Overwintering and Productivity of Scots Pine in a Changing Climate

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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 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).

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

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 growing 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).

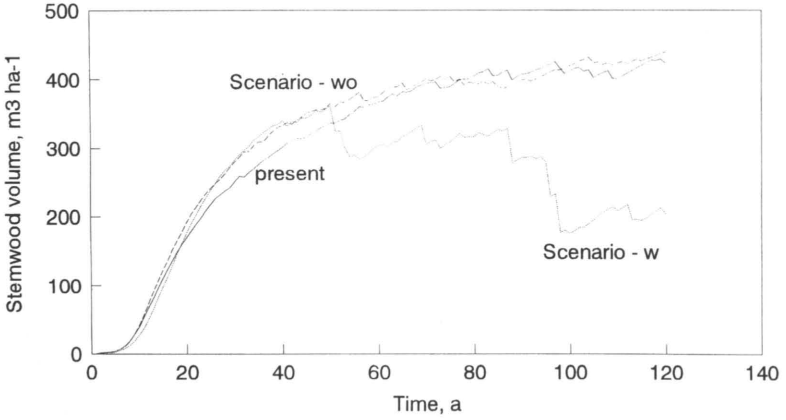

Fig. 1. Simulated development of stemwood volume in a Scots pine stand in southern Finland, in the present climate and in a scenario climate assuming an increase of 4.1 °C in the annual mean temperature during the first 50 years. Simulations for scenario climate with (Scenario-w) and without (Scenario-wo)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

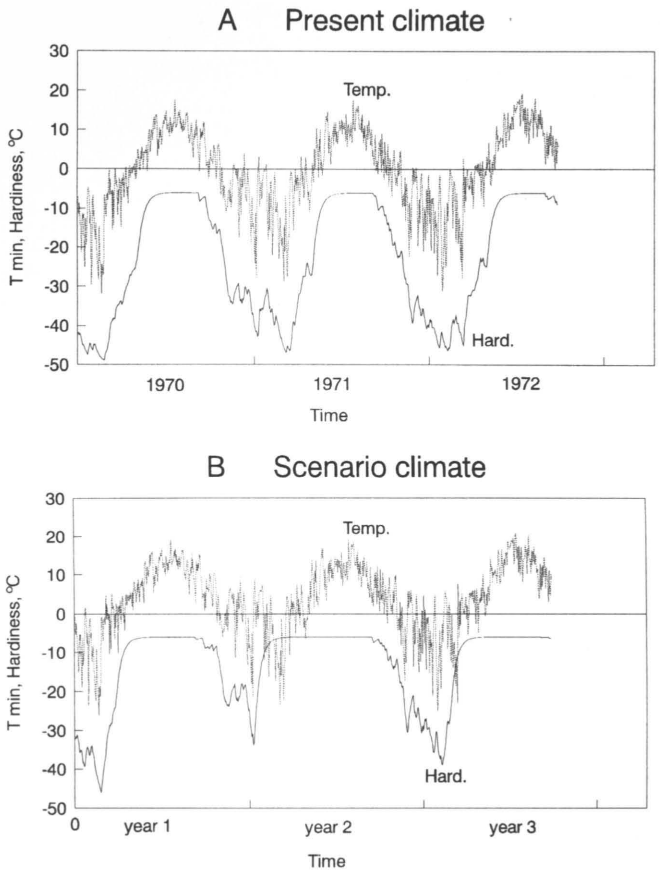

Fig. 2. Daily minimum temperatures and simulated frost hardiness of Scots pine trees over three years in Jyväskylä, central Finland, for (A) present climate and (B) scenario climate. Temperature data for the years 1–3 in (B) were constructed by increasing the daily mean and minimum temperatures for the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

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

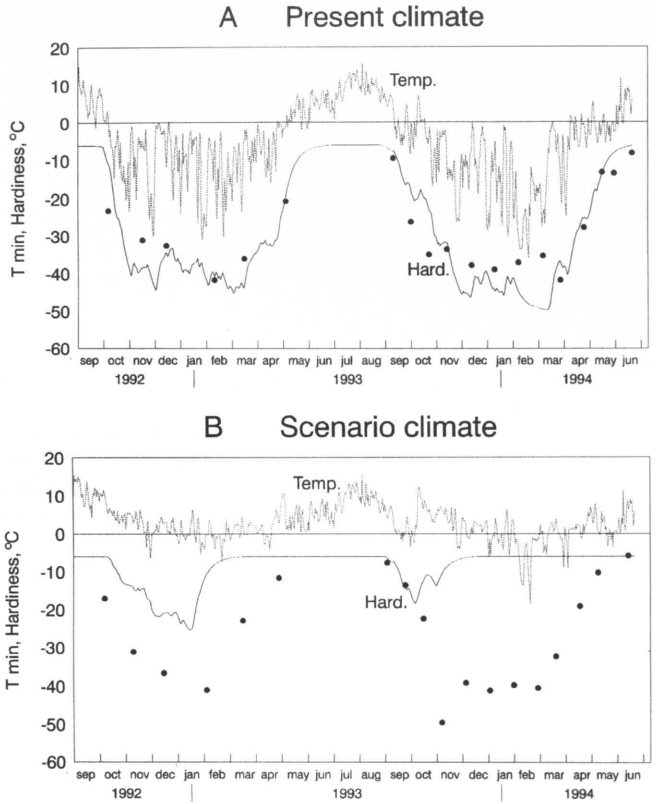

Fig. 3. Daily minimum temperatures (broken line), tree frost hardiness predicted by the overwintering submodel (solid line), and measured needle frost hardiness of Scots pine saplings (dots) in Mekrijärvi, eastern Finland. (A) Saplings growing under natural temperature conditions, (B) saplings growing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

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