

Late Termination of Freezer Storage Increases the Risk of Autumn Frost Damage to Norway Spruce Seedlings

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Over the last few years it has become increasingly common in artificial forest regeneration to extend the planting period by using freezer-stored seedlings for early summer plantings. Developmentally, however, planted freezer-stored seedlings lag behind seedlings planted earlier in the spring. As freezer-stored seedlings also start hardening later, they are more susceptible to early autumn frosts, especially in years when the thermal growing season ends and the first autumn frosts come earlier than usual. By means of computer simulations with a simple temperature sum model and long-term air-temperature data from three locations in Finland, we examined the effect of the freezer-storage termination date on the risk of autumn frost damage to the seedlings. The long-term simulations revealed a drastic effect of year-to-year variation in the thermal conditions during the growing season on the occurrence of autumn frost damage. Such results provide crucial information complementary to those obtained in field experiments, which are always restricted to a relatively short time period. Together with earlier field data, the present results suggest that at an average regeneration site in central Finland, the planting of seedlings whose storage has terminated on 15 June and 22 June involve autumn frost damage every tenth and every fifth year, respectively. The sensitivity analysis revealed that the temperature sum requirement of maturation has a great effect on the risk of autumn frost damage, thus pinpointing the need for experimental studies addressing this ecophysiological trait of the seedlings.

Keywords autumn frost damage, day degrees, freezer storage, growing season, Norway spruce, simulation

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1 Introduction

Traditionally, plantings in artificial forest regeneration have been done with dormant seedlings. This is because the seedlings have been considered to withstand the stresses of transportation and planting better during dormancy than after the onset of growth. However, as the time window from the thawing of snow and ground frost to the onset of seedling growth is relatively narrow, spring plantings with dormant seedlings have had to be done in a great hurry. One traditional way to overcome this problem has been to plant part of the seedlings in the autumn, after they have attained dormancy (Antola and Lehto 1969). More recently, plantings with actively growing seedlings have also produced promising results (Revel et al. 1990, Grossnickle and Folk 2003, Luoranen et al. 2005, 2006).

The time window for planting dormant seedlings in the spring can be extended and the great hurry avoided by freezer-storing the seedlings. This method has been successfully used in northern Europe and North America for more than fifty years (Yli-Vakkuri et al. 1968, Brown 1973, Camm et al. 1994). The viability of the seedlings is sustained relatively long in freezer storage, so that there are normally no problems about the onset of growth even in late plantings (Ericsson et al. 1983, Luoranen et al. 2005, Helenius et al. 2005) except after very long storage, which may decrease the carbohydrate reserves (Ritchie 1982, Jiang et al. 1994) and dry out the seedlings through transpiration. In their development over the growing season, however, freezer-stored seedlings lag behind seedlings planted earlier in the spring. Thus freezer-stored seedlings also start hardening later, which makes them more susceptible to early autumn frosts than seedlings planted earlier, especially in years when the thermal growing season ends and the first autumn frosts come earlier than usual.

The risk of autumn frost damage can be studied in field experiments by varying the date of storage termination of the planting stock (Ericsson et al. 1983, Raulo et al. 1994, Luoranen et al. 2005). As this experimental design simulates real-life practice, the method produces reliable results. However, as thermal conditions vary drastically from year to year (Koski and Sievänen 1985), the interpretation of the results is not straightforward. From a single one-year experiment, one can

only infer how long the storage termination can be postponed in years with similar summer and autumn thermal conditions. If the thermal growing season of the experimental year happens to be warmer and longer than average, the experiment produces an over-optimistic recommendation of the latest possible termination date. Similarly, an unusually cold and short growing season results in an over-cautious recommendation. For reliable information, the experiment needs to be repeated over several years, since the effects of the termination date can be studied only for the year when the seedlings were planted, not for later years. In order to properly account for the year-to-year variation in the climatic conditions, the experiments would need to be repeated over several decades, but that is not possible in practice.

Since the 1960s, the annual cycle of forest trees has been studied by means of various simulation models (for a recent review, see Hänninen and Kramer 2007). The effect of year-to-year variation in climatic conditions on the survival and growth of trees can be studied with the simulation models by using long-term climatic data as input (Cannell 1985, Häkkinen and Hari 1988, Hänninen 1991, Kramer 1994, Linkosalo et al. 2000). The purpose of the present study was to examine, by means of a simple temperature sum model and long-term air-temperature data, the effect of the storage termination date on the risk of autumn frost damage to freezer-stored Norway spruce (*Picea abies* (L.) Karst.) seedlings. Long-term air-temperature data from three locations in Finland were used in the study, with the main emphasis on the central Finland location. At this location, the model parameterization was tested with independent field data from an earlier study (Luoranen et al. 2005). For the other two locations, no such data were available, so that their results are presented in a condensed form here, mainly for the purposes of a sensitivity analysis of the model parameters.

