A Simulation Model for the Annual Frost Hardiness and Freeze Damage of Scots Pine

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The changes in the frost hardiness of Scots pine were modelled by a dynamic model where the input variables were temperature and photoperiod and the phase of annual development. The damage caused by freezing was described by the sigmoidal relationship between the relative needle damage and freezing temperature. The model simulations were carried out using temperature data from two sites in central Finland—Suonenjoki and Tampere. The validity of the frost hardiness model was tested with measured frost hardiness data from Suonenjoki. The effects of climatic warming were also simulated by increasing temperature of the long-term climatic data. Genotypic differences in chilling requirement, which determines the timing of the reduction of hardening competence, were included in the simulations. The simulated needle damage increased as a result of climatic warming, and the differences in the chilling requirement had a stronger effect on the amount of damage in the warmed climate than in the present climate. A large variation between years was found in the level of damage.   © 1996 Annals of Botany Company

INTRODUCTION

The observed climatic warming is expected to cause changes in the productivity of boreal forests. Several ecosystem models predict that the climatic changes will increase the growth of forests due to increased temperature and a prolonged growing season (e.g. Kellomäki and Kolström, 1994; Väisänen, Strandman and Kellomäki, 1994). Climatic warming may, however, also cause disturbances in the annual growth cycle of trees. For example, the onset of premature growth during early spring or late winter may expose the trees to damage caused by subsequent frosts, as demonstrated by Hänninen (1991) with the aid of computer simulations. In recent field experiments simulating climatic warming in open-top chambers, the frost hardening of Scots pine was delayed in autumn, and dehardening was hastened and the onset of growth advanced several weeks in spring (Repo, Hänninen and Kellomäki, 1996). These results suggest that the possibility of freeze damage should be taken into account in the ecosystem models predicting the response of forests to climatic warming (Kellomäki *et al.*, 1992; Kellomäki, Hänninen and Kolström, 1995).

In the frost hardiness models previously developed for Scots pine (*Pinus sylvestris* L.), air temperature and photoperiod have been used to describe the development of frost hardiness. Repo, Mäkelä and Hänninen (1990) introduced a model with a linear relationship between the prevailing air temperature and the stationary level of frost hardiness, i.e. the target level which determines the direction of the change in frost hardiness. The rate of change of frost hardiness was assumed to be dependent on the difference between the prevailing frost hardiness and the stationary level, and on the value of the time constant. Kellomäki *et al.*

(1992) modified the model of Repo *et al.* (1990) by dividing the annual cycle of trees into three periods (growth, lignification and dormancy), which included different frost hardiness responses to the environment.

Leinonen *et al.* (1995) and Leinonen, Repo and Hänninen (1996*a*) developed the model of Repo *et al.* (1990) further by introducing an additive effect of temperature and photoperiod on frost hardiness. This model was accurate in predicting the frost hardening in autumn, but overestimated the hardiness during dehardening in spring. This result showed that the models must be closely related to the development of the annual growth cycle of trees and the gradual change in the environmental response of frost hardiness must be included.

One aim of this study was to develop a model for the frost hardiness and freeze damage of conifers covering the entire annual growth cycle. Another aim was to demonstrate model simulations which predict the amount of needle damage to Scots pine caused by freezing in the present climate and in the predicted conditions of climate warming.

MODEL FOR FROST HARDINESS

The structure of the present model is based on three main aspects observed in the changes of frost hardiness of Scots pine: (1) the response of frost hardiness to the environment gradually changes depending on the phase of the annual development (e.g. Valkonen *et al.*, 1990; Repo 1991); (2) photoperiod has an essential role in hardening but little or no effect in dehardening (e.g. Aronsson, 1975; Christersson, 1978; Leinonen, Repo and Hänninen, 1996*b*); and (3) frost hardiness fluctuates according to temperature fluctuations

(Nilsson and Walfridsson, 1995; Beuker, 1996; Leinonen *et al.*, 1996*b*).

