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

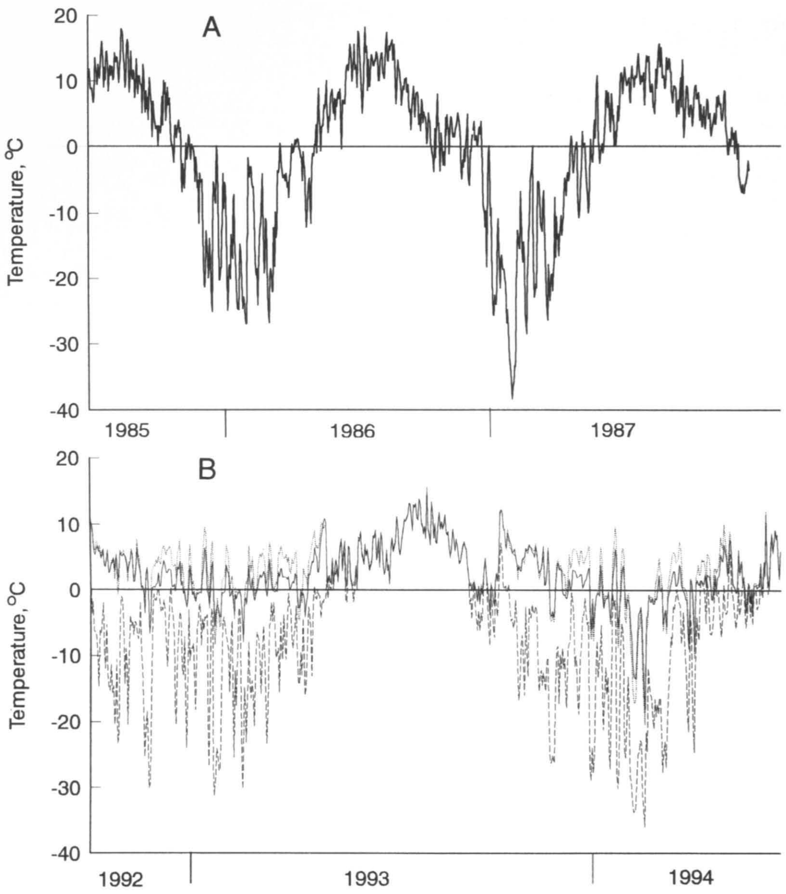

Fig. 1. (A) Daily minimum temperatures during the experiment in Suonenjoki. (B) Daily minimum temperatures during the experiment in Mekrijärvi, control treatment (– – –), moderately elevated temperature (——) and highly elevated temperature (········).

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:

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

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:

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

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:

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

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:

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

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:

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

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 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.

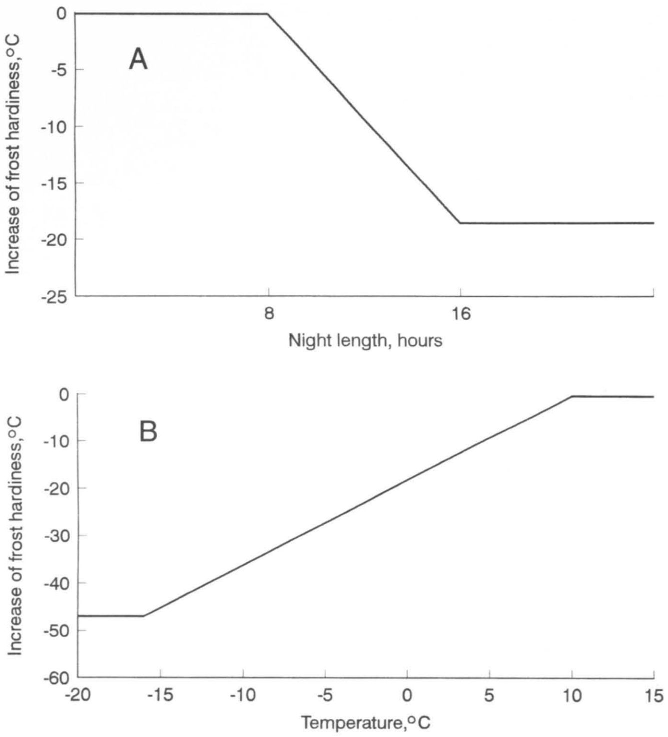

Fig. 2. (A) Dependence of the increase of the stationary level of frost hardiness on photoperiod as used in the additive model. (B) Dependence of the increase of the stationary level of frost hardiness on temperature as used in the additive model.