2 Material and Methods

2.1 The Air-temperature Data

Long-term air-temperature data collected by the Finnish Meteorological Institute at three loca-

Table 1. The three locations for the simulations, with characteristics of their air-temperature data

	Coordinates	Altitude (m asl)	Years (no. of years)	Temp sum, d.d. ^{a)}		
				Min	Mean	Max
Jokioinen	60°48'N, 23°30'E	104	1959–2002 (44)	981	1261	1536
Jyväskylä	62°24'N, 25°40'E	139	1952–2002 (51)	892	1149	1435
Kajaani	64°16'N, 27°40'E	147	1952–1999 (48)	806	1051	1287

^{a)} Temperature sum of the thermal growing season

tions in Finland were used in the study (Fig. 1). The data from the different locations covered slightly different periods, so that 44–51 years were included in the simulations (Table 1), which employed the daily mean temperature, $T_{\text{mean}}(t)$, determined by observations made in standard meteorological screens at the height of two metres above ground, and the daily minimum temperature, measured at the height of five centimetres from the soil surface.

2.2 The Simulations

The development of the seedlings after the planting was simulated by means of a simple temperature sum model with the threshold temperature at +5 °C:

$$R(t) = \begin{cases} 0 & T_{\text{mean}}(t) < 5^\circ\text{C} \\ T_{\text{mean}}(t) - 5 & T_{\text{mean}}(t) \geq 5^\circ\text{C} \end{cases} \quad (1)$$

where $R(t)$ = the daily accumulation rate of temperature sum units (day degrees (d.d.) day⁻¹). The risk analysis was based on two parameters: first, the minimum temperature sum of maturation, TS_{min} (d.d.), i.e. the temperature sum required for the growth phase and the subsequent lignification phase (Kellomäki et al. 1992, 1995, Leinonen 1996), and second, the frost hardiness, H (°C), of the seedlings prevailing during the growth and lignification phases. As the frost hardiness was described by a single parameter instead of using a dynamic model variable for it, the changes taking



Fig. 1. The locations of the study. The filled circles indicate the three locations whose long-term temperature data was used in the simulations (Table 1). The unfilled circles indicate two central Finnish locations related to the simulations carried out for Jyväskylä: the model used in the simulations was parameterized on the basis of previous experimental results from a Sulkava provenance of Norway spruce seedlings (Koski and Sievänen 1985), and the parameterization was tested against previous results from a field experiment carried out in Suonenjoki (Luoranen et al. 2005). For details, see Materials and Methods.

place in it during the growth and lignification phases were deliberately neglected. To compensate for this, a sensitivity analysis with a broad range of parameter values was carried out on the value of frost hardiness, H (see section 2.3).

For each year, the values of two variables were obtained for output of the simulations: first, the maturation day, i.e. the day when the temperature sum attained the value of TS_{\min} , and second, the stress temperature, T_{stress} ($^{\circ}\text{C}$), i.e. the lowest of the daily minimum temperatures between 1 August and the maturation day. Frost damage was considered to occur in the years when the daily minimum air temperature dropped below the frost hardiness H on any day between 1 August and the maturation day, i.e. during the years when

$$T_{\text{stress}} < H \quad (2)$$

Frost damage was also considered to occur in the years when TS_{\min} was not attained until the end of October. In the simulations, the seedlings did not complete their maturation before the onset of winter in those cases.

The risk of frost damage for the entire simulation period was determined as the percentage of years with simulated damage occurring. The risk was calculated for 60 consecutive termination dates, the first being 1 June and the last, 30 July.

2.3 The Parameterization of the Model

Unfortunately, the literature offers no data for the value of the minimum temperature sum, TS_{\min} , as such, so that the determination of that parameter value must be based on indirect evidence. Koski and Sievänen (1985) found that in a Sulkava, Finland, provenance of Norway spruce (Fig. 1), the height growth stopped at 700 d.d. in the second year. After growth cessation, further accumulation of temperature sum is required for the lignification of the seedlings; accordingly, for the Sulkava provenance the value of TS_{\min} would be higher than 700 d.d. However, the empirical temperature sum observed by Koski and Sievänen (1985) for growth cessation was obviously higher than the corresponding minimum value. This is because in the case of free height growth, such as that of second-year seedlings of Norway spruce, growth

Table 2. The parameter values used in the simulations. TS_{\min} =minimum temperature sum of maturation, H =frost hardiness during growth and lignification. BE=best-estimate value of the parameter. For TS_{\min} , the low and high values were determined by decreasing and increasing the BE value by ten per cent, respectively. Note that for H , ‘low’ indicates hardy and ‘high’ susceptible seedlings.

	TS_{\min} , d.d.			H , $^{\circ}\text{C}$		
	Low	BE	High	Low	BE	High
Jokioinen	691	768	845	-7	-5	-3
Jyväskylä	630	700	770	-7	-5	-3
Kajaani	756	640	704	-7	-5	-3

cessation does not occur at a constant temperature sum. Rather, as shown by Koski and Sievänen (1985), the required temperature sum decreases with increasing night length, so that in a cool summer, growth stops at a lower temperature sum than in an average summer. Unfortunately, Koski and Sievänen (1985) did not provide data for this relationship in second-year seedlings of Norway spruce. Thus, in the absence of accurate data, we simply assumed that the empirical temperature sum (700 d.d.) reported by Koski and Sievänen (1985) for growth cessation was observed in an average year. We further assumed that the temperature sum required for lignification after growth cessation would be identical to the difference between the minimum temperature sum requirement for growth cessation and the corresponding empirical value observed by Koski and Sievänen (1985). On the basis of this inference, we set 700 d.d., i.e. the value observed by Koski and Sievänen (1985) for growth cessation, as the best estimate of the value of TS_{\min} for the Sulkava provenance. This was also in accordance with Koski’s (1999) suggestion.