The fluctuation in frost hardiness caused by environmental factors is described by the feedback control, i.e. the daily change of frost hardiness is dependent on the difference between the stationary (target) level of frost hardiness [$\hat{R}(t)$] and the actual frost hardiness [$R(t)$] according to a first-order dynamic process (Repo *et al.*, 1990):

$$\frac{\mathrm{d}R(t)}{\mathrm{d}t} = \frac{1}{\tau}[\hat{R}(t) - R(t)], \qquad (1)$$

where τ is the time constant.

The stationary level of frost hardiness is modelled as a function of the additive effect of night length and temperature (Leinonen *et al.*, 1995, 1996*a*), and the effect of the annual development of trees described by the hardening competence (C_R), which indicates the capacity of environmental factors (i.e. short photoperiod, low temperatures) to induce or retain frost hardiness.

$$\hat{R}(t) = \hat{R}_{min} + C_R \times [\Delta\hat{R}_T(t) + \Delta\hat{R}_P(t)], \qquad (2)$$

where $\hat{R}_{min}$ is the minimum level of frost hardiness, $\Delta\hat{R}_T(t)$ the increase in the stationary level of frost hardiness induced by temperature and $\Delta\hat{R}_P(t)$ the increase in the stationary level of frost hardiness induced by night length.

The effect of temperature on the stationary level of frost hardiness is modelled by a piece-wise linear function (Repo *et al.*, 1990; Leinonen *et al.*, 1995, 1996*a*):

$$\left.\begin{aligned}
\Delta\hat{R}_T(t) &= \Delta\hat{R}_{Tmax} - \frac{\Delta\hat{R}_{Tmax}}{(T_1 - T_2)}[T(t) - T_2], \quad T_2 \leqslant T(t) \leqslant T_1 \\
\Delta\hat{R}_T(t) &= 0, \qquad\qquad\qquad\qquad\quad T(t) > T_1 \\
\Delta\hat{R}_T(t) &= \Delta\hat{R}_{Tmax}, \qquad\qquad\qquad T(t) < T_2,
\end{aligned}\right\} \quad (3)$$

where $\Delta\hat{R}_{Tmax}$ is the maximum level of the increase of frost hardiness induced by temperature, $T(t)$ the daily minimum temperature, and T_1 and T_2 the upper and lower limits of the effective temperature range required to effect the increase in frost hardiness.

The effect of increasing night length on the stationary level of frost hardiness is also modelled by a piece-wise linear function (Kellomäki *et al.*, 1992; Bigras and D'Aoust, 1993; Leinonen *et al.*, 1995, 1996*a*):

$$\left.\begin{aligned}
\Delta\hat{R}_P(t) &= \frac{\Delta\hat{R}_{Pmax}}{(NL_2 - NL_1)}[NL(t) - NL_1], \quad NL_1 \leqslant NL(t) \leqslant NL_2 \\
\Delta\hat{R}_P(t) &= 0, \qquad\qquad\qquad\qquad NL(t) < NL_1 \\
\Delta\hat{R}_P(t) &= \Delta\hat{R}_{Pmax}, \qquad\qquad\quad NL(t) > NL_2,
\end{aligned}\right\} \quad (4)$$

where $\Delta\hat{R}_{Pmax}$ is the maximum level of the increase of frost hardiness induced by night length, $NL(t)$ the daily night length, and NL_1 and NL_2 the lower and upper limits of the effective range of night length required to effect the increase in frost hardiness.

Since decreasing night length was found in previous studies (Aronsson, 1975, Leinonen *et al.*, 1996*b*) to have

little or no effect on the dehardening of Scots pine, during decreasing night length the following is assumed:

$$\Delta\hat{R}_P(t) = \Delta\hat{R}_{Pmax}. \qquad (5)$$

When the hardening competence reaches its minimum level during the active growth phase ($C_R = 0$, see details below),

$$\Delta\hat{R}_P(t) = 0. \qquad (6)$$

In order to determine the hardening competence, the phase of the annual cycle for each day must be determined. The timing of each phase can be calculated as a function of environmental factors. Several models for this purpose have been developed (for references, see Hänninen, 1990; Kramer, 1994*a*). In this study, the sequential model originally developed by Sarvas (1972, 1974) and reformulated by Hänninen (1990), Kellomäki *et al.* (1992) and Kramer (1994*a*) is used. In this model the annual growth cycle of trees is divided into four separate phases, i.e. active growth, lignification, rest and quiescence.

