiversity oriented management of production forests to the need of protection areas
— the degree of naturalness of forests

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Conservation in Boreal Forests under Conditions of Climate Change

Nigel Dudley, Jean-Paul Jeanrenaud and Adam Markham

1 Introduction

Addressing the potential impact of climate change on boreal forest ecosystems will require a range of new conservation techniques. This offers opportunities for WWF (the World Wide Fund for Nature) to combine a number of its specialised field and policy activities into an integrated strategy.

During the early 1990s, the scope of WWF's forest policy work has broadened from a focus on tropical moist forests to a more general consideration of all the world's forests (Dudley 1992). Several major new projects, in Scandinavia, Alaska and more recently in Russia, mean that the organisation has given boreal forest issues a much higher priority than has been the case in the past. More recently, WWF's Forest Advisory Group agreed a Global Forest Strategy and several National Organisations have drawn up and published complementary forest strategies for their own countries. At the same time, WWF has been active in conservation planning aimed at reducing the impact of climate change on biodiversity (Peters and Lovejoy 1992) and in funding research into global warming and the impacts on biodiversity. Confronting the problems raised by climate change within boreal forests also allows WWF to combine policy work with a range of new and existing field programmes. The existence of WWF national organisations or project offices in most of the countries possessing boreal forests ensures that policies and programmes can be directly related to regional conditions.

Climate change is only one of a series of threats currently facing boreal forests. Four key impacts can be identified:

- forest management and particularly timber extraction
- other industrial sectors, including mineral mining
- tropospheric pollution from wet acid deposition, gases and particulates
- stratospheric changes, including ozone depletion and global warming.

Any management systems designed to reduce the impacts of climate change therefore have to be integrated with other conservation strategies and with broader management priorities.

The following paper looks at some of the conservation issues raised by climate change in boreal ecosystems, and at some preliminary conservation strategies for reducing harmful impacts on biodiversity. A concluding section discusses potential conflicts between management for climate change and other conservation priorities.

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2 Climate Change and Conservation

Climate change poses a number of problems for conservation organisations, from the perspective of both strategy and allocation of resources. While

the evidence for the existence of climate change continues to grow, ecological impacts are still uncertain and unpredictable. There is not much to suggest that this will change in the short term. Planning conservation strategies that take account of global warming is not easy when there are many computer models of climate change, sometimes predicting very different ecological effects. Whilst conservation organisations can learn a great deal from climate models, in practice staff often have to take an educated guess at what might happen in the future from the best available evidence, and stay flexible enough to modify plans as better information becomes available.

Prediction of global warming also adds significant new pressures to organisations and institutions that are often already stretched to their limits dealing with current environmental problems. The fact that the threats from climate change remain imperfectly quantified, and are at least to some extent still in the future, can make it difficult to argue for the diversion of time and funds from other projects that are considered to be more pressing. Yet failure to include climate change impacts in current conservation planning might lead to decisions being made that will soon be out of date. There has been a lively debate about how much time and resources should be devoted to climate change work.

In addition, climate change generates some philosophical problems for many non governmental organisations (NGOs). On the whole, conservation groups have argued that environmental problems should be tackled at source rather than by attempting to reduce impacts. For example, in the acid rain debate, NGOs have been virtually unanimous in proposing cuts to sulphur and nitrogen oxide emissions rather than supporting liming programmes on freshwaters and soils. Conservation planning for climate change implies a tacit admission that pollution from greenhouse gases, mainly from the rich countries, will remain at high enough levels to continue affecting the climate. Many organisations feel more at ease with campaigning for a reduction in pollution emissions than with assuming that impacts will occur and making plans accordingly.

3 Climate Change in the Boreal Forest

Climate change could result in some particularly extreme problems for the boreal forest biome. However, conservation biologists also have opportunities in boreal regions that are denied to them in many other parts of the world. If decisive action is taken now, there is a good chance of developing policies that could, in time, avoid many of the worst impacts of climate change in this region. This could also help us to gain knowledge that would have relevance in other ecosystems as well. A summary of the problems and opportunities in boreal forests is presented below, and expanded in the following section:

Boreal forests – problems:
- acute changes are predicted
- a lack of expertise exists in international conservation organisations
- political problems in some areas.

Boreal forests – opportunities:
- conservation issues are relatively simple
- biodiversity in the region is relatively limited in terms of number of species
- boreal forests are in relatively good condition
- forest management strategies in boreal regions are currently in a state of flux.

