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# Autumn frost hardiness in Norway spruce plus tree progeny and trees of the local and transferred provenances in central Sweden

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**Summary** Reforestation with provenances from locations remote from the planting site (transferred provenances) or the progeny of trees of local provenances selected for superior form and vigor (plus trees) offer alternative means to increase yield over that obtained by the use of seed from unselected trees of the local provenance. Under Swedish conditions, Norway spruce (*Picea abies* (L.) Karst.) of certain transferred provenances generally has an advantage in productivity relative to the local provenance comparable to that of progeny of plus trees. The aim of this study was to explore the extent to which productivity gains achieved by provenance transfer or the use of plus tree progeny are associated with reductions in autumn frost hardiness, relative to that of trees of the local provenance. In a field trial with 19-year-old trees in central Sweden, bud hardiness was tested on four occasions during the autumn of 2002. Trees of the local provenance were compared with trees of a south Swedish provenance originating 3° of latitude to the south, a Belarusian provenance and the progeny of plus trees of local origin. The Belarusian provenance was the least hardy and the local provenance the most hardy, with plus tree progeny and the south Swedish provenance being intermediate in hardiness. Both the Belarusian provenance and the plus tree progeny were significantly taller than trees of the other populations. Within provenances, tree height was negatively correlated with autumn frost hardiness. Among the plus tree progeny, however, no such correlation between tree height and autumn frost hardiness was found. It is concluded that although the gain in productivity achieved by provenance transfer from Belarus was comparable to that achieved by using the progeny of plus trees of the local provenance, the use of trees of the Belarus provenance involved an increased risk of autumn frost damage because of later hardening.

*Keywords: Belarus, electrolyte leakage, frost tolerance, Picea abies, tree breeding.*

## Introduction

The source of seed for reforestation can have a marked impact on the performance of the resulting stand. To achieve high survival and avoid climate-induced damage, the growth rhythm of the trees needs to be adapted to the local climate. Often, reforestation is undertaken either with trees of a provenance remote from the planting site (transferred provenance) or with the progeny of trees of the local provenance that have been selected for superior form and vigor (plus trees), with the aim in either case being to increase yield relative to that possible with the local provenance. However, anticipated gains in productivity by these means may be offset by damage resulting from greater early summer or autumn frost.

Norway spruce (*Picea abies* (L.) Karst.) is the most commonly planted tree species in Sweden (Anonymous 2004). A north- to northwest-ward transfer of Norway spruce seed sources has been recommended in Sweden to increase yield and reduce spring frost damage. Increased yields by means of provenance transfers have been confirmed in several studies (Langlet 1960, Rosvall and Ericsson 1981, Persson and Persson 1992, Skrøppa and Magnussen 1993). Bud break is usually later in material derived from north-transferred provenances than in local provenances (Worrall 1975). Belarusian provenances, in particular, are known to break bud later when grown in Sweden, and they thus tend to be less affected by early summer frosts than Scandinavian provenances (Hannerz 1994). However, the increase in yield achieved by the use of north-transferred provenances is generally accompanied by delays in shoot growth cessation and increased risk of autumn-frost damage (Langlet 1960, Persson and Persson 1992, Skrøppa and Magnussen 1993).

Stem volume growth of plus tree progeny is estimated to be approximately 10% greater than that of the local provenance (Rosvall et al. 2001). Similar yield increases have been claimed for stands established with north-transferred provenances.

Non-juvenile plus tree progeny de-harden slightly later in spring than trees of the provenance local to the planting site, but do not differ in needle frost hardiness in autumn (Westin et al. 2000*a*). However, mitotic bud activity ceases later in autumn in plus tree progeny than in trees of the local provenance (Westin et al. 2000*b*), indicating that the formation of needle primordia, which is an important determinant of the length of the following year's shoot, continues later in the autumn in the plus tree progeny. It has also frequently been observed that young seedlings of Norway spruce plus tree progeny cease growth and harden later in autumn than seedlings of the local provenance (Johnsen and Apeland 1988, Dæhlen et al. 1995, Hannerz and Westin 2000).