During the rest phase trees have no capacity to grow in any environmental conditions. Rest is broken as a result of chilling temperature. The daily rate of rest break (M_{chl}) is calculated as a function of daily mean temperature [$T_{mean}(t)$] (Sarvas, 1974; Hänninen, 1990; Kramer 1994*a*):

$$\left.\begin{aligned}
M_{chl} &= 0, & T_{mean}(t) &\leqslant T_{min} \\
M_{chl} &= \frac{T_{mean}(t) - T_{min}}{T_{opt} - T_{min}}, & T_{min} < T_{mean}(t) &\leqslant T_{opt} \\
M_{chl} &= \frac{T_{mean}(t) - T_{max}}{T_{opt} - T_{max}}, & T_{opt} < T_{mean}(t) &\leqslant T_{max} \\
M_{chl} &= 0, & T_{mean}(t) &> T_{max}
\end{aligned}\right\} \quad (7)$$

The state of rest break (S_{chl}) is calculated as an integral of M_{chl} from the beginning of the rest period (t_1) (Kramer, 1994*a*):

$$S_{chl} = \sum_{t_1}^{t} M_{chl} \qquad (8)$$

Rest is completed when S_{chl} attains the critical value CU_{crit} (arbitrary chilling units, CU).

After rest completion the daily rate of ontogenetic development (M_{frc}) is calculated as a nonlinear function of daily mean temperature (Sarvas, 1972; Hänninen, 1990, Kramer, 1994*b*):

$$\left.\begin{aligned}
M_{frc} &= 0, & T(t) &\leqslant 0\ ^\circ\mathrm{C} \\
M_{frc} &= \frac{1}{1 + \mathrm{e}^{-b[Tmean(t) - c]}}, & T(t) &> 0\ ^\circ\mathrm{C}.
\end{aligned}\right\} \quad (9)$$

The state of ontogenetic development (S_{frc}) is calculated by integrating M_{frc} from the beginning of the quiescence period (t_2) (Kramer, 1994*a*).

$$S_{frc} = \sum_{t_2}^{t} M_{frc} \qquad (10)$$

Bud burst occurs when S_{frc} attains the critical value FU_{crit} (arbitrary forcing units, FU).

In the model of Kellomäki *et al.* (1992), the timing of growth cessation was determined as a function of night length and temperature sum (Koski and Selkäinaho, 1982; Koski and Sievänen, 1985). In the present model developed for Scots pine, however, the growth cessation is determined only as a function of temperature sum, due to the predetermined growth of this species (e.g. Koski and Sievänen, 1985). Growth cessation occurs when the linear temperature sum (day °C, threshold temperature = 5 °C) attains the critical value TS_{crit}.

After growth cessation, the state of lignification TS_{lgn} is calculated as a linear temperature sum (threshold temperature = 5 °C). When TS_{lgn} attains the critical value $TS_{critlgn}$, the rest phase begins (Kellomäki *et al.*, 1992).

The value of hardening competence ranges between 0 (no capacity to harden) and 1 (capacity to maximum hardiness). During the rest phase the hardening competence is assumed to remain at its maximum level, i.e.

$$C_R = 1. \tag{11}$$

During the quiescent phase, the hardening competence decreases in connection with the ontogenetic development towards bud burst and reaches its minimum during the beginning of the active growth period (Leinonen *et al.*, 1996*b*). Therefore, the prevailing value of the hardening competence is modelled as a function of the state of ontogenetic development S_{frc} [eqn (9)]. Consequently, the hardening competence during the quiescent and active growth phases is:

$$C_R = \max[1 - (S_{frc}(t)/FU_{critR}), 0], \tag{12}$$

where $S_{frc}(t)$ is the state of ontogenetic development, and FU_{critR} the critical state of ontogenetic development when the hardening competence reaches its minimum level ($C_R = 0$). The value of FU_{critR} is higher than the critical temperature sum for bud burst (FU_{crit}), since Scots pine needles are still frost-hardened at the time of onset of height growth (Leinonen *et al.*, 1996*b*; Repo *et al.*, 1996).