Most models of climate change predict relatively acute changes in the boreal region. Increases are expected in mean annual temperature, and in the frequency and severity of both storms and fires (Shugart et al. 1992). Some researchers suggest that 40 per cent of boreal forests could disappear and be replaced by temperate forests and/or tundra (Solomon 1993), although there are wide variations in predictions from different models. Many tree species will be unable to disperse fast enough to keep pace with changing conditions (Davies 1989) and are therefore likely to undergo a net decline.

In practice, if the predicted changes come about they will not in the short term mean that the biome will undergo abrupt changes in vegetation patterns, but rather that an increasing proportion of the boreal forest will be growing in sub-optimal conditions, and therefore under extra stress.

Changes in storm damage and fire frequency would have an important impact on ecology, and warmer conditions are also likely to allow the spread of additional pest species. The challenge for conservation biologists will be to design management systems and protected area strategies that give the boreal forest ecosystem as much resilience as possible to survive and adapt to changing conditions.

Working in boreal forests also creates a range of institutional problems for conservation organisations such as WWF. During the 1980s, international attention was focused on issues related to the loss of tropical forests to the extent that status of and threats to temperate and boreal forests were, until recently, comparatively ignored. Until the mid 1990s, WWF had no staff working specifically on boreal forest issues, even within those countries in North America and Scandinavia where there were active WWF National Organisations. Whilst this situation has now changed, expertise in boreal regions continues to lag behind that in other biomes. Lack of institutional expertise adds further blocks to progress in this area and lack of political will in some countries has allowed conservation problems to develop relatively unchallenged.

However, the boreal forest zone also has some advantages when compared with other regions. These could combine to make the region an ideal testing ground for theories of conservation biology and climate change.

Conservation issues within the boreal region are relatively simple compared with other parts of the world. The official bodies charged with management and regulation of the forest estate are well trained and equipped when compared to those in most tropical countries. Land tenure disputes, while still important particularly in parts of Canada and Russia, are less acute than in almost any sizeable tropical rainforest region. Infrastructure and the facilities for the training of foresters and conservation biologists are already well developed in most countries of the region, and many boreal countries have substantial research programmes looking at both sustainable forest management and at the impacts of climate change on the region. On a global scale, it should be noted that this stability relies heavily on what happens in the former USSR. Future political and economic developments in the Russian Federation, which holds the largest proportion of remaining boreal forest, could reduce the comparative advantages listed above.

Biodiversity is also simple compared with the tropics and even with most temperate forests. Boreal forests are dominated by a few genera of trees and speciation is similarly limited amongst most groups of lower plants and animals, although the extent of within-species genetic variation in the biome is still relatively unknown. Boreal forest conservation strategies therefore have the advantage of being developed to protect a relatively small number of species. Boreal forests are also, on a global scale, in better condition than either tropical or temperate forests, and large tracts of semi-natural or old-growth forest remain in Russia, Canada and Alaska.

In addition, forest management and conservation policies are currently being rewritten in several boreal countries, with new laws recently introduced into Sweden and Finland, new policies being developed in the Russian Federation, and legal and management changes initiated at a provincial level in Canada. Attitudes towards forest management, and particular towards the importance of biodiversity, the role of fire in the landscape and the importance on non-wood forest products, has changed enormously in the last few years. The forest industries throughout the region have become used to a measure of change and development; it may therefore be an apt time to introduce policies aimed specifically at addressing threats from climate change.

4 A Strategy for Conservation in Boreal Forests under Conditions of Climate Change

Over the last three years, WWF has been drawing up strategies for conservation on a global, regional and national level. The *Global Forest Strategy*, which included input from 27 national organisations and 13 programme offices, draws up a detailed framework for addressing environmental and social problems in forests, within the context of five key objectives:

- Establishment of an ecologically representative network of protected areas covering at least 10 per cent of the world's forest area by the year 2000, demonstrating a range of socially and environmentally appropriate models;
- Environmentally appropriate, socially beneficial and economically viable forest management outside protected areas, to achieve sustainable management, including no net deforestation, by the year 2000;
- Development and implementation of ecologically and socially appropriate forest restoration programmes;
- Reduction of forest damage from global change, including a decrease of pollution below damage thresholds, as measured by critical loads;
- Use of forest goods and services at levels that do not damage the environment, to attain a level of use of forest goods and services within the regenerative capacity of the forest estate.

Within the context of forest management and protection in the boreal region, the first and second objectives are the most important. The existence of large tracts of biologically-rich old-growth forest means that WWF's target of setting aside 10 per cent of forest in reserves is more achievable within the boreal zone than in other areas. Canada is already committed to setting aside 12 per cent of its territory into ecologically-representative protected areas.