For the provenances of the other two locations, Jokioinen and Kajaani, we had no empirical biological data. The best estimate of TS_{\min} for them was determined on the basis of a principle generally known as ‘Linsser’s Law’ (Linsser 1867). According to this principle, the provenances of a given tree species have adapted to their local climates so that the critical temperature

sum required by a given developmental event is a fixed proportion of the mean total temperature sum of the growing season at the native growing site of the provenance. Thus the critical temperature sum is lower in northern than in southern locations. Sarvas (1966a,b, 1967) presented evidence for the principle in the case of the annual regenerative cycle of boreal trees. On the basis of this reasoning, we assumed that the ratio between TS_{\min} and the mean temperature sum of the growing season was the same for the three locations of the present study. For Jyväskylä we had $TS_{\min}=700$ d.d. (Table 2) and the mean temperature sum of the growing season = 1149 d.d. (Table 1); thus the ratio for Jyväskylä was $700 \text{ d.d.} / 1149 \text{ d.d.} = 0.609$. As the mean temperature sums for Jokioinen and Kajaani were 1261 d.d. and 1051 d.d., respectively (Table 1), we got $TS_{\min} = 0.609 \times 1261 \text{ d.d.} = 768 \text{ d.d.}$ for Jokioinen and $TS_{\min} = 0.609 \times 1051 \text{ d.d.} = 640 \text{ d.d.}$ for Kajaani (Table 2).

In order to account for the uncertainties about the value of TS_{\min} , a sensitivity analysis with two optional values of TS_{\min} was carried out. The optional values were determined by decreasing or increasing the best-estimate values by 10 per cent (Table 2).

According to Bigras et al. (2001), growing organs of the conifer species can be killed by temperatures ranging from -2° to -8°C . Vaarataja (1954), on the other hand, observed that young succulent shoots were killed when the temperature was from -3°C to -6°C . The lethal temperature for the current shoot of conifers, then, had to be about -5°C on average, and accordingly we picked this value as the best estimate of H . The determination of the value of the frost hardiness parameter H is complicated by the fact that it does not stay constant over the growth and lignification phases. Rather, the seedlings and trees typically harden slightly towards the end of the summer (Repo 1992). However, as we did not want to complicate our analysis with details of the hardening process, we accounted for them by a sensitivity analysis of the value of the parameter H . In addition to the best-estimate $H = -5^{\circ} \text{C}$, we also carried out the analysis with the values of $H = -3^{\circ} \text{C}$ and $H = -7^{\circ} \text{C}$ (Table 2). The value of $H = -3^{\circ} \text{C}$ obviously underestimates the hardiness, since during the latter part of summer, i.e. during

the time critical for the present study, the hardiness of the seedlings exceeds -3°C . This value was chosen for the purposes of the sensitivity analysis and for illustration.

2.4 Testing the Model Parameterization for the Jyväskylä Location

The best-estimate model parameterization used for Jyväskylä ($TS_{\min} = 700$ d.d., $H = -5^{\circ} \text{C}$, Table 2) was tested against field data independently gathered at the Suonenjoki Research Unit of the Finnish Forest Research Institute ($62^{\circ}39' \text{N}$, $27^{\circ}03' \text{E}$, 142 m asl, Fig. 1) by Luoranen et al. (2005). They did an experimental study of the effect of the storage termination date on the risk of autumn frost damage to freezer-stored Norway spruce seedlings. The experiments were carried out in 2000 and 2001. The storage termination date was varied from 11 May to 17 August in 2000 and from 24 May to 19 July in 2001. The experiment was facilitated by the fact that the thermal conditions during the two years were different: the temperature sum of the growing season was 1265 d.d. in 2000 and 1346 d.d. in 2001 (Luoranen et al. 2005).

In the present study, we used the air-temperature data from Suonenjoki for testing the model parameterization. We used the daily mean temperature, measured in a standard meteorological screen at the height of two metres above ground, and the daily minimum temperature, measured at the height of five centimetres from the soil surface. For each termination date, we calculated the temperature sum (Eq. 1) accumulated from the storage termination date to the first day when the air temperature dropped below -5°C (= the best-estimate value of parameter H). The percentage of damaged seedlings observed by Luoranen et al. (2005) for each termination date was then plotted against the corresponding temperature sum. According to the model's predictions –

- (i) the data plotted for the two years should follow a common pattern, with the data points falling approximately on the same line,
- (ii) the damage percentage should be close to zero in the early termination dates with relatively high temperature sums, and
- (iii) with successively later termination dates, the

damage percentage in both years should start to increase when the corresponding temperature sum is reduced to the value of $TS_{\min}=700$ d.d., and this should happen regardless of the termination date after which this value was attained.