During the lignification phase the hardening competence is assumed to return to its maximum level, and this development is calculated as a function of temperature sum:

$$C_R = TS_{lgn}/TS_{critlgn} \tag{13}$$

where TS_{lgn} is the state of lignification as determined by a linear temperature sum, and $TS_{critlgn}$ the critical state of lignification when the hardening competence reaches its maximum level and the trees enter the rest phase.

MODEL FOR FREEZE DAMAGE

The relative effect of freeze damage for each temperature at each level of frost hardiness is modelled according to a logistic function:

$$I = \frac{1}{1 + e^{B(R-T)}}, \tag{14}$$

where I is the index of injury (proportion of damaged needle area) at temperature T, R the level of frost hardiness and B the slope parameter (Leinonen *et al.*, 1996*b*).

Since the shape of the curve for the index of injury changes in respect to the level of hardiness (R), the value of the slope parameter (B) is modelled as follows:

$$B = \alpha + \beta e^{\gamma R}. \tag{15}$$

In the simulations, the index of injury is calculated for each day, and the maximum of these daily values during the frost-exposed period of each year is used to represent the annual reduction of the needle area.

MODEL PARAMETERS

The parameters for Scots pine used in the simulations were obtained from the literature and unpublished experimental results (Table 1). The rate of development during the rest and quiescence phases is described by parameters T_{min}, T_{opt}, T_{max}, b and c. For these parameters, as well as for parameter FU_{crit}, the values of Scots pine estimated by Kramer (1994*b*) were used. The value for CU_{crit} was estimated from the data of Leinonen (1996) for the Finnish Scots pine origin. The value of TS_{crit} estimated from a Scots pine stand in southern Finland (Raulo and Leikola, 1974) was used. The temperature sum for lignification ($TS_{critlgn}$) was calculated from the period between the end of shoot elongation and the end of needle elongation of Scots pine (Repo, 1992). The parameters for frost hardiness [Eqns (3), (4)] were obtained from other sources (Aronsson, 1975; Christersson, 1978; Leinonen *et al.*, 1996*a*). The temperature sum for minimum hardening competence (FU_{critR}) was calculated from the data of Leinonen *et al.*, 1996*b*, and the parameters for freeze damage were also estimated using the same data. The index of injury was estimated visually, and eqn (14) fitted