The main objectives of this study were to determine to what extent the superior growth in central Sweden of the progeny of plus trees of local origin and north-transferred provenances, relative to that of the unselected local provenance, is associated with reduced autumn frost hardiness. We examined material from a 19-year-old Norway spruce plantation that included stands of the local provenance, north-transferred provenances, and progeny of plus trees of local origin. We tested the hypotheses that: (1) the north-transferred provenances and progeny of plus trees of local origin undergo frost hardening of buds later in the autumn than unselected trees of the local provenance; and (2) the time of autumn bud hardening is associated with height growth in trees of the local provenance, but that this relationship is weaker in plus tree progeny.

## Materials and methods

### *Field experiment and material*

Two-year-old container-grown seedlings were planted in May 1986 in a trial located at 60°03′ N, 18°29′ E, 15 m a.s.l., about 80 km north of Stockholm (S22F842B4 Forsbol) on a flat, fertile site (site index G32 according to Hägglund and Lundmark 1981) with a thin peat cover. The site is considered to be frost-prone. The overall survival rate in the trial was 86% in autumn 2000.

The study material was separated into four groups. (1) Progeny of 10 families selected for superior form and yield that originated in central Sweden (the counties of Värmland, Närke and Dalarna, 59°37′–61°42′ N, mean 60°23′ N). Seed was collected after open pollination of grafted trees in a seed orchard (453-SörAmsberg) located in the center of the area from which the plus trees originated (plus tree progeny). (2) Progeny of unselected trees from four natural stands in central Sweden (59°51′–61°05′ N, mean 60°24′ N) (the local provenance). (3) Progeny from unselected trees in three natural stands in southern Sweden (56°33′–58°34′ N, mean 57°29′ N) (south Swedish provenance). (4) Progeny of unselected trees of three natural stands in Belarus (54°18′–56°30′ N, mean 55°17′ N) (Belarusian provenance).

Trees were planted in single-tree plots with one replicate randomly assigned to each of 20 blocks. For this study, we used a total of 100 trees distributed over nine of the original 20 blocks in the field experiment. Five trees were randomly selected in each of the following: ten plus tree families, four local stands, three south-Swedish stands and three Belarusian stands. In the statistical analysis, the trees in blocks 7–9 were considered to belong to the same block, making seven blocks in total.

### *Sampling and artificial freeze testing*

Tree heights and survival were recorded in the autumn of 2000, when the trees were 17 years old. Twigs were sampled for freeze testing on August 21, September 11, October 2 and October 30, 2002. On each sampling date, 10 current-year twigs were cut from the three uppermost whorls of each tree and placed separately in plastic bags that were sealed and stored on ice in a cooler. The cooler was transported by air the same day to the laboratory at Skogforsk's field station at Ekebo 55°58′ N, 13°54′ E, where the sampled twigs were stored for 1–2 days at +5 °C in darkness until freeze tested. The twigs from each tree were divided into five groups: one was held at +5 °C as a control; the others were frozen to different temperatures selected according to the results of pre-tests on a small sample of twigs collected a week before the main sampling.

Twigs, still sealed in plastic bags, were placed in each of four chest freezers (Tefcold A/S, Denmark) in which the temperature was lowered at 5 °C $h^{-1}$ until the test temperature was reached. The test temperature was maintained for 2 h and the temperature was then increased at 5 °C $h^{-1}$ to +5 °C.

Buds of the test twigs were excised and an incision was made just above the uppermost needle base, at the bottom of the lower bud scales (just below the embryonic shoot). Two buds from each tree and test temperature were placed separately in plastic vials containing 15 ml of deionized water and incubated on a gravity shaker at +5 °C for 48 h. The vials were then warmed to room temperature, and electrolytic conductivity of the water measured with a Schott CG 853 conductivity meter (Schott, Mainz, Germany). After the first assessment of conductivity, the vials were placed in a water bath and boiled for 1 h. After cooling to room temperature, the vials were again placed on a gravity shaker at +5 °C for 48 h, warmed to room temperature, and the conductivity remeasured.

