Growth Cessation and Autumn-frost Hardiness in One-year-old *Picea abies* Progenies from Seed Orchards and Natural Stands

MATS HANNERZ[1] and JOHAN WESTIN[2]

[1]*The Forestry Research Institute of Sweden, Uppsala Science Park, SE-751 83 Uppsala, Sweden and* [2]*The Forestry Research Institute of Sweden, PO Box 3, SE-918 21 Sävar, Sweden*

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One-year-old seedlings of Norway spruce [*Picea abies* (L.) Karst.] from seed orchards and natural stands were compared with respect to growth cessation and autumn-frost hardiness. The correlation among traits related to growth, growth cessation and frost hardiness on the same plants in two sets of environmental conditions was assessed. Total height, the degrees of shoot lignification and frost hardiness, and the timing of height growth cessation and budset were recorded at two nurseries in central and northern Sweden. Nine seed-orchard seed-lots were compared with seed from 26 natural stands originating from 56° N to 66° N in Sweden. Latitude explained 55–87% of the statistical variation among stands in the analysed traits at the central nursery and 49–84% at the northern nursery. On average, the seed-orchard progeny performed similarly to progeny from natural stands located 1–2° south of the origin of the seed-orchard clones. Reference material representing a geographical gradient was found to be a valuable aid when interpreting the results of growth cessation and frost-hardiness evaluations. *Key words: budset, clinal variation, early test, freeze test, Norway spruce.*

INTRODUCTION

Norway spruce (*Picea abies* (L.) Karst) is the tree species most commonly used for artificial reforestation in Sweden. To meet the needs for improved reforestation material, clonal seed orchards based on phenotypically selected plus-trees have been established extensively, beginning in the late 1950s. To optimize yield and limit the risk of frost damage, there must be a good match between the genetic and physiological characteristics of the seed-orchard material and conditions at the reforestation site. Genetic origin affects the growth rhythm of the plant material and, hence, the risks of frost damage. For example, early budburst increases the risk of late spring frost damage (Langlet 1960) and late growth cessation renders the plants more vulnerable to autumn frost (Krutzsch 1974). Results from provenance trials indicate that Norway spruce can be transferred to regions far from its source at limited risk (Giertych 1976, Persson & Persson 1992). In Sweden a northward transfer of stand seed is commonly motivated by its potential to establish highly productive stands (Rosvall & Ericsson 1981, Anon. 1998), despite the later shoot growth cessation associated with such transfers (Worall 1975, Skrøppa & Magnussen 1993).

Experiences from provenance research can be used to develop guidelines for where to use particular seed-orchard progeny, provided that the growth rhythm of plus-trees, as a group, is fairly equal to that of the mean of the populations from which they were selected. However, the growth rhythm of seed-orchard crops can deviate from that of unselected trees, owing to the differential effects of the parental environment during pollination and seed-ripening (Johnsen & Skrøppa 1996), contamination from background pollen (Paule et al. 1993) and other factors. Year-crops from the same seed orchard can also differ in growth rhythm or frost hardiness owing to annual variation in weather conditions (Kohmann & Johnsen 1994, Daehlen et al. 1995).

Consequently, there are several reasons why the growth rhythms of seed-orchard crops need to be determined. Spring phenology is commonly estimated in terms of the timing of budburst, a trait that is highly heritable and stable over years and test conditions (Worall 1973, Ekberg et al. 1985, Hannerz 1999). The environmental and genetic control of growth cessation in the autumn is more complex, being determined primarily by photoperiod, but also by temperature (Dormling et al. 1968, Christersson 1978). A variety of traits has been employed to rank

Table 1. *Average clonal origin, seed-orchard location and seed weight of seed-orchard seed-lots in the study*

Seed orchard lot/seed yr	Clonal origin		Seed orchard location		Seed weight
	Latitude	Altitude	Latitude	Altitude	1000-grain, g
444-Ön, all clones/1989	57.8	60	60.2	60	7.83
444-Ön, southern clones/1989	58.3	118	60.2	60	8.74
487-Lustnäset/1989	59.0	120	59.6	60	7.44
453-SörAmsberg/1989	60.0	230	60.5	155	7.48
444-Ön, local clones/1989	60.2	41	60.2	60	6.39
128-Grånäs/1989	60.4	370	60.6	155	6.79
31-Högseröd/1989	61.0	400	55.8	115	6.09
31-Högseröd/1990	61.0	400	55.8	115	7.48
26-Jung, northern clones/1989	63.5	340	58.3	70	5.96

genotypes or provenances of Norway spruce in autumn phenology: frost tolerance of young seedlings in laboratory tests (Johnsen & Apeland 1988, Johnsen 1989, Pulkkinen 1993), timing of budset (Krutzsch 1986, Skrøppa 1988), degree of stem lignification (Pulkkinen 1993), degree of lignification of the year-rings (Dietrichson 1969), shoot dry-matter content (Rosvall-Åhnebrink 1985) and shoot elongation pattern (Eriksson & Gagov 1976, Skrøppa & Magnussen 1993). Consistent test results can be obtained by performing the tests under thoroughly controlled and defined conditions, e.g. in growth chambers, or by relating the performance of a provenance or genotype to that of a well-tested reference set. The latter approach is routinely used for assessing the frost hardiness of Scots pine seed crops in Sweden (Andersson 1986). In these tests, the frost hardiness of the tested material is expressed in relation to the hardiness of natural stands along a latitudinal gradient. To the authors' knowledge, a corresponding system for Norway spruce has yet to be developed.