TABLE 1. *Values of parameters used in the model simulations*

| Parameter	Value	Unit	Source
Model for the annual cycle			
T_{min}	−13·8	°C	Kramer, 1994*b*
T_{opt}	−1·2	°C	Kramer, 1994*b*
T_{max}	16·5	°C	Kramer, 1994*b*
b	0·11	°C	Kramer, 1994*b*
c	37·6	°C	Kramer, 1994*b*
CU_{crit}	28	CU	Leinonen, 1996
FU_{crit}	2·4	FU	Kramer, 1994*b*
TS_{crit}	510	d °C	Raulo and Leikola, 1974
$TS_{critlgn}$	300	d °C	Repo, 1992
Model for frost hardiness			
$\hat{R}_{min}$	−4·5	°C	Repo, 1992
T_1	10	°C	Aronsson, 1975
T_2	−16	°C	Leinonen *et al.*, 1996*a*
NL_1	10	h	Aronsson, 1975
NL_2	16	h	Aronsson, 1975
$\Delta\hat{R}_{Tmax}$	−47	°C	Leinonen *et al.*, 1996*a*
$\Delta\hat{R}_{Pmax}$	−18·5	°C	Christersson, 1978
			Leinonen *et al.*, 1995*a*
τ	5	d	Repo and Pelkonen, 1986
			Repo *et al.*, 1990
FU_{critR}	4·5	FU	Leinonen *et al.*, 1996*b*
Model for freeze damage			
α	−0·1435	°C^{-1}	Present study
β	−1·4995	°C^{-1}	Present study
γ	0·1071	°C^{-1}	Present study
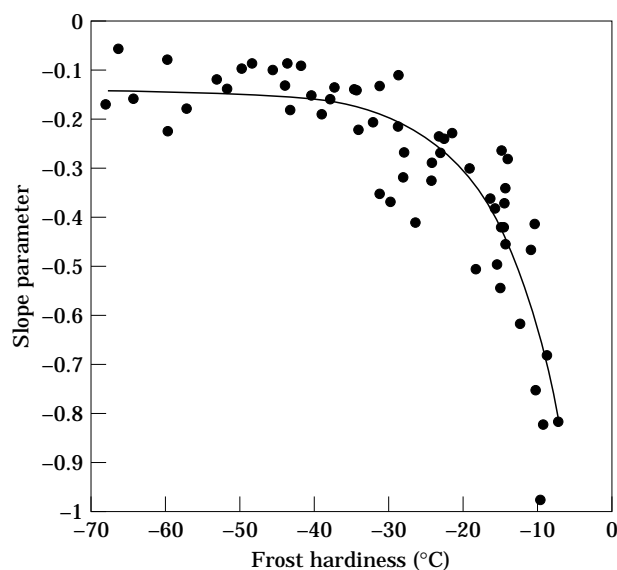
FIG. 1. Relationship between the slope parameter (*B*) of the curve of the index of injury and the level of frost hardiness. Observed values (●) (Leinonen *et al.*, 1996*b*) and fitted curve [eqn (15)] (——).

for each freezing test. Since the slope of the curve for index of injury changed, depending on the level of frost hardiness, the relationship between the slope parameter B and frost hardiness [eqn (15)] was determined using nonlinear regression (Fig. 1).

MODEL SIMULATIONS

The simulations were carried out using temperature data from two sites in central Finland: Suonenjoki Research Station, 62°40′ N, 27°00′ E (3-year period) and Tampere, 61°28′ N, 23°44′ E (15-year period). The Tampere data was used to represent the present climate in Finland, and the scenario for future climate with climatic warming (Kettunen *et al.*, 1987) was simulated by raising the daily mean temperature (input of the model for annual development) and minimum temperature (input of the hardiness model) according to the predicted increase of mean temperature for each month (Table 2).

TABLE 2. *Increase of monthly mean temperatures (°C) according to the scenario for future climatic warming (*Kettunen* et al., 1987)*

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

The validity of the model was tested by comparing the frost hardiness data from Suonenjoki, measured using the impedance method and visual damage scoring (Repo, 1992). The data indicate that the model is accurate during the most frost-sensitive phases in autumn and spring, when the level of frost hardiness is low but the occurrence of frost is possible (Fig. 2).

The simulation results carried out with the data from Tampere indicate that in the present climate the level of needle damage is low during most of the simulation years (Fig. 3). The highest level of damage occurred during winter 1986–87, when the midwinter temperature was exceptionally low. When the effects of climatic warming were simulated, needle damage increased in most of the years included in the simulations (Fig. 3). The reason for this is that increased temperature accelerates the development towards bud burst and thus decreases the hardening competence. Only during winter 1986–87 did the simulated freeze damage decrease as a result of climatic warming since in this case the main factor affecting freeze damage was not the timing of dehardening but rather the absolute minimum winter temperature.

Since the timing of the rest break is essential in determining the timing of the reduction of the hardening competence, the simulations were also carried out by changing the value of CU_{crit} to represent different tree genotypes (cf. Hänninen 1991, 1996; Leinonen, 1996). According to the results, in the present climate the values of CU_{crit} ranging from 20 to 35 had only a minor effect on the amount of needle damage (Table 3). Conversely, when the effects of climatic warming were simulated, the occurrence of needle damage was highly dependent on the value of CU_{crit} used (Table 3).