Frost hardiness was estimated by an index expressing the relative (percent) injury resulting from freezing to temperature $t$. The index was calculated for each sampled tree and test temperature according to Flint et al. (1967): $I_t = 100(R_t - R_0)/(1 - R_0)$, where $I_t$ = Index of Injury, in this study referred to as "relative injury," $R_t = L_t/L_k$; $R_0 = L_0/L_d$, where $R_t$ is relative conductivity of the sample exposed to temperature $t$; $R_0$ is relative conductivity of the unfrozen control sample; $L_t$ is conductance of leachate from the sample frozen at temperature $t$; $L_k$ is conductance of leachate from the sample frozen at temperature $t$ and then heat-killed; $L_0$ is conductance of leachate from the unfrozen sample; and $L_d$ is conductance of leachate from the corresponding heat-killed, unfrozen control sample.

### *Statistical analyses*

Relative injury was analyzed separately for each sample according to Model 1:

$$y_{ijkl} = \mu + \text{group}_i + \text{block}_j + \text{temp}_k + e_{ijkl} \quad (1)$$

where $y_{ijkl}$ = individual observation of each trait (relative injury and tree height); μ = overall mean; $\text{group}_i$ = fixed effect of genetic group $i$ ($i$ = 1, … 4); $\text{block}_j$ = fixed effect of block $j$ ($j$ = 1, … 7); $\text{temp}_k$ = fixed effect of freezing temperature ($k$ = 1, … 4); and $e_{ijkl}$ = a random residual term.

A corresponding model (Model 2) excluding the temperature factor was used to analyze differences in tree height:

$$y_{ijk} = \mu + \text{group}_i + \text{block}_j + e_{ijk} \quad (2)$$

Differences between groups were analyzed with Tukey's test.

The relationships between relative injury and tree height were assessed by the calculation of Pearson product-moment correlations.

*Temperature in the field trial*

Temperature in the field was monitored with a Tinytag sampler at a height of 1 m in two openings in the field trial. The first part of autumn was relatively warm and the first night with temperatures below 0 °C occurred on September 2 (Figure 1). Several nights with temperatures below –5 °C occurred around September 25, between the second and third samplings. The lowest temperature (–16 °C) occurred on October 20.

## Results

Bud hardiness increased over the experimental period. On August 21, buds from all groups of trees were damaged by freezing to –10 °C, whereas on October 30, there was minimal damage even after freezing to –45 °C (Figure 2). The effects of group, block and temperature on the relative injury index were significant ($P < 0.05$) on all occasions, except October 30 when the group effect was insignificant ($P = 0.079$; Table 1). The Belarusian provenance was significantly less hardy than the local provenance on all occasions except October 30 (Table 2). The south Swedish provenance and the progeny of plus trees of local origin were intermediate in hardiness, and could not be distinguished from one another. Plus tree progeny were significantly less hardy than the local provenance on all occasions up to October 2, and significantly more hardy than the Belarusian provenance on August 21 and October 2. The south Swedish provenance tended to be less hardy than the local provenance, but the difference was significant only on September 11. The pattern was reversed on October 30, with the Belarusian provenance being the most hardy and the local provenance the least hardy; however, injury on this date was slight, and most trees remained undamaged after freezing to –45 °C. The Belarusian provenances and the plus tree progeny were significantly taller than the local provenance (Table 2), whereas the south Swedish provenance was of intermediate height.

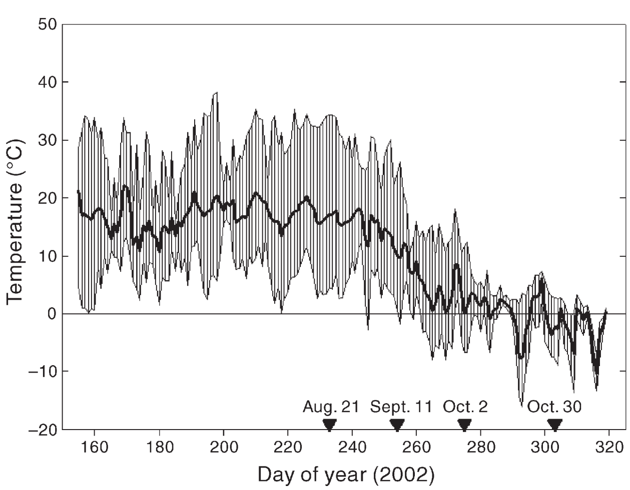


Figure 1. Daily maximum, mean and minimum temperatures during autumn 2002. The arrows indicate the four dates of freeze testing.