3 Results

3.1 The Parameterization of the Model for Jyväskylä

The results of the independent field test agreed with the model's predictions (i)–(iii) (Fig. 2). With the exception of one outlier for 2001, the data for the two years fell onto a common line. The damage percentage was generally zero or close to zero in the early terminations with relatively high temperature sums. With successively later terminations and lower temperature sums, the damage percentage started to increase on 22 June 2000 and 5 July 2001. Despite the 13-day difference in the termination dates between the two years, the temperature sum accumulation after the terminations was a little below 800 d.d. in both cases. In the next terminations, that is 6 July 2000 and 19 July 2001, the temperature sum accumulation decreased to roughly 600 d.d., and the damage percentage increased to over 20 per cent. These findings show that the value of $TS_{\min}=700$ d.d. used in the present study is close to the minimum in the distribution of TS_{\min} within the Norway spruce populations that have been studied. In practical applications, little if any damage is allowed, so that the value used in the calculations should be near the minimum observed in the population. Altogether, then, the test results of the parameter values against independent field experiments provided support for the best-estimate parameter values ($TS_{\min}=700$ d.d., $H=-5$ °C) used to simulate long-term data in the present study.

3.2 The Maturation and Low-temperature Stress of the Seedlings at Jyväskylä

With the 1 June termination dates, the simulated maturation day varied between 25 July (1972)

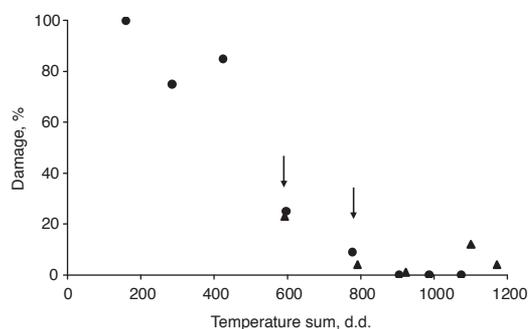


Fig. 2. Results of the empirical test of the best-estimate parameter values used for Jyväskylä ($TS_{\min}=700$ d.d., $H=-5$ °C, Table 2): dependence of the percentage of damaged freezer-stored Norway spruce seedlings in central Finland (Suonenjoki) on the temperature sum accumulated between the day of storage termination and the first day with a minimum air temperature $T_{\min}<-5$ °C in the years 2000 (circles) and 2001 (triangles). The termination dates and the damage data were obtained from Luoranen et al.'s (2005) field experiment, and the temperature sums were calculated in this study. In the critical part of the curve (the arrows), the corresponding termination dates are 22 June 2000 and 5 July 2001 (right-hand arrow) and 6 July 2000 and 19 July 2001 (left-hand arrow). For further explanations, see text.

and 10 September (1962) but fell on the first half of August in most cases (Fig. 3a). The stress temperature was close to zero in most cases (Fig. 3b). The lowest value $T_{\text{stress}}=-3.9$ °C occurred in 1987, when a cool summer postponed the maturation day till September (Fig. 3a). The stress temperature did not drop below -5 °C in any year (Fig. 3b), so that no simulated autumn frost damage occurred with the 1 June termination dates.

Terminating the storage one week later, on 8 June, postponed the average maturation day till mid-August (Fig. 4a). The range of maturation days also widened, so that in 1962 the maturation day was reached only on 21 September and in 1987 as late as 6 October (Fig. 4a). The stress temperature was again near zero in most cases, but in three years it dropped below -5 °C: in 1962 the $T_{\text{stress}}=-5.6$ °C, in 1984 the $T_{\text{stress}}=-5.4$ °C,

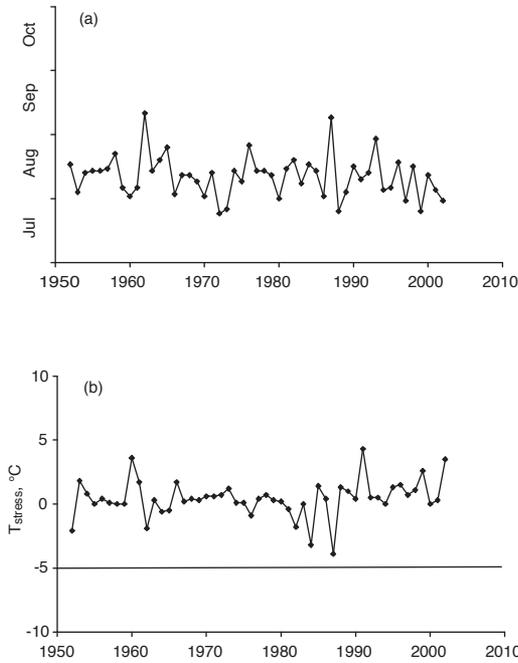


Fig. 3. The simulated development and autumn frost damage of freezer-stored Norway spruce seedlings at the Jyväskylä location (Fig. 1) after storage termination on 1 June in each of the years 1952–2002. (a) The maturation day, i.e. the day when the temperature sum calculated from the termination date attained the value of $TS_{min} = 700$ d.d., which was required for completing the growth and lignification phases. (b) The stress temperature T_{stress} = the lowest of the daily minimum temperatures occurring each year between 1 August and the maturation day. The frost hardness assumed during the growth and lignification phases ($H = -5$ °C) is marked with a horizontal line. T_{stress} did not drop below H during any year, so that no frost damage occurred in the simulation.

and in 1987 the $T_{stress} = -6.6$ °C (Fig. 4b). In these three years, simulated frost damage took place.