DISCUSSION

Model

The present study introduces a model in which the response of frost hardiness of trees to environmental factors is dependent on the annual development. A similar approach was previously used in the model of Kobayashi, Fuchigami and Weiser (1983), where the phase of annual development is described by degree growth stage (°GS) (Fuchigami *et al.*, 1982), and by Kellomäki *et al.* (1992). The model of Kellomäki *et al.* (1992), like the present model, is based on the fluctuating development of frost hardiness, but their model does not include the gradual change in the environmental response of frost hardiness. Furthermore, in their model, the additive effect of temperature and photoperiod on the level of frost hardiness during the hardening phase is not taken into account.

The assumption of the fluctuating development of frost hardiness of Scots pine in the model (Repo *et al.*, 1990; Leinonen *et al.*, 1995, 1996*a*) has been supported by recent experimental results with Scots pine (Nilsson and Walfridsson, 1995; Beuker, 1996; Leinonen *et al.*, 1996*b*), and earlier observations with other species (Proebsting, 1963; Sakai and Larcher, 1987). Furthermore, the additive effect of temperature and night length on frost hardiness has been found in several woody species (Chen and Li, 1978; Greer, 1983), including Scots pine (Christersson, 1978;
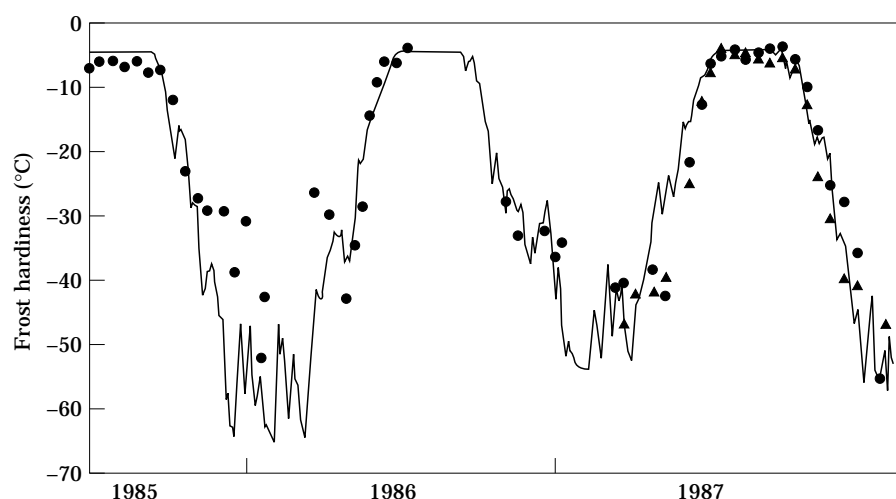
Fig. 2. Model-predicted (——) and measured frost hardiness using impedance method (●) and visual damage scoring (▲).
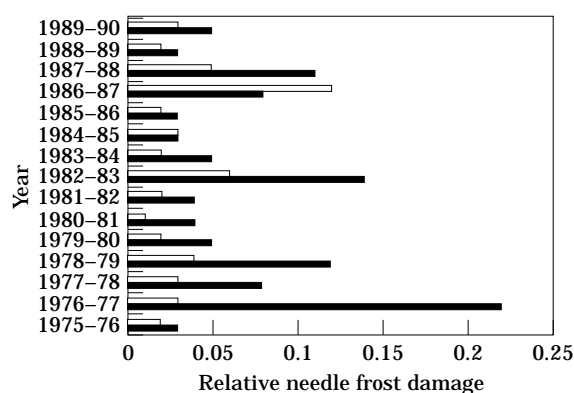

Fig. 3. Model-predicted relative needle damage (maximum of daily values during each frost-exposed season) in present climate and in the scenario climate for future climatic warming. □, Present; ■, scenario.