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-

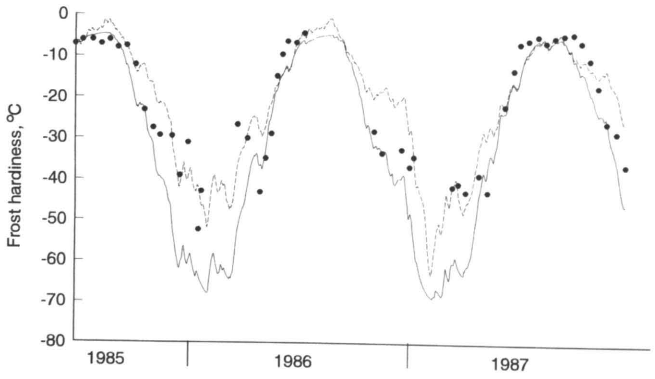

Fig. 3. Frost hardiness as estimated by the impedance method (●), predicted by the temperature model (– – –) and by the additive model (——) in the experiment in Suonenjoki.

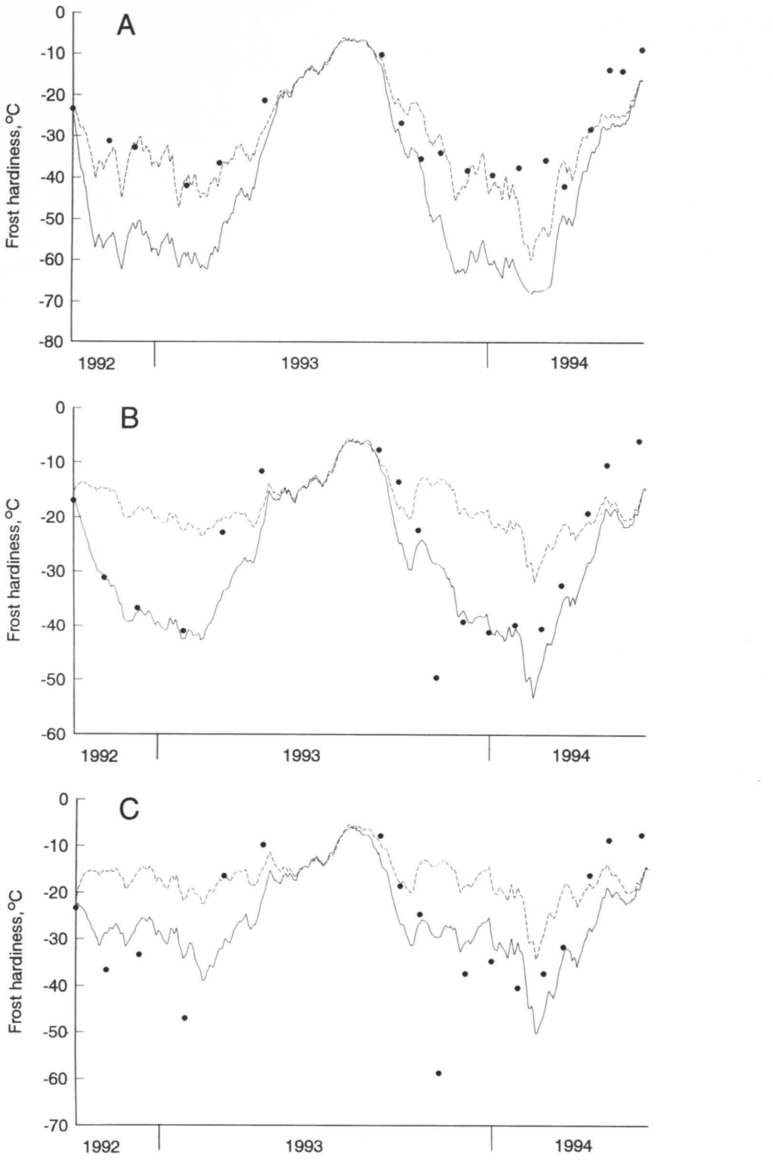

Fig. 4. Frost hardiness as estimated by the electrolyte leakage method (●), predicted by the temperature model (– – –) and by the additive model (——) in the experiment in Mekrijärvi. (A) control treatment, (B) moderately elevated temperature and (C) highly elevated temperature.