The aim of the study presented here on 1-yr-old Norway spruce seedlings was to compare progeny from seed orchards with progeny from natural stands along a latitudinal gradient, in terms of their timing of growth cessation and frost hardiness.

MATERIALS AND METHODS

The test material consisted of nine open-pollinated seed-lots from well-established grafted clonal seed orchards (SO) (Table 1) and, as references, 26 natural-stand (NS) seed-lots (Fig. 1). The NS seed-lots were part of a gene-bank of autochthonous stands collected in 1983 by the National Board of Forestry in Sweden (Krutzsch 1986). The SO seed-lots were

collected in seed orchards composed of clones (plus-trees selected for superior height) of various origins. The seed orchards can be roughly classified according to clonal origin and seed-orchard location, into four classes: SO with a clonal origin similar to the seed-orchard location (453-SörAmsberg, 128-Grånäs); SO with clones transferred to a southern location (31-Högseröd, 26-Jung); SO with a mixed clonal origin composed of clones collected from a range of locations from Poland in the south to local origins in the north (444-Ön); and SO with clones selected locally but with an uncertain origin, presumably originating in central Europe (487-Lustnäset). In seed orchard 444-Ön, seed was only collected from clones with origins in southern Sweden (southern clones) or from clones with origins similar to the seed-orchard location (local clones). In seed orchard 26-Jung clones with origins in northern Sweden (northern clones) were used.
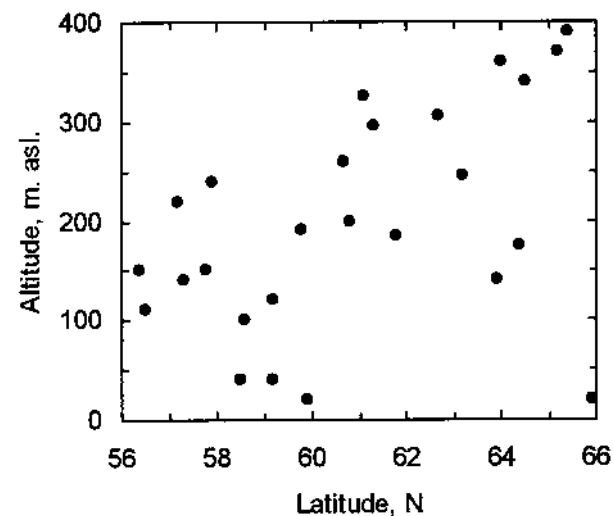

Fig. 1. Origin (latitude and altitude) of the natural stands included in the experiments.
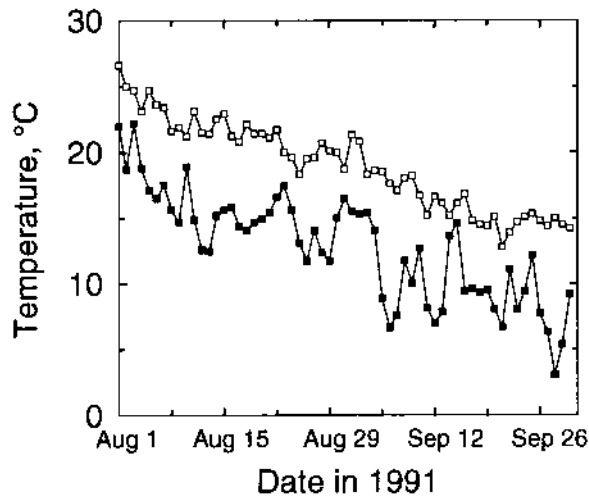
Fig. 2. Daily mean temperatures in the greenhouse at Sävar (□), and outdoors at Brunsberg (■) during August and September, 1991.

The study was performed at the Brunsberg (59.7° N) and Sävar (63.9° N) nurseries. At each of the nurseries the same 26 NS seed-lots were used. Two SO seed-lots were tested only at Sävar (128-Grånäs and 26-Jung). All other seed-lots were tested at both locations. The seeds were sown in peat-filled containers in greenhouses on May 25 (Brunsberg) and May 30 (Sävar) in 1991. The seedlings at Brunsberg were moved outdoors on August 1, while those at Sävar were kept in a greenhouse throughout the test period. During the common greenhouse period regular greenhouse conditions were applied at both locations (temperature approx. 20–30°C). The temperature conditions in August and September are shown in Fig. 2. The seedlings were only exposed to natural day lengths. At both sites there were four replicates, each with an 18-seed plot per SO seed-lot and a six-seed plot per NS seed-lot.

The proportion of seeds that germinated and formed seedlings was 94% at Brunsberg and 80% at Sävar. Germination showed a random pattern; thus, the correlation for frequency of establishment was low between Brunsberg and Sävar ($r = 0.06$). The lowest proportion of established seedlings registered for a single NS seed-lot was 46% at Brunsberg and 54% at Sävar. For the SO material, the corresponding figures were 79% and 76%. Thus, the number of tested seedlings at each nursery was between 11 and 24 for the NS seed-lots and between 55 and 72 for the SO seed-lots.