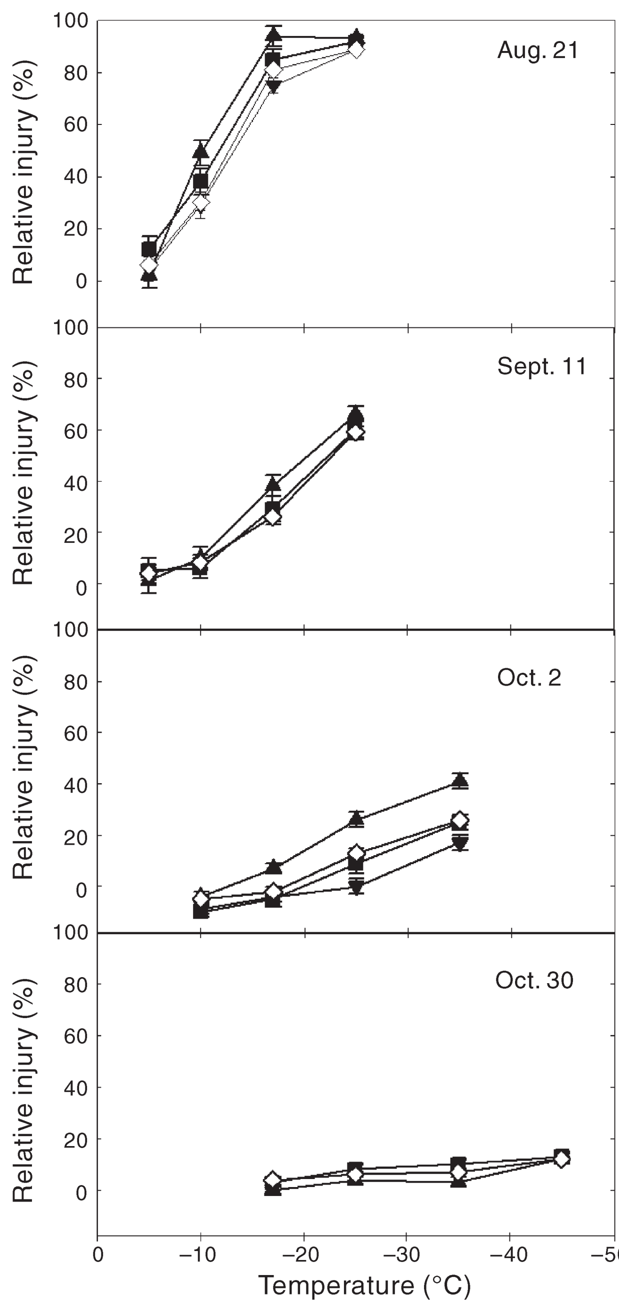


Figure 2. Relative injury for the four test dates and test temperatures (▲ = Belarusian stands, $n = 15$; ■ = south-Swedish stands, $n = 15$; ▼ = local stands, $n = 20$; ◇ = plus trees, $n = 50$). Vertical bars indicate standard errors.

Table 1. Summary of ANOVA of the model $y_{ijkl} = \mu + group_i + block_j + temp_k + e_{ijkl}$, where $y$ = relative injury at each sampling occasion), group = genetic group (local provenance, south Swedish stands, Belarusian provenance or plus tree progeny) and temp = freezing temperature.

| Factor | df | ms | $F$ | $P$ |
|---|---|---|---|---|
| *Relative injury on August 21* | | | | |
| Group | 3 | 1600.42 | 5.48 | 0.0011 |
| Block | 6 | 671.65 | 2.30 | 0.0342 |
| Temp | 3 | 172844.42 | 591.38 | < 0.0001 |
| Error | 387 | 292.27 | | |
| *Relative injury on September 11* | | | | |
| Group | 3 | 1695.07 | 6.02 | 0.0005 |
| Block | 6 | 2057.79 | 7.31 | < 0.0001 |
| Temp | 3 | 64388.42 | 228.75 | < 0.0001 |
| Error | 383 | 281.48 | | |
| *Relative injury on October 2* | | | | |
| Group | 3 | 2359.38 | 13.25 | < 0.0001 |
| Block | 6 | 446.88 | 2.51 | 0.0214 |
| Temp | 3 | 15578.15 | 87.51 | < 0.0001 |
| Error | 386 | 178.02 | | |
| *Relative injury on October 30* | | | | |
| Group | 3 | 167.03 | 2.28 | 0.079 |
| Block | 6 | 227.16 | 3.10 | 0.0056 |
| Temp | 3 | 1007.29 | 13.74 | < 0.0001 |
| Error | 385 | 73.31 | | |