With the 15 June termination dates, the average maturation day was in late August (Fig. 5a). There were four exceptional years with a later-than-usual maturation day, including 1987, when the minimum temperature sum for maturation was not attained until the end of October, so that the simulated seedlings did not mature before

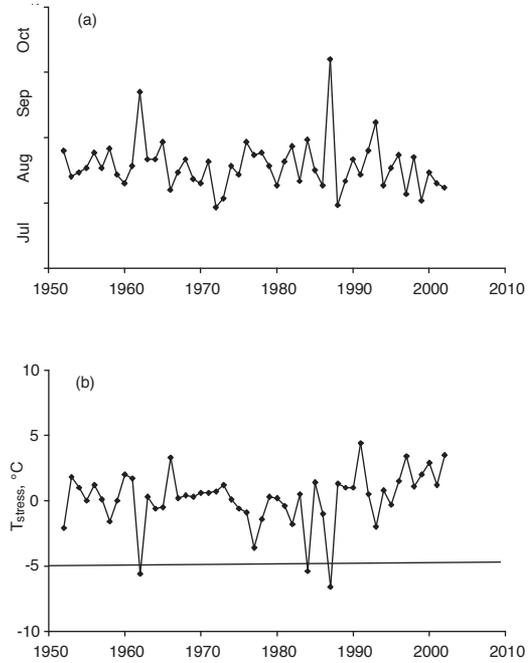


Fig. 4. As in Fig. 3, except that the termination date each year was 8 June. Frost damage occurred in three years of the simulated period.

the onset of winter. The stress temperature was still near zero in most cases, but the number of damage years with $T_{stress} < -5$ °C now amounted to five (Fig. 5b).

Terminating the storage on 22 June postponed the average maturation day till the beginning of September. In one year the maturation day was in early October, and in seven years the minimum temperature sum for maturation was not attained until the end of October (Fig. 6a). The number of damage years with $T_{stress} < -5$ °C rose to ten, even though in most years T_{stress} was still near zero (Fig. 6b).

With the 1 July termination dates, the minimum temperature sum for maturation was not attained until the end of October in 16 years, and among the other years the stress temperature T_{stress} dropped below -5 °C in 12 years (data not shown). Simulated frost damage thus occurred in 28 years, but even with this late termination, there were 23 years free of simulated frost damage.

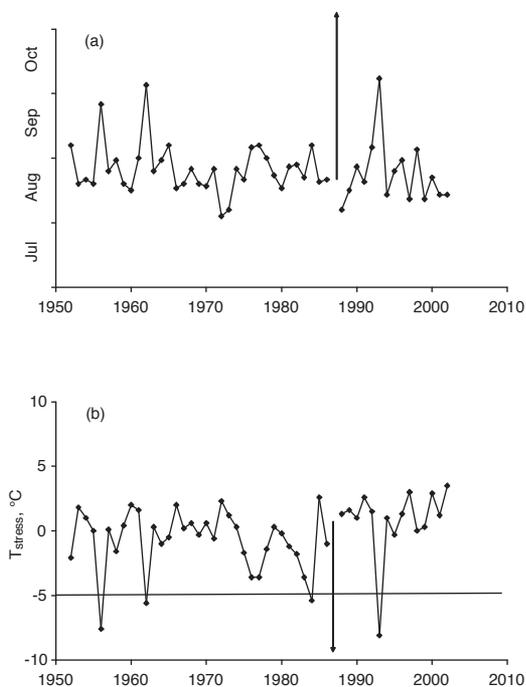


Fig. 5. As in Fig. 3, except that the termination date each year was 15 June. The missing values in the data marked with arrows indicate the year (1987) when the temperature sum $TS_{min}=700$ d.d. was not attained until the end of the simulation (October 31), i.e. the year when the simulated seedlings did not mature before the onset of winter. Frost damage occurred in five years of the simulated period.

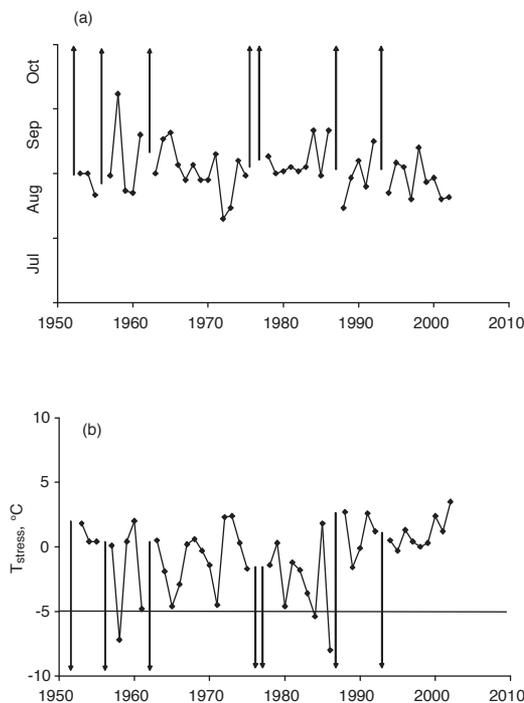


Fig. 6. As in Fig. 3, except that the termination date each year was 22 June. The missing values in the data marked with arrows indicate the seven years when the temperature sum $TS_{min}=700$ d.d. was not attained at the end of the simulation (October 31), i.e. when the simulated seedlings did not mature before the onset of winter. Frost damage occurred in ten years of the simulated period.