All seedling traits were measured during their first growing season (Table 2). Seedling height (HEIGHT) was measured at the end of the growing season. Height growth cessation (relative height, RELHT) was measured as the proportion of the final height that was reached by August 13 at the Brunsberg nursery. The frequency of terminal budset was registered on one occasion each at Sävar and Brunsberg (BUDSET). The proportion of the stem that was lignified (LIGNIF) was estimated once at each nursery by measuring the length of the green, non-woody upper part of the stem, in contrast to the non-green (white or brown) woody lower part. The non-green part of the stem was assumed to be more lignified than the green part. Following a period with daily high temperatures of over 20°C, the seedlings at Brunsberg were exposed to a naturally occurring night frost on September 7. The minimum temperature at the seedling level was not recorded, but was estimated to be at least −2°C. The occurrence of damage on the seedlings was registered 17 days later (FROST). An artificial freeze test was performed in Sävar in early October in two batches with two replications in each batch (treated as four replicates in the analysis) when all seedlings were visually lignified. The air temperature was decreased to −20°C at a rate of 5°C h⁻¹, held at −20°C for 3 h and then thawed at a rate of 5°C h⁻¹. Freeze-tested seedlings were thereafter transferred to growth-promoting conditions and, after another 3 weeks, needle damage was classified as follows: 0 = no visible damage; 1, 2, 3, 4 and 5 = 1–19%, 20–39%, 40–59%, 60–79% and

Table 2. *List of traits analysed*

Trait	Description and date of assessment
Brunsberg	
HEIGHT	Total seedling height (24 Sept), mm
BUDSET	Presence of visible bud (29 Aug), 0/1
LIGNIF	Lignified proportion of the stem (29 Aug), %
RELHT	Relative height (height on 13 Aug as a percentage of final height)
FROST	Presence of frost damage (24 Sept), 0/1
Sävar	
HEIGHT	Total seedling height (16 Sept), mm
BUDSET	Presence of visible bud (16 Sept), 0/1
LIGNIF	Lignified proportion of the stem (16 Sept), %
FREEZE	Damage score after freeze-test, transformed with normal scores (7 Oct)

80–99% of the needles discoloured, respectively; and 6 = all needles discoloured (FREEZE).

Damage scores from the freeze test were linearized by transformation to normal-score values (Gianola & Norton 1981), which form a normal distribution with a mean of 0 and a variance of 1 within each of the replicates. To avoid negative values the mean is set to $+5$ standard deviation units, i.e. normal score $+5$.

The effects of seed-lot on each trait were analysed by two linear models. HEIGHT, RELHT, LIGNIF, BUDSET and FROST were analysed using one linear model (1), run separately with data from each of the two sites, and FREEZE was analysed using another linear model (2):

$$y_{ij} = \mu + a_i + b_j + e_{ij} \quad \text{(HEIGHT, RELHT, LIGNIF, BUDSET, FROST)} \quad (1)$$

$$y_{ij} = \mu + a_i + e_{ij} \quad \text{(FREEZE)} \quad (2)$$

where y_{ij} = mean value of seed-lot i in replicate j, μ = overall mean, a_i = fixed effect of seed-lot i, b_j = fixed effect of replicate j, e_{ij} = random residuals, $\sim N(0, \sigma_e^2)$.

Mean values for each seed-lot were estimated as least square means (LSMEANS) by the SAS Procedure GLM (SAS Institute. Cary, NC, USA). Product-moment correlations were calculated between all traits, where significant differences ($p = 0.05$) existed between seed-lot means, using the default settings of the SAS Procedure CORR (SAS Institute, Cary, NC, USA).

The relationship between the effect of NS seed-lots and the latitude of their origin was calculated using the following regression function:

$$y_i = a + b \, (\text{lat}_i + e_i) \quad (3)$$

where y_i = effect of NS seed-lot i, a and b = regression coefficients, lat_i = latitudinal origin of seed-lot i, e_i = random residual, $\sim N(0, \sigma_e^2)$. Models with altitude as an additional independent variable were also tested.

When calculating the regression functions, NS seed-lots from north of 64° N were excluded for BUDSET, FROST and LIGNIF at Brunsberg because by the time of measurement seedlings from these seed-lots had completed budset and lignification, and appeared to be unaffected by the frost.

Similarly, NS seed-lots from south of 58° N were excluded for HEIGHT at Sävar because seedlings from these seed-lots did not appear to have entered
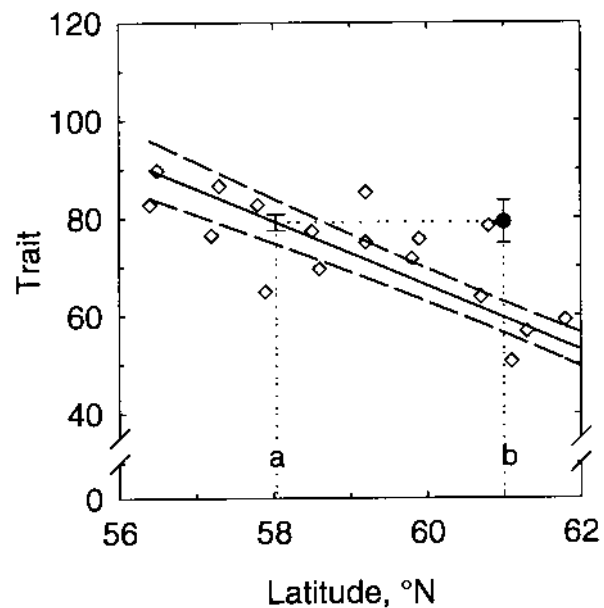