Table 3. Pearson product-moment correlations between relative injury and tree height. Correlations computed for provenance means ($n$ = 10) and plus tree progeny means ($n$ = 10). Significant correlations are in boldface.

| Date | Provenance | Plus trees |
|---|---|---|
| August 21 | 0.47 | 0.43 |
| September 11 | 0.58 | –0.13 |
| October 2 | **0.80** | 0.09 |
| October 30 | –0.53 | 0.10 |

Within the three provenances, the correlation between tree height and relative injury was significant on October 2 (Table 3 and Figure 3), indicating that the tallest trees were the least hardy. For plus tree progeny, the correlation between tree height and relative injury was not significant (Figure 3).

## Discussion

The hypothesis that north-transferred provenances harden later in central Sweden than the local provenance was confirmed. The south Swedish provenance was significantly less hardy than the local provenance on September 11, with a 3 °C difference in critical temperature for frost injury. The north-transferred Belarus provenance was significantly less hardy than the local provenance on all occasions up to October 2. Our results confirm previous observations of differences in autumn hardiness among populations of Norway spruce. Beuker et al. (1998) showed that provenances from latitude 60° N harden about a month later than provenances from latitude 66–67° N. Similarly, Westin et al. (2000*a*) found that populations originating from latitude 58–63° N harden later, on average, than populations originating from latitude 63–68° N. Hardiness is negatively related to growth activity, as demonstrated by Westin et al. (2000*b*), who showed that southern populations are mitotically active later in the autumn than northern populations.

Shoot elongation continues until later in the year in southern populations than in northern populations of Norway spruce (e.g., Skrøppa and Magnussen 1993). Prolongation of growth and consequent reductions in autumn frost hardiness following northward transfer have been demonstrated in many other species: e.g., Sitka spruce (*Picea sitchensis* (Bong.) Carr.) (Cannell and Sheppard 1982), inland Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) (Rehfeldt 1983), Scots pine (*Pinus sylvestris* L.) (Persson and Stähl 1990) and western hemlock (Kuser and Ching 1980).

The hypothesis that plus tree progeny harden later in the autumn than unselected trees of the local provenance was confirmed. The plus tree progeny were significantly less hardy on September 11 and October 2 than trees of the local provenance. The hardiness of the plus tree progeny was comparable with that of the south Swedish provenance, located on average 3° of latitude south of the local stands from which the plus trees originated. This difference is consistent with results obtained with 1-year-old Norway spruce seedlings, where growth cessation and autumn frost hardiness of plus tree progeny corresponded to that of natural stands located 1–2° of latitude south of the origin of the plus trees (Hannerz and Westin

Table 2. Least square means of relative injury and tree height from Model 2. Within a column, values followed by the same letter are not significantly different at $P > 0.05$.

| Group | Relative injury (%) | | | | Tree height (cm) |
|---|---|---|---|---|---|
| | Aug. 21 | Sept. 11 | Oct. 2 | Oct. 30 | |
| Local provenance | 48.1 b | 18.8 b | 4.3 c | 8.7 b | 298.8 b |
| South Swedish provenance | 55.7 ab | 26.8 a | 8.0 bc | 8.5 ab | 334.3 ab |
| Belarusian provenance | 58.6 a | 30.4 a | 18.5 a | 5.1 a | 440.9 a |
| Plus tree progeny | 50.7 b | 26.1 a | 11.1 b | 7.1 b | 426.1 a |