3.3 The Risk of Autumn Frost Damage at the Three Locations

3.3.1 The Best-estimate Values of the Parameters

At Jyväskylä, the risk of frost damage was zero in the 1–5 June terminations (Fig. 7a). With later terminations, the risk increased almost linearly until 22 June, when it reached the 20 per cent level. With terminations done on 25 June or later, the risk started to increase at a considerably higher rate than earlier (Fig. 7a).

At Jokioinen, a slight risk of frost damage (2 per cent) was observed even in the earliest terminations (Fig. 8a). This was caused by a single

event of night frost, with the temperature below -5 °C, occurring before the date of maturation. Otherwise, the risk curve is almost identical to that for Jyväskylä, reaching the 20 per cent level on 21 June (Fig. 8a).

At Kajaani, too, a frost-damage risk of 2 per cent was observed as early as the 1 June terminations (Fig. 9a). There, however, the risk stayed at its initial low level until 13 June. With later terminations, the risk level of 20 per cent was reached on 26 June (Fig. 9a).

3.3.2 Sensitivity Analyses of the Parameters

The results show that the simulated risk of autumn

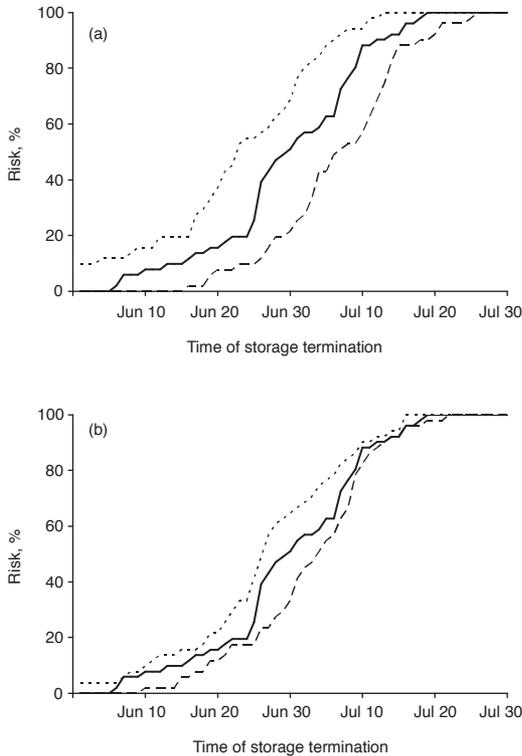


Fig. 7. The simulated dependence of the risk of autumn frost damage on the storage-termination date of freezer-stored Norway spruce seedlings at the Jyväskylä location in 1952–2002 (Fig. 1, Table 1). The risk was determined as the percentage of years when frost damage occurred in the simulation (for details, see Material and Methods and Figs. 3–6). In figures 7 (a) and 7 (b), the thick continuous lines denote the risk calculated from the best-estimate values of the two model parameters (Table 2). The thin dotted lines indicate simulations with the high value and the thin dashed lines, simulations with the low value of the analysed parameter (Table 2). Fig. 7 (a) presents the sensitivity analysis of the minimum temperature sum of maturation, TS_{\min} , and Fig. 7 (b), that of the frost hardness during the growth and lignification phases, H .

frost damage was sensitive to the value of the minimum temperature sum, TS_{\min} , that was used in the simulations (Fig. 7a–9a). At Jyväskylä, for instance, an increase of 10 per cent in the parameter value speeded up the attainment of the 20 per cent risk level by 10 days, from 22 June

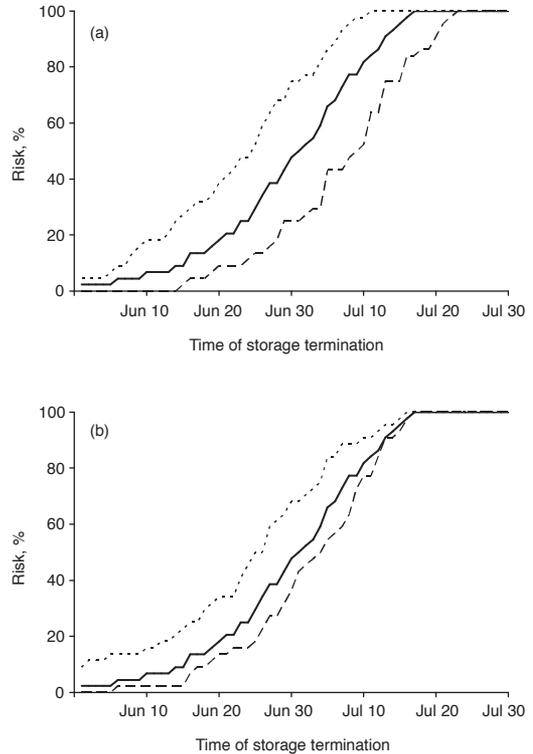


Fig. 8. As in Fig. 7, except that the simulations are for the Jokioinen location in 1959–2002 (Fig. 1, Tables 1 and 2).

to 12 June, and a corresponding decrease in the parameter value delayed the attainment by six days, from 22 June to 28 June (Fig. 7a).