Fig. 3. Example of standardized latitude *a* for a SO seed-lot (●), with the latitudinal origin *b* and the latitude deviation, *a–b*. The regression line of all NS seed-lots (—) and the 95% confidence limits (---) are shown together with mean values of individual NS seed-lots (◇) in the actual range of latitudes. The standard error of the regression function at the standardized latitude and the standard error for the SO seed-lot are indicated by vertical bars.

the growth-cessation phase. Furthermore, NS seed-lots from north of 62° N were excluded for FREEZE at Sävar because seedlings from these seed-lots appeared to be unaffected by the freeze test.

The mean values obtained for the SO seed-lots were used to calculate the "standardized latitude of origin", hereafter referred to as "standardized latitude", based on the regression functions for the NS seed-lots (Fig. 3). The standard error of the regression function, at the standardized latitude, was calculated from the 95% confidence interval of the regression function. Standard errors of the estimated standardized latitudes were obtained by pooling the standard error of the regression function and the standard error of the test materials [eq. (4)]. The upper and lower limits of the standard error were resolved with the regression function (3) to a latitude interval:

$$SE_{est} = \sqrt{(SE_1^2 + SE_2^2)} \quad (4)$$

where SE_{est} = the pooled standard error for the estimated standardized latitude of the test material, SE_1 = standard error for the regression function at

the standardized latitude, and SE_2 = standard error for the test material.

RESULTS

Analysis of variance showed a significant effect ($p < 0.0001$) of seed-lot for all of the tested traits. The effect of replicate was significant ($p < 0.05$) for all traits except for HEIGHT in Sävar, LIGNIF in Brunsberg and BUDSET in Brunsberg. All assessed traits showed pronounced clinal variation with latitude (Fig. 4). Seedlings originating from northern NS seed-lots had shorter stems, ceased height growth earlier and were hardier than those originating from southern NS seed-lots. Latitude explained 82–87% of the statistical variation for traits measured at the

Brunsberg nursery, with the exception of frost damage (55%). Latitude explained a smaller part of the statistical variation for traits measured at the Sävar nursery (49–85%). At Brunsberg, the altitude of the NS seed-lots had significant effects only on HEIGHT, BUDSET and LIGNIF, and increased the coefficient of determination (R^2) by 0.08, 0.03 and 0.03, respectively. Altitude did not significantly affect any of the traits measured at Sävar.

In terms of height and phenology, the SO seed-lots resembled NS seed-lots originating south of the origin of the SO clones (Table 3). The average deviation between the original and standardized latitude was 0.9–1.8° for traits measured at Brunsberg and 1.5–2.3° for traits measured at Sävar.
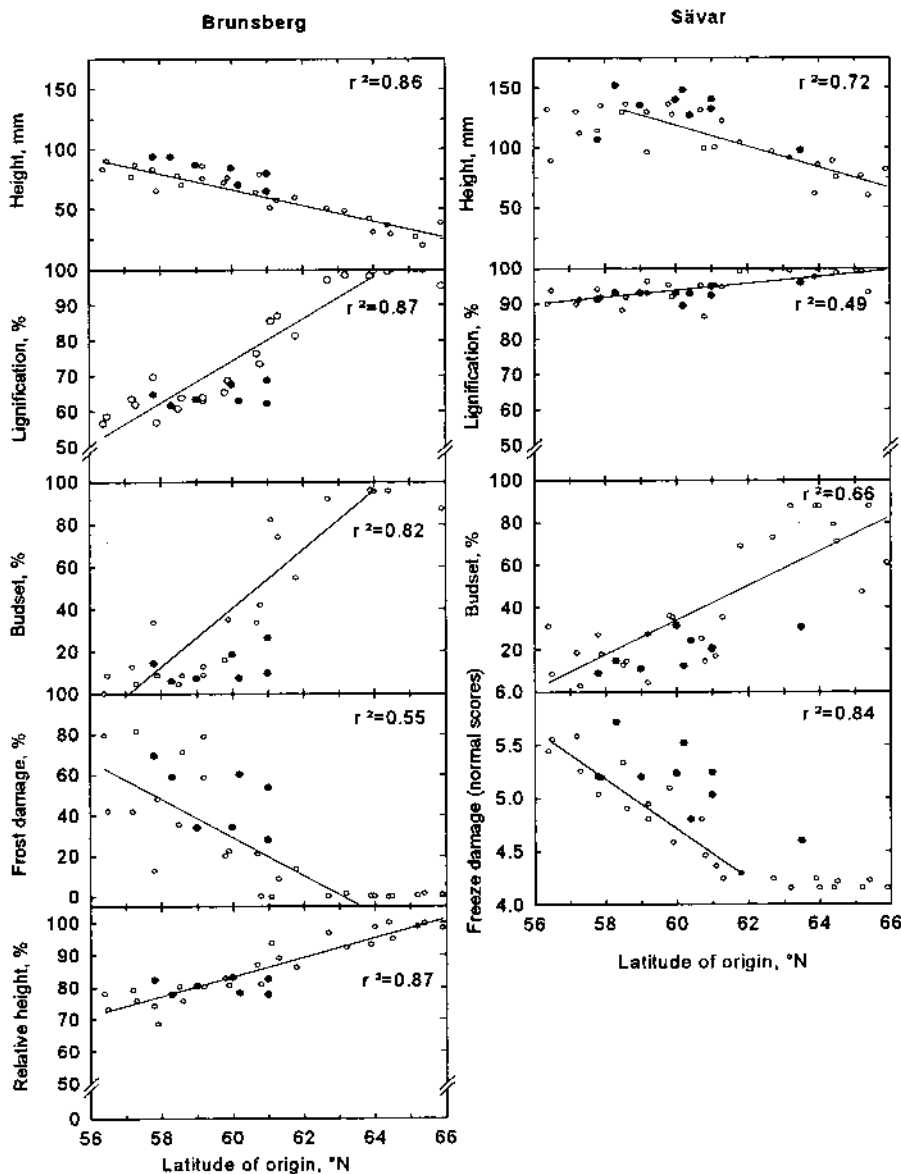