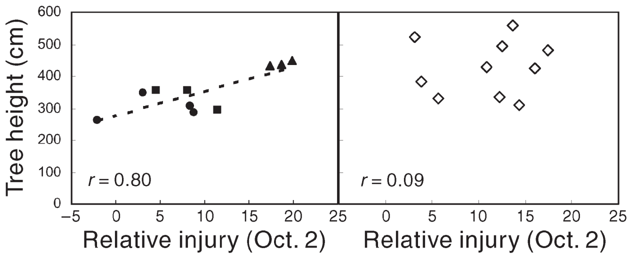


Figure 3. Pearson product-moment correlation between relative injury on October 2 and tree height for stands (left diagram, $n = 10$) and plus tree progeny (right diagram, $n = 10$). Symbols: ▲ = the Belarusian provenance; ■ = the south Swedish provenance; ▼ = the local provenance; and ◇ = the plus tree progeny.

2000). In their study on mature trees, Westin et al. (2000*a*) detected no differences in the autumn hardening of needles between selected plus trees and natural stands from the same latitude. Despite the absence of differences in hardiness, mitotic activity continued later into the autumn in the buds of the plus trees than in buds of the local provenance, which is likely indicative of reduced bud hardiness (Westin et al. 2000*b*).

The hypothesis that late autumn hardening contributes more to the superior growth of north-transferred provenances than that of selected plus trees was partly confirmed. Plus tree progeny and the Belarusian provenance were similar in height, and over 40% taller, on average, than the local provenance, yet the Belarusian provenance was significantly less hardy than the plus tree progeny on August 21 and October 2. The hardiness of the plus tree progeny corresponded to that of the south Swedish provenance, although the south Swedish provenance was 20% shorter than the plus tree progeny, and 10% taller than the local provenance. Our results support the hypothesis that correlation between relative frost injury and height growth is weaker in plus tree progeny than in unselected trees of any particular provenance. However, because the south Swedish and Belarusian provenances fall into distinct groups with respect to relative frost injury (Figure 3), we cannot exclude the possibility that factors other than late autumn hardening contribute to the superior growth of the Belarusian provenance. At the end of October, trees of the Belarusian provenance were hardier than the plus tree progeny, and the local provenance was the least hardy. However, the differences were small, and most trees sustained little damage after freezing to −45 °C.

Height growth in this and other studies indicated that transferring populations a modest latitudinal distance does not reduce their growth. Nevertheless, the late autumn hardening of the Belarusian provenance implies an increased risk of autumn frost damage to buds, which could lead to an increased percentage of stem forking.

Westin (2000) concluded that differences in both growth and hardiness between a local population and plus trees selected from the same population reflect differences in the duration of growth. However, our results and those of others indicate that additional factors are partly responsible for the superior growth of plus tree progeny. For example, studies with Norway spruce have shown that selection for growth within families has little or no effect on either the duration of growth or autumn frost hardiness (Skrøppa and Magnussen 1993, Ekberg et al. 1994, Johnsen and Østreng 1994). Furthermore, the relationship between time of bud set and frost hardiness, which is usually strong among population means, is weaker among families from the same population (Johnsen and Skrøppa 2000). Results similar to ours were obtained in a study with western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), in which local selected material was found to be as frost hardy as local unselected material, but north- transferred populations were less hardy (Hannerz et al. 1999*a*). The growth of the locally selected and north- transferred material was similar.

An alternative possible explanation for the superior growth of plus tree progeny and north-transferred provenances is that the growth period is extended by an earlier start. However, Westin et al. (2000*a*) found that bud burst was later in plus trees than in unselected populations, whereas in a subsequent unpublished study, they found that bud break occurred 8–13 days later in Belarusian provenances than in local stands. In a study of half-sib families of Norway spruce in trials at various locations in central Sweden, Hannerz et al. (1999*b*) demonstrated a positive correlation between date of bud burst and growth that could be explained partly by late flushing varieties being less prone to frost damage and partly by a positive correlation between late flushing and late growth cessation. Families with late growth cessation can exploit the growing season more fully. We speculate that, in our plus tree progeny, the duration of growth contributes to the observed gain, but that a higher growth rate was more important.

In conclusion, the results show that improvement in yield through northward transfer of provenances from Belarus is accompanied by an increased risk of autumn frost damage. Yield improvement through the use of plus tree progeny may also be associated with an increased risk of autumn frost damage, though the risk may be less than with the use of transferred provenances.

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