In contrast, the sensitivity of frost damage risk to the value of frost hardness (H) turned out to be relatively low (Figs. 7b–9b). Even so, the results obtained at Jokioinen with $H = -3$ °C indicated considerably higher risks than the other values of H (Fig. 8b). Obviously, however, this theoretical result of the sensitivity analysis does not reflect a real risk to the seedlings (see Material and Methods).

4 Discussion

Due to various uncertainties, the results of the present study should be treated with caution. The development of the seedlings was simulated by

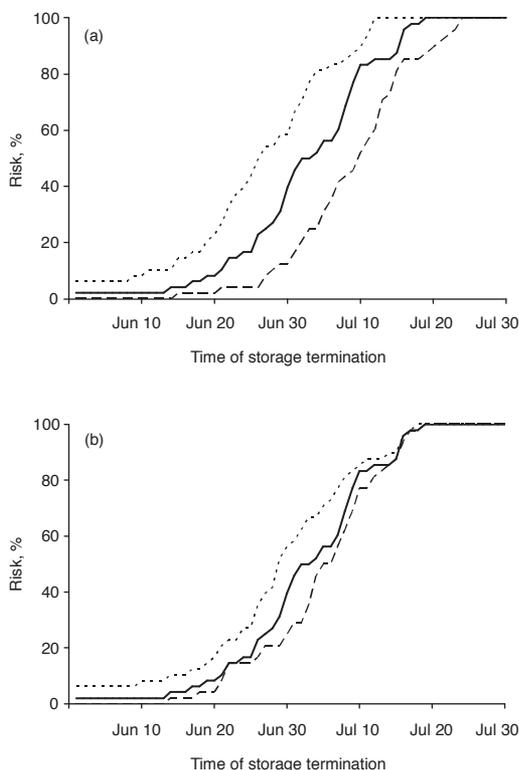


Fig. 9. As in Fig. 7, except that the simulations are for the Kajaani location in 1952–1999 (Fig. 1, Tables 1 and 2).

means of a simple temperature sum model, where the effects of night length on growth cessation and hardening of the seedlings (Dormling et al. 1968, Aronsson 1975, Christersson 1978, Koski and Sievänen 1985, Zhang et al. 2003, Partanen 2004), for instance, were not explicitly addressed. However, night length cannot induce growth cessation before a certain phase of the active period is attained, and attaining this phase requires a certain accumulation of temperature sum (Fuchigami et al. 1982). If such a temperature sum requirement did not exist, there would be no problems with late plantings of freezer-stored seedlings. However, as such a requirement does exist, the accumulation of temperature sum was also the focus of the present study. Furthermore, the effects of night length were implicitly addressed in the present study because the joint-factor model of Koski and Sievänen (1985), which synthesises

the effects of night length and temperature sum accumulation on growth cessation, was used in the indirect inference in order to determine the value of the minimum temperature sum of maturation, TS_{\min} .

Day-degree models have been used with several values of the threshold temperature (Wielgolaski 1999). In Finland, the value of $+5\text{ }^{\circ}\text{C}$ has normally been used in ecophysiological studies of trees (Sarvas 1967, Hari and Häkkinen 1991), and that was also used in the present study (Eq. 1). It was actually the only possibility, for the value of $+5\text{ }^{\circ}\text{C}$ is the one used in the joint-factor model of Koski and Sievänen (1985). Thus, as Koski and Sievänen's (1985) model was applied in the present study to infer the value of the parameter TS_{\min} , the use of any other value than $+5\text{ }^{\circ}\text{C}$ for the threshold temperature would have made the temperature sum scale used in the present study incomparable with that used in Koski and Sievänen's (1985) study. Actually, all day-degree models with different values for the threshold temperature are piece-wise linear approximations of the real non-linear air-temperature response of the rate of development (Sarvas 1972, Hänninen 2006), but as the real physiological non-linear response is only rarely available, one has to resort to the use of the day-degree approximations.

The parameter values were based on indirect inference, as no direct data was available for them. In the cases of Jokioinen and Kajaani in particular, we had to resort to theoretical reasoning. Furthermore, the hardening of the seedlings was regarded as a stepwise process: it was assumed that before the maturation day their frost hardiness equalled a given value (best-estimate $H = -5\text{ }^{\circ}\text{C}$) and that after the maturation day the seedlings were hardy enough to tolerate any temperature occurring at their growing site. In real life, the frost hardening of the seedlings is a gradual process, and frost damage may also occur after the seedlings have matured and hardened to tolerate low wintertime temperatures (Bigras et al. 2001, Luoranen et al. 2008). Furthermore, the temperature data used in the study were measured in standard meteorological stations. It goes without saying that such data does not account for the micrometeorology of individual forest regeneration sites in the region.