TABLE 3. *Model predicted mean and maximum annual needle damage during a 15-year period in present and scenario climate with different values of* CU_{crit}

	CU_{crit}		
	20	28	35
Present, mean	0·06	0·03	0·02
max	0·21	0·12	0·07
Scenario, mean	0·18	0·07	0·05
max	0·46	0·22	0·18

on the level of frost hardiness (Leinonen *et al.*, 1996*b*). During the quiescence phase, the accumulation of temperature sum promotes development towards bud burst and decreases hardening competence (Proebsting, 1963). During the lignification phase the effect of high temperatures is the opposite. After growth cessation the trees use their energy resources to develop a freeze tolerance (cf. Fuchigami, Weiser and Evert, 1971; Harrison, Weiser and Burke, 1978), and high temperatures are needed for this development. In the present model, the hardening competence reaches its maximum level when the needle elongation is completed. This is supported by the observations on the timing of the beginning of rapid hardening (Repo, 1992). The lignification phase of the model can be seen as comparable to the 'stage I acclimation' presented by Fuchigami *et al.* (1982).

The present study is an attempt to develop a model in which a biological interpretation can be found for all the model parameters, where the values of each are dependent on properties of each tree genotype. For this reason the model may be used in different environmental conditions, for example, in the changing climate. Limitations on the use of models based on biological processes are a result of the large amount of experimental work and long-term field observations necessary to determine the genotypic variation in the environmental response. However, detailed models describing the dynamics of frost hardiness are needed to include short-term fluctuation, which is essential for the process of freeze damage.

Bervaes, Ketchie and Kuiper, 1978) during hardening, while temperature has been found to be the most important factor affecting the development of hardiness during dehardening (Van den Driessche, 1969; Aronsson, 1975).

Hardening competence is an essential concept in describing the seasonal behaviour of frost hardiness. This concept permits a differentiation between the indirect (long-term) effect of temperature and the direct (short term) effect

Simulations

The comparison of the simulation results to the measured frost hardiness data from Suonenjoki can be considered an independent test of the model, since the parameters of the model describing hardening and dehardening were obtained from sources other than these data. On the other hand, it is not possible to validate the model for relative needle damage in field conditions. However, the high freeze damage during winter 1986–87 predicted by the model is in good

agreement with field observations. Following that winter, considerable needle loss in conifers was observed in Finland, and the most obvious reason was frost damage caused by exceptional weather conditions (Jalkanen, 1988; Jukola-Sulonen, 1990).

The model simulations indicate that trees growing in the present climate adequately tolerate freezing during all phases of the annual growth cycle. The timing of the onset of the quiescence phase of Scots pine, as described by parameter CU_{crit}, has in previous studies been found to vary greatly both within populations (Hänninen, 1990) and between origins (Leinonen, 1996). This variation, however, seemed to be relatively insignificant in regard to the level of freeze damage. This is due to the fact that although the rest phase ends early, i.e. the value of CU_{crit} is small, high temperatures causing ontogenetic development towards bud burst and the simultaneous loss of hardening competence seldom occur during winter in the present climate.

In the changed climate, the temperature in winter rises more frequently to the effective range (above 0 °C) and causes ontogenetic development and the loss of hardening competence. Therefore, bud burst was hastened and the freeze damage increased compared to the present climate and with all values of CU_{crit} used (cf. Hänninen, 1991). In the base simulation ($CU_{crit} = 28$) the maximum relative needle damage during the 15-year period was quite moderate (about 20 %). With the lower value of CU_{crit}, a damage of nearly 50 % occurred during some years. The results suggest that the strongly-developed protection against freeze damage in local origins in the present climate may partly be lost in the changed climate. The year to year variation in climatic conditions in the warmed climate seemed to have an even more significant effect on the level of freeze damage than in the present climate. This is, however, largely dependent on the variation of temperature in the future climate (Repo *et al.*, 1996). In the simulations only the level of temperature was increased and the variation was kept at the same level as in the present climate. If the temperature fluctuation decreases in connection with temperature rise, the probability of freeze damage may also decrease.

ACKNOWLEDGEMENTS

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