Fig. 4. Mean values of seedling height, budset frequency, degree of lignification, freeze-damage score, frost-damage frequency and relative height as a percentage of final height for seed-lots from natural stands (open symbols), seed orchards (filled symbols) and regression line for NS seed-lots plotted against latitude of origin.

Table 3. *Deviation between latitude of clonal origin and standardized latitude for SO seed-lots*

Seed-lot	Brunsberg					
	HEIGHT	LIGNIF	BUDSET	FROST	RELHT	Mean[b]
444-Ön, all clones	−1.9 (–)	0.6 (0.4)	0.3 (0.5)	−2.1 (–)	0.5 (0.6)	−0.2
444-Ön, southern clones	−2.4 (–)	−0.4 (0.4)	−0.8 (0.5)	−1.5 (1.1)	−0.2 (0.6)	−0.7
487-Lustnäset	−2.0 (0.7)	−0.9 (0.4)	−1.4 (0.4)	0.5 (1.0)	−0.0 (0.6)	−0.5
453-SörAmsberg	−2.7 (0.7)	−1.2 (0.4)	−1.6 (0.4)	−0.5 (1.0)	−0.1 (0.6)	−0.9
444-Ön, local clones	−0.7 (0.7)	−2.1 (0.4)	−2.6 (0.4)	−3.5 (1.0)	−1.9 (0.6)	−2.5
31-Högseröd, yr 1989	−3.0 (0.7)	−1.9 (0.4)	−2.0 (0.4)	−0.9 (1.0)	−1.3 (0.6)	−1.5
31-Högseröd, yr 1990	−0.7 (0.7)	−3.1 (0.4)	−3.2 (0.4)	−3.6 (1.0)	−2.9 (0.6)	−3.2
Mean[a]	−2.1	−1.5	−1.8	−1.8	−0.9	

Seed-lot	Sävar				
	HEIGHT	LIGNIF	BUDSET	FREEZE	Mean[b]
444-Ön, all clones	3.6 (–)	−0.8 (1.6)	−0.9 (1.0)	0.1 (0.7)	−0.5
444-Ön, southern clones	−2.1 (–)	0.7 (1.5)	−0.7 (1.0)	−2.6 (–)	−0.9
487-Lustnäset	−0.9 (–)	−0.0 (1.5)	−1.9 (0.9)	−1.1 (0.7)	−1.0
453-SörAmsberg	−2.4 (–)	−1.0 (1.4)	−0.4 (0.9)	−2.2 (0.7)	−1.2
444-Ön, local clones	−3.5 (–)	−5.1 (1.6)	−2.9 (0.9)	−3.6 (0.7)	−3.9
128-Grånäs	−1.3 (1.4)	−1.7 (1.4)	−1.6 (0.9)	−0.8 (0.7)	−1.4
31-Högseröd, yr 1989	−2.5 (1.4)	−2.8 (1.4)	−2.6 (0.9)	−3.3 (0.7)	−2.9
31-Högseröd, yr 1990	−3.5 (–)	−0.1 (1.3)	−2.7 (0.9)	−2.3 (0.7)	−1.7
26-Jung, northern-clones	−1.1 (1.4)	−1.4 (1.4)	−4.0 (1.0)	−3.0 (0.9)	−2.8
Mean[a]	−1.8	−1.5	−1.8	−2.3	

[a] Mean of SO seed-lots common to Brunsberg and Sävar.
[b] Mean of LIGNIF, BUDSET, FROST and RELHT at Brunsberg and LIGNIF, BUDSET and FREEZE at Sävar.
A negative deviation implies that the performance of the SO progeny resembles that of progeny from NS with a more southerly origin. Pooled standard error of the estimates is in parentheses. Errors could not be estimated for values for SO seed-lots outside the range of values included in the regression.