Despite the shortcomings, the study provided valuable information on the topic. The shorten-

ing of the thermal growing season is a real-life problem for planting freezer-stored seedlings in early summer (Luoranen et al. 2005). For examining this phenomenon, a simple temperature sum model may be regarded as a sufficient tool; this notion is supported by the results of the test carried out in the present study with independent data from a previous field experiment (Luoranen et al. 2005, Fig. 2).

This study revealed the great importance of year-to-year variation in the thermal conditions for the risk of frost damage to freezer-stored seedlings. At Jyväskylä, for instance, the risk of frost damage started to increase when the storage termination was delayed by just a few days from the beginning of June (Fig. 7). Yet our calculations revealed periods of several years without any frost damage occurring even if the termination took place as late as 22 June. One such period was from the mid-1960s to the mid-1970s (Fig. 6b). Field experiments carried out in all those years would suggest that termination on 22 June involves no risk of autumn frost damage, even though there is an obvious risk, of approximately 20 per cent, of frost damage occurring. Due to the aforementioned uncertainties, it is not possible to determine the risk exactly, but for the practical forester in the Jyväskylä region it is enough to know that with termination on 22 June, frost damages will probably occur every fifth year. This rule of thumb needs to be revisited if the micrometeorology of the regeneration site is exceptional. Whether this is the case can often be inferred from previous experiences and the geomorphology of the site. At frost-prone sites the risks are considerably higher than those indicated in the present study.

The sensitivity analyses of the present study revealed that the assessment of the risks of using freezer-stored seedlings was sensitive to the thermal requirement of the seedlings (Figs. 7a–9a) but much less so to the details of the frost hardiness of the seedlings (Figs. 7b–9b). These findings suggest that the critical issue in using freezer-stored seedlings in plantings is whether a sufficient temperature sum accumulates after the storage termination before the end of the thermal growing season. The detailed dynamics of the hardening process play a smaller role. After maturation, and even during it, increasing night length and decreasing air temperature cause the

seedlings to harden (Aronsson 1975, Christerson 1978, Kellomäki et al. 1992, 1995, Leinonen 1996). Though these processes are crucial for the climatic adaptation of forest trees and also for several issues in practical forestry, such as the assessment of the need to protect seedlings at nurseries from autumn frost, they play a minor role in the assessment of the risk of autumn frost damage to freezer-stored seedlings used in early summer plantings.

The present simulation results accord with the available empirical data from field experiments. Luoranen et al. (2005) found autumn frost damage occurring when freezer storage of the seedlings was terminated after mid-June in 2000 and the first autumn frosts came at the beginning of September. On the other hand, they also observed that in 2001, when the first autumn frosts did not occur until the end of September, the percentages of damaged seedlings were much lower even with the July terminations. These findings were further quantified in the present study, where Luoranen et al.'s (2005) field data were used for testing the parameterization of the model. The results of the independent test provided support for the model and its parameterization for the study (Fig. 2). Considering the inconclusive background of the parameter values (see Material and methods), the results of the independent test greatly improved the reliability of the simulation results calculated for Jyväskylä (Figs. 3–7).

The computational results of the present study may also be used to examine the results of field experiments if sufficient temperature data for the experimental site is available. Assume, for instance, that severe autumn frost damage occurred after a 15 June storage termination. The method of the present study could then be used to examine how common the thermal conditions of that year were at the site. The occurrence of severe damage does not necessarily imply a recommendation not to terminate the storage on 15 June if the computational analysis reveals that the thermal conditions inducing frost damage that year were rare at the site. Similarly, even several years with no damage after termination on a given day do not necessarily imply a recommendation to terminate the storage on that day if the computational analysis reveals that the thermal conditions were exceptionally favourable in those years.

In the long run, climatic warming may push back the latest possible storage terminations. Following the approach that is nowadays frequently used in studies assessing the effects of climatic warming on the annual cycle of forest trees (Cannell 1985, Kramer 1994, Linkosalo et al. 2000, Hänninen 2006), it would be quite straightforward to introduce any warming scenario into the computations carried out in the present study. This is not recommended, however, because the time spans of climatic warming and forest regeneration are different. In the former the time span is decades, whereas for the topic of the present study, i.e. the use of freezer-stored seedlings, the critical time span was the year-to-year variation in the thermal conditions over just a few years ahead.

In conclusion, the present study revealed and quantified the great effect of year-to-year variation in the growing season's thermal conditions on the risk of autumn frost damage to freezer-stored Norway spruce seedlings. Considered together with earlier results from field experiments, the present results suggest that at an average forest regeneration site in central Finland (such as Jyväskylä), storage terminations on 15 June and 22 June involve autumn frost damage every tenth and every fifth year, respectively. The damage is not necessarily lethal, but at least it reduces growth and predisposes the seedlings to secondary damage. At frost-prone sites the plantings should be carried out as early as the spring climatic conditions allow. For the other two regions addressed in the present study, no data from field experiments were available for testing the parameterization of the model. The results obtained for those regions, then, should be considered at this stage mainly as a contribution to the sensitivity analysis rather than a solid basis for recommendations for forest regeneration. The sensitivity analysis revealed the great effect of the temperature sum requirement of maturation on the risk of autumn frost damage, thus pinpointing the need for experimental studies addressing this ecophysiological trait of the seedlings.

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