However, climate change creates additional problems for reserve management, and should therefore influence decisions about the selection of reserves. Shifting geographical and climatic zones may mean that areas that were ecologically valuable when a reserve was created become less suitable over time. Extreme weather events could further weaken protected ecosystems. Damage from climate change does not respect the boundaries of protected areas. The ability of atmospheric pollution to damage reserve areas has already been demonstrated (Fry and Cooke 1984). Similar deterioration is likely to affect boreal regions in the future as a consequence of climate change.

Whilst there can be no way of avoiding all such impacts, WWF has drawn up a preliminary set of criteria for maximising the chances of selecting protected areas that will be robust enough to preserve biodiversity during times of rapidly changing weather patterns (based on Markham et al. 1993).

Reserves should:

- be as large as possible, to give space for plants and animals to migrate within the protected area if climatic conditions change;
- have more than one protected area per habitat type, ideally at some distance apart, so as to maximise the chances that at least one area will remain in conditions suitable for its continued survival;
- have altitudinal and latitudinal variation, to maximise the potential for migration if climate changes;
- have topographic variation, including valleys and areas where microclimate is likely to remain fairly stable;
- place zones of transition between one habitat type and another within the core of reserve rather than at the edge, so that once again there is space for expansion or contraction of habitat types within the protected area;
- ideally be close to other reserves or to similar habitat outside reserves to allow migration if necessary;
- include buffer zones where management is carried out sensitively enough to protected the main core of the reserve;
- have flexible zoning of reserve boundaries if possible, such that the reserve can, through negotiation, be relocated in the future if changing conditions make this necessary.

In addition, two other factors are important:

- consideration should be given to the development of corridors of natural or semi-natural habitat between reserves to aid migration (although further study is required as to the role that these might also play in spreading pests, diseases and alien species);
- existing stresses, including air pollution, fire mismanagement and invasion by alien species, should be minimised to give the ecosystem as great a chance as possible of coping with a changing climate.

5 Discussion

WWF has concluded (Peters and Lovejoy, 1992 and Markham et al. 1993) that conservation strategies aimed at combatting climate change need not be in direct conflict with other conservation planning requirements. Two effects were possible: climate change might provide additional arguments for implementing some existing conservation strategies; and in other cases might suggest the need for additional, complementary, procedures. The ten procedures outlined above fall into this category. More recently, proposals have emerged for ways to address the impacts of climate change that would certainly have detrimental impacts on existing conservation plans. These include:

- removal of dead timber and dying trees to reduce methane emissions from decaying vegetable matter
- disturbance of forests to introduce extra dynamism into ecosystems and thus help them adapt to a changing climate
- select useful species and genotypes
- enhance available nutrients
- control stand density
- change rotations.

Most of these proposals are, in effect, arguing for a continuation, or introduction, of intensive forestry practices. At a time when these are being questioned in several boreal countries, for both social and ecological reasons, it appears that in this case climate change is being used as a justification for forest practices that fly in the face of widely accepted conservation priorities.

WWF has always been cautious in both its predictions about global warming and its approach to management for climate change. Short-term measures that risk immediate environmental damage in the cause of addressing a possible future threat are therefore in opposition to its approach. At the same time, enough evidence has emerged about the likelihood that global warming is already underway to justify taking action to alleviate some of the ecological effects. WWF therefore proposes that, in the short term, management steps taken to address climate change in the boreal region should be confined to those which have an additional conservation effect, or at least are not in opposition to existing conservation priorities. This win-win climate scenario minimises the risks of causing secondary ecological damage in attempting to address problems of global warming.

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Climate Change, Biodiversity and Boreal Forest Ecosystems

Peer-reviewed papers selected from the International Boreal Forest Research Association Conference held in Joensuu, Finland, 30 July–5 August, 1995

Edited by E. Korpilahti, S. Kellomäki and T. Karjalainen

The predicted increase of temperature and CO_2 in the atmosphere associated with the climate change will create major changes in ecological communities and the distribution of species in the boreal zone. The area of boreal forests will most probably decrease, tree species compositions will change and the boreal zone will move 500–1000 kilometers further north. The boreal zone has experienced climate change in the past when the ice sheets retreated before the present inter-glacial period. A drastic difference between the climatic warming at the beginning of the present inter-glacial and the predicted climate change is the rate of temperature increase. It is of utmost importance to increase scientific knowledge about how ecosystems may respond to environmental changes. An understanding of these responses should be achieved at all hierarchical levels of ecosystems over long enough periods of time.

This book contains nearly thirty articles from a global group of experts providing scientific, economic, and policy perspectives on **Climate Change, Biodiversity and Boreal Forest Ecosystems**. These articles will serve to complement the scientific basis for the sustainable management of boreal forest resources and provide new perspectives for the development of constructive policies to improve management strategies for preserving the vitality of boreal forests and their potential as a source of economic and social well-being.

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