Standard errors for the standardized latitudes in the Brunsberg experiment averaged 0.6°, with the smallest errors for LIGNIF (0.4) and the largest for FROST (1.1) (Table 3). Standard errors were generally higher at Sävar, being 0.7–1.0 for BUDSET and FREEZE and over 1.4° for HEIGHT and LIGNIF.

Significant correlation coefficients calculated for NS seed-lots at Brunsberg were high (> 0.88) between all traits measured except for FROST, but were lower between traits measured only at Sävar (0.49–0.71) (Table 4). The correlation between the same traits measured at both locations was relatively high (0.59–0.87) except for between FROST at Brunsberg and HEIGHT and LIGNIF at Sävar.

DISCUSSION

In accordance with many previous studies on Norway spruce in Fennoscandia (e.g. Dietrichson 1969, Rosvall & Ericsson 1981, Ekberg et al. 1985, Pulkkinen 1993), strong clinal variation with latitude was found, whereas the effect of altitude was weak or absent. However, significant effects of altitude on the timing of budset have been found in other studies (e.g. Krutzsch 1986). The material used in this study was not optimal for evaluating the relative effects of latitude and altitude, since material from high altitudes tended to originate from more northern latitudes (Fig. 1). The small, but statistically significant, effects of altitude on HEIGHT, BUDSET and LIGNIF in Brunsberg might have been a result of genetic differences, but other explanations are also possible. Low-altitude sites generally provide more favourable climates for seed development than sites at high altitudes. Studies of first-year seedlings might therefore detect altitudinal effects resulting from differences in physiological properties of the seed, e.g. germination rates or germination energy, rather than in genetic properties.

The phenology of the SO progeny corresponded to that of progeny from NS located to the south of the origin of the SO clones (Table 3, Fig. 4). Southward transfer of clones in combination with background pollination may have caused the differences in the phenology of the SO progeny compared with the NS progeny of similar origin. However, transfer of clones could explain the deviation in phenology for only two of the seed orchards, 26-Jung and 31-Högseröd, since the other orchards were all located close to or north of the geographical origin of the clones. Internal background pollination with southerly pollen may explain the deviation in phenology of local clones in 444-Ön, as clones with considerably more southerly origins exist in the seed orchard. The generally negative deviations in phenology between SO seed-lots and comparable NS seed-lots are probably not related solely to pollination with pollen of southern origin. Factors such as seed-orchard environment or genetic differences between selected plus-trees and unselected trees may also contribute to the phenological deviation.

The female flowering environment appears to influence the growth rhythm and autumn-frost hardiness of Norway spruce progeny (as reviewed by Johnsen & Skrøppa 1996). Important factors appear to be temperature and photoperiod during pollination and fertilization. Observed effects of flowering environment include changes in growth rhythm and reductions in autumn-frost hardiness in trees up to 17 yrs old (Edvardsen et al. 1996). No genetic difference in autumn-frost hardiness was observed between first-year seedlings of plus-trees and unselected trees from northern Norway (Johnsen & Østreng 1994). It is not possible to separate effects of seed-orchard environment or genetic differences between selected plus-trees and unselected trees using results from the present study.

Experience gained in connection with provenance-transfer work in Sweden (e.g. Rosvall & Ericsson 1981, Werner & Karlsson 1982, Persson & Persson 1992, Hannerz 1993) suggests that a northward transfer of 2–4° of latitude in Sweden will enhance growth without sacrificing adaptation. Based on the present results, we recommend that material from seed orchards composed of domestic plus-trees be used at latitudes similar to the latitude of origin of the parental clones or slightly to the north. In seed orchards located far south of the origin of the SO clones, this recommendation might be modified based on knowledge of background pollination, internal pollination, early tests of progenies or results from field trials.

The ultimate purpose of early tests is to identify test traits that correspond to target traits in the field. If the goal is to estimate autumn-frost hardiness under field conditions, a two-step procedure can be followed: (1) find traits that are correlated with frost hardiness in early tests; and (2) determine whether these traits are correlated with frost hardiness in field trials.

The study presented here focused on the first step. No direct comparisons between first-year traits and field performance were made. The strong clinal variation with latitude suggests indirectly that all of the

Table 4. *Estimated product-moment correlations between traits in NS seed-lots (n = 26) at the test locations Brunsberg and Sävar*

	Brunsberg					Sävar			
	HEIGHT	LIGNIF	BUDSET	FROST	RELHT	HEIGHT	LIGNIF	BUDSET	FREEZE
B HEIGHT	–	**−0.89**	**−0.88**	**0.68**	**−0.90**	**0.78**	**−0.67**	**−0.82**	**0.68**
B LIGNIF		–	**0.98**	**−0.78**	**0.92**	**−0.74**	**0.73**	**0.84**	**−0.87**
B BUDSET			–	**−0.82**	**0.89**	**−0.74**	**0.70**	**0.81**	**−0.84**
B FROST				–	**−0.69**	0.48	**−0.44**	**−0.62**	**0.59**
B RELHT					–	**−0.78**	**0.71**	**0.79**	**−0.69**
S HEIGHT						–	**−0.49**	**−0.69**	0.51
S LIGNIF							–	**0.71**	**−0.38**
S BUDSET								–	**−0.48**
S FREEZE									–