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 Mekrijärvi, 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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References

Aronsson, A. 1975. Influence of photo- and thermoperiod on the initial stages of frost hardening and dehardening of phytotron-grown seedlings of Scots pine (Pinus silvestris L.) and Norway spruce (Picea abies (L.) Karst.). Studia Forestalia Suecica 128: 5–20.

Burr, K.E., Tinus, R.W., Wallner, S.J. & King, R.M. 1990. Comparison of three cold hardiness tests on conifer seedlings. Tree Physiology 6: 351–369.

Cannell, M.G.R., Murray, M.B. & Sheppard, L.J. 1985. Frost avoidance by selection for late budburst in Picea sitchensis. Journal of Applied Ecology 22: 931–941.

Chen, H.-H. & Li, P.H. 1978. Interactions of low temperature, water stress, and short days in the induction of stem frost hardiness in red osier dogwood. Plant Physiology 62: 833–835.

Christersson, L. 1978. The influence of photoperiod and temperature on the development of frost hardiness in seedlings of Pinus silvestris and Picea abies. Physiologia Plantarum 44: 288–294.

Deans, J.D. & Harvey, F.J. 1995. Phenologies of sixteen European provenances of sessile oak growing in Scotland. Forestry 68: 265–273.

Flint, H.L., Boyse, B.R. & Beattie, D.J. 1967. Index of injury – a useful expression of freezing injury to plant tissues as determined by the electrolytic method. Canadian Journal of Plant Science 47: 229–230.

Greer, D.H. 1983. Temperature regulation of the development of frost hardiness in Pinus radiata D. Don. Australian Journal of Plant Physiology 10: 539–547.

— & Warrington, I.J. 1982. Effect of photoperiod, night temperature, and frost incidence on development of frost hardiness in Pinus radiata. Australian Journal of Plant Physiology 9: 333–342.

Hänninen, H. 1991. Does climatic warming increase the risk of frost damage in northern trees? Plant, Cell and Environment 14: 449–454.

— 1995a. Effects of climatic change on trees from cool and temperate regions: an ecophysiological approach to modelling of bud burst phenology. Canadian Journal of Botany 73: 183–199.

— 1995b. Assessing ecological implications of climatic change: can we rely on our simulation models? Climatic Change 31: 1–4.

— , Kellomäki, S., Laitinen, K., Pajari, B. & Repo, T. 1993. Effect of increased winter temperature on the onset of height growth of Scots pine: a field test of a phenological model. Silva Fennica 27: 251–257.

Jonsson, A., Eriksson, G., Dormling, I. & Ifver, J. 1981. Studies on frost hardiness of Pinus contorta Dougl. seedlings grown in climate chambers. Studia Forestalia Suecica 157: 1–47.

Kellomäki, S., Hänninen, H. & Kolström, M. 1995. Computations on frost damage to Scots pine under climatic warming in boreal conditions. Ecological Applications 5: 42–52.

— , Väisänen, H., Hänninen, H., Kolström, T., Lauhanen, R., Mattila, U. & Pajari, B. 1992. A simulation model for the succession of the boreal forest ecosystem. Silva Fennica 26: 1–18.

Leinonen, I, Repo, T., Hänninen, H. & Burr, K. E. 1995. A second order dynamic model for frost hardiness of trees. Annals of Botany 76: 89–95.

Murray, M.B., Cannell, M.G.R. & Smith, R.I. 1989. Date of budburst of fifteen tree species in Britain following climatic warming. Journal of Applied Ecology 26: 693–700.

Repo, T. 1991. Rehardening potential of Scots pine seedlings during dehardening. Silva Fennica 25: 13–21.

— 1992. Seasonal changes of frost hardiness in Picea abies and Pinus sylvestris in Finland. Canadian Journal of Forest Research 22: 1949–1957.

— , Hänninen, H. & Kellomäki, S. 1996. The effect of the long-term elevation of air temperature and CO_2 on frost hardiness of Scots pine. Plant, Cell and Environment 19: 209–216.

— , Mäkelä, A. & Hänninen, H. 1990. Modelling frost resistance of trees. Silva Carelica 15: 61–74.

Sutinen, M.-L., Palta, J. P. & Reich, P. B. 1992. Seasonal differences in freezing stress resistance of needles of Pinus nigra and Pinus resinosa: evaluation of the electrolyte leakage method. Tree Physiology 11: 241–254.

Valkonen, M.-L., Hänninen, H., Pelkonen, P. & Repo, T. 1990. Frost hardiness of Scots pine seedlings during dormancy. Silva Fennica 24: 335–340.

Total of 24 references