B: Brunsberg; S: Sävar.
Significant correlations ($p < 0.05$) are indicated in bold.

measured phenological traits reflect the same photoperiodically controlled adaptive process of growth cessation. A corresponding clinal variation in growth rhythm and frost-related damage in the field has been shown previously (Langlet 1960, Ekberg et al. 1991, Persson & Persson 1992, Skrøppa & Magnussen 1993). In addition to the photoperiodically controlled adaptive process, plants show high plasticity and high capacity for acclimation, both of which can be of major adaptive significance (Junttila 1996). Temperature may modify all the traits investigated in the study, as well as the adaptive processes of growth cessation and development of autumn hardiness under field conditions. Therefore, different traits of first-year seedlings may be interchangeably used, when the purpose is to rank populations for differences in growth cessation under the current test conditions. However, there is still a need to determine whether these traits are correlated with differences in growth and frost hardiness among populations in field trials, and whether such data can also be used for discerning differences among families or genotypes.

In this study, strong correlations at the population level were found among growth-cessation traits and between these traits and frost hardiness (Table 4). Based on the present findings, it can be concluded that the timing of budset or height growth cessation, or the degree of shoot lignification, or frost hardiness can be used independently as indicators of growth cessation and frost hardiness, at least at the population level. A prerequisite is that the traits must be measured at a time when the resolution among the tested seed-lots is high. Strong correlations among timing of budset, shoot lignification and frost hardiness in first-year seedlings at the population level have also been reported in other studies on Norway spruce (Johnsen & Apeland 1988, Skrøppa 1991, Pulkkinen 1993). However, both Skrøppa (1991) and Johnsen & Apeland (1988) found that the relationship between frost hardiness and the timing of budset was much weaker among families than among populations.

A disadvantage of using natural-stand seed-lots as reference materials is that the tests cannot be reproduced using the same material since cones are often collected from harvested trees. Furthermore, a large number of natural stands is required to obtain stable regression functions. The availability of a reproducible reference set of thoroughly tested full-sib families, with less phenotypic variation, would make

it possible to reduce the number of reference materials, compared with the situation where natural stands are used. Furthermore, the latitudinal range of the tested seed-lots should be considered in the experimental design. Norway spruce populations have critical night lengths ranging from 2–3 h in northern Sweden to 10 h in central Europe (Ekberg et al. 1979). Too large differences in critical night length among populations tested in the same experiment might involve problems with cultivation and interpretation of the growth cessation (Fig. 4). The photoperiodic conditions of the test should not deviate too much from those of the tested seed-lots.

In summary, first-year seedlings from seed orchards of Norway spruce located within the area of origin of the plus-trees exhibited phenological characteristics corresponding to natural-stand progeny from 1–2° of latitude further south. Reference material from natural stands representing a wide latitudinal range can be used effectively to characterize the phenology of the tested material. Timing of budset and height growth cessation, degree of shoot lignification and damage level after freeze testing can be independently used as indicators of autumn phenology. However, the measurements must be made at a time when the test materials display a large degree of variation. Future studies should emphasize the correlation between first-year phenological traits and target traits in the field.

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REFERENCES

Andersson, B. 1986. Freezing tests of Scots pine (*Pinus sylvestris* L.) seed orchard crops. *In* Lindgren, D. (ed.). Provenances and Forest Tree Breeding for High Latitudes. Dept of Forest Genetics and Plant Physiology, Swed. Univ. of Agric. Sci., Umeå. Report 6: 99–111. ISBN 91-576-2813-0.

Anon. 1998. www.svo.se, Skogsstyrelsens föreskrifter och allmänna råd till skogsvårdslagen (1979: 429), Användning av skogsodlingsmaterial och utländska trädarter, Skogsstyrelsens författningssamling. National Board of Forestry. ISSN 0347-5212.

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

Daehlen, A. G., Johnson, Ø. and Kohmann, K. 1995. Autumn frost hardiness in young seedlings of Norway spruce from Norwegian provenances and seed orchards. Skogforsk Research Paper 1/95, 24 pp. ISBN 82-7169-70 1-3. (In Norwegian with English summary).

Dietrichson, J. 1969. The geographic variation of spring-frost resistance and growth cessation in Norway spruce (*Picea abies* (L.) Karst.). Medd. Norske Skogforsøksvesen 27: 91–104.

Dormling, I., Gustafsson, Å. & von Wettstein, D. 1968. The experimental control of the life cycle in *Picea abies* (L.) Karst. I. Some basic experiments on the vegetative cycle. Silva Genet. 17: 44–64.

Edvardsen, Ø. M., Johnsen, Ø. & Dietrichson, J. 1996. Growth rhythm and frost hardiness in northern progeny trials with plants from Lyngdal seed orchard. Skogforsk Research Paper 9/96, 9 pp. ISBN 82-7169-4. (In Norwegian with English summary.)

Ekberg, I., Eriksson, G. & Dormling, I. 1979. Photoperiodic reactions in conifer species. Holarctic Ecol. 2: 255–263.

Ekberg, I., Eriksson, G. & Weng, Y. 1985. Between- and within-population variation in growth rhythm and plant height in four *Picea abies* populations. Studia Forestalia Suecica 167, 14 pp. ISBN 91-576-2233-7.

Ekberg, I., Eriksson, G. & Nilsson, C. 1991. Consistency of phenology and growth of intra and interprovenance families of *Picea abies*. Scand. J. For. Res. 6: 323–333.

Eriksson, G. & Gagov, V. 1976. Growth differences within full-sib families of *Picea abies* (L.) Karst. Studia Forestalia Suecica 130, 25 pp. ISBN 91-38-02753-4.

Gianola, D. & Norton, H. W. 1981. Scaling threshold characters. Genetics 99: 357–364.

Giertych, M. 1976. Summary of the results of the IUFRO 1938 Norway spruce (*Picea abies* (L.) Karst.) provenance experiment. Height growth. Silva Genet. 25: 154–164.

Hannerz, M. 1993. Norway spruce provenances in central Sweden – height growth and damage in a 12-year-old provenance trial. The Forestry Research Institute of Sweden, Uppsala. Redogörelse No. 1, 23 pp. ISSN 1103-4580. (In Swedish with English summary.)

Hannerz, M. 1999. Evaluation of temperature models for predicting bud burst in Norway spruce. Can. J. For. Res. 29: 9–19.

Johnsen, Ø. 1989. Freeze-testing young *Picea abies* plants. A methodological study. Scand. J. For. Res. 4: 351–367.

Johnsen, Ø. & Apeland, I. 1988. Screening early autumn frost hardiness among progenies from Norway spruce seed orchards. Silva Fennica 22: 203–212.

Johnsen, Ø. & Østreng, G. 1994. Effects of plus tree selection and seed orchard environment on progenies of *Picea abies*. Can. J. For. Res. 24: 32–38.

Johnsen, Ø. & Skrøppa, T. 1996. Adaptive properties of *Picea abies* progenies are influenced by environmental signals during sexual reproduction. Euphytica 92: 67–71.

Junttila, O. 1996. Plant adaptation to temperature and photoperiod. Agricultural and Food Science in Finland 5: 251–260.

Kohmann, K. & Johnsen, Ø. 1994. The timing of bud set in seedlings of *Picea abies* from seed crops of a cool versus a warm spring and summer. Silva Genet. 43: 329–333.

Krutzsch, P. 1974. The IUFRO 1964/68 provenance test with Norway spruce (*Picea abies* (L.) Karst.). Silva Genet. 23: 58–62.

Krutzsch, P. 1986. An investigation on budset in Norway spruce (*Picea abies*). *In* Lindgren, D. (ed.). Provenances and Forest Tree Breeding for High Latitudes. Dept of Forest Genetics and Plant Physiology, Swed. Univ. of Agric. Sci., Umeå. Report 6: 21–32. ISBN 91-576-2813-0.

Langlet, O. 1960. Mellaneuropeiska granprovenienser i svenskt skogsbruk. *In* Kungl. Skogs- och Lantbruksakad. Tidskrift 5–6: 259–329. (In Swedish with German summary.)

Paule, L., Lindgren, D. & Yazdani, R. 1993. Allozyme frequencies, outcrossing rate and pollen contamination in *Picea abies* seed orchards. Scand. J. For. Res. 8: 8–17.

Persson, A. & Persson, B. 1992. Survival, growth and quality of Norway spruce (*Picea abies* (L.) Karst) provenances at the three Swedish sites of the IUFRO 1964/68 provenance experiment. Dept of Forest Yield Research, Swed. Univ. of Agric. Sci., Garpenberg. Report 29, 67 pp. ISSN 0348-7636.

Pulkkinen, P. 1993. Frost hardiness development and lignification of young Norway spruce seedlings of southern and northern Finnish origin. Silva Fennica 27: 47–54.

Rosvall, O. & Ericsson, T. 1981. Transfer effects of *Picea abies* in northern Sweden. *In* Föreningen Skogsträdförädling och Institutet för skogsförbättring, Uppsala. Årsbok 1981, pp. 85–115. (In Swedish with English summary.)

Rosvall-Åhnebrink, G. 1985. Invintring av plantor för höstplantering eller vinterlagring. Swed. Univ. of Agric. Sci., Skogsfakta Konferens 7: 33–37. (In Swedish). ISBN 91-576-2370-8

Skrøppa, T. 1988. The seed weight did not affect first years bud-set in *Picea abies*. Scand. J. For. Res. 3: 437–439.

Skrøppa, T. 1991. Within-population variation in autumn frost hardiness and its relationship to bud-set and height growth in *Picea abies*. Scand. J. For. Res. 6: 353–363.

Skrøppa, T. & Magnussen, S. 1993. Provenance variation in shoot growth components of Norway spruce. Silva Genet. 42: 111–120.

Werner, M. & Karlsson, B. 1982. Results from a series of Norway spruce provenance trials within southern and central Sweden. *In* Föreningen skogsträdsförädling och Institutet för skogsförbättring, Uppsala. Årsbok 1982, pp. 90–158. (In Swedish with English summary.)

Worall, J. 1973. Seasonal daily and hourly growth of height and radius in Norway spruce. Can. J. For. Res. 3: 501–511.

Worall, J. 1975. Provenance and clonal variation in phenology and wood properties of Norway spruce. Silva Genet. 24: 2–5.