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## Parental Environment Effects on Cold Acclimation and Height Growth in Lodgepole Pine Seedlings

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### Abstract

Lodgepole pine stands from a number of seed sources were established in different commercial forest environments in northern Sweden in the 1970's as part of the introduction effort of this species. Parental environment effects (aftereffects) were studied in progeny from stands originating from two seed sources (Fireside and Toad River, British Columbia), with each seed source grown in six different Swedish environments. The occurrence of aftereffects on cold acclimation (freezing damage and mortality) and height growth of the progeny was investigated in the greenhouse and freezing chamber. One growing season height and cold acclimation differed significantly among stand sites, though the magnitude of the site effect was relatively small. Seedlings were taller at lower elevations, at higher site indexes and in longer growing degree-days environments. With longer growing degree-days freezing damage was significantly lower in the Fireside origin, but not significantly higher in the Toad River origin. Height and resistance to cold damage were positively correlated in the Fireside origin but not in the Toad River origin. The results suggest that aftereffects could be manipulated to benefit reforestation by choosing the proper combination of genetic materials and environments for seed production. Aftereffects could also constitute a problem for tree breeding, because the environment in which a seed sample is produced could be confounded with its inherent genetic value.

*Key words:* Seed origin, freezing test, aftereffects, growing degree-day, tree breeding.

### Introduction

It is well accepted in tree breeding that establishing seed orchards in more southern or warmer regions usually results in

early flowering, higher seed production, heavier seed, and higher seed germination rates (e.g. SCHMIDTLING, 1984, 1987). These types of beneficial effects, known as “aftereffects”, are caused by the difference between the original and present environment where the seed is produced. Aftereffects can also influence adaptive traits. Indeed, several studies have shown that Norway spruce (*Picea abies*) raised from seed produced under milder environments grew faster, flushed later in the spring and set buds later in the autumn, had a longer shoot elongation period, and were therefore more sensitive to cold conditions than those of the same genetic composition produced under harsher environments (BJØRNSTAD, 1981; JOHNSEN, 1989a and b; JOHNSEN et al., 1995, 1996; SKRØPPA, 1994; JOHNSEN and SKRØPPA, 1996). Aftereffects in *Picea abies* might last for many years (JOHNSEN, 1989b; JOHNSEN and SKRØPPA, 1996) or possibly indefinitely. Similar observations have been made in *Picea glauca* (STOEHR et al., 1998) and *Pinus sylvestris* (LINDGREN and WANG, 1986; DORMLING and JOHNSEN, 1992; ANDERSSON, 1994; LINDGREN and WEI, 1994). Aftereffects in

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adaptive traits were also caused by differences in temperature during sexual reproduction (KOHMANN and JOHNSEN, 1994; JOHNSEN et al., 1996). However, most early studies involved grafts grown in environments that are very different from forest stands.

Cold acclimation and height growth are probably the most important silvicultural considerations to the success of reforestation in the harsh north. Cold acclimation determines the survival rate of a plantation, which in turn affects its productivity (NILSSON and ERIKSSON, 1986). Aftereffects therefore are of importance in plant production. Information about the influence of aftereffects on cold acclimation is, therefore, critical for producing seedlings to achieve high rates of survival to ensure reforestation success. The effects of aftereffects on growth may not persist indefinitely. Fast growing seedlings at an early age are likely to out-compete wild grasses and shrubs in forest conditions, thus resulting in high survival rates. Differences in cold resistance and growth may be due to differences in seed production environments, which may be negatively correlated (e.g. LINDGREN and WEI, 1994). Therefore both should be taken into account whenever aftereffects are found to be significant.

A quick and precise method to detect the occurrence of aftereffects in seedlings/saplings would be to use controlled environments (such as freezing chambers and greenhouses). Freezing test provide useful information on the cold acclimation of seedlings which are good predictors of survival in forest sites (e.g. NILSSON and ERIKSSON, 1986). LINDGREN and NILSSON (1992) studied the cold acclimation of *Pinus sylvestris* and *P. contorta* by testing the freezing tolerance of detached needles.

Most seed used for commercial, scientific or tree improvement purposes has been and continues to be harvested from forest stands. No previous studies on the effect or magnitude of aftereffects in a range of forest environments have been carried out. At least these results are not subject to criticism because of possible severe confounding by genetic differences, selection, adaptation or pollen migration. In this study we investigate the magnitude of aftereffects in the progeny of different forest stands where the effect of other factors than aftereffects should be small.

## Materials and Methods

### Material Structure

Canadian seed sources (origins) of lodgepole pine (*Pinus contorta* spp. *latifolia*) were used to establish "test" stands in different environments in Sweden by Svenska Cellulosa Aktie-

bolaget in early 70's. These "test" stands represented the later phase of preparations for a large-scale introduction of this species into Northern Sweden (LINDGREN, 1993). In this study, two seed sources from British Columbia (B.C.) Canada were selected: one from Toad River, B.C. (58°52'N, 122°21'W, 760 m elevation) and the other from Fireside, B.C. (59°40'N, 127°10'W, 750 m elevation). For each seed source, stands established on six different Swedish sites were used. Geographic location and growing degree-days (GDD) together with temperature  $\geq +5^\circ\text{C}$  for each site were used to describe the site environment (Table 1). GDD was the mean daily temperature above  $+5^\circ\text{C}$  accumulated over a year. The technique and meteorological data used for deriving the GDD were described by LINDGREN (1994).

The two seed sources were represented by a single bag of seeds from a single collection in a "naturally wild" forest. Because the stands originated from the same two seed sources they should be genetically identical. The stand size per site was about 20 hectares. Each chosen stand was estimated to have at least 1000 living lodgepole pine trees per hectare left (thus more than half of the initially planted) to ensure that selection had not changed the genetic composition of the stand. In the surrounding areas, either there was no other lodgepole pine planted, or the planted trees were too young to produce pollen. Presumably, for each origin, there was no differentiation in the genetic contribution of male or female gametes among sites and progenies from six chosen stands had the same or very similar genetic structure.

In September 1995, open-pollinated seeds were collected from at least 20 trees along a transect through the central part of each stand. At least 20 cones were harvested from each tree. In a few stands cone production limited the number of sampled trees. Seeds were extracted from cones for each tree, and the filled seed for each tree (family) was weighted. For the present study, 11 half-sib families (maternal half-sib families from 11 trees) were chosen to represent each stand. Half-sib families represented by poor or low-weight seeds were not used. Therefore, the experimental material had a hierarchical structure: 6 different sites nested within each of two Canadian origins and 11 half-sib families nested within each site.

### Greenhouse Material

Forty-four styrofoam containers, each having 7x12 cells (3.7 cm in diameter and 11 cm in depth), were filled with basic nourished forest peat and arranged into 4 replications for four different freezing tests in a greenhouse. Seeds were sown in

Table 1. – Six test stand sites, locations and growing degree-days (GDD) for each of two Canadian lodgepole pine seed sources (Toad River and Fireside).

Stand site	Toad River					Fireside					
	Site code	Lat	Long	Elev (m)	GDD	Stand site	Site code	Lat	Long	Elev (m)	GDD
Pausele	24	64°52'	17°51'	320	737	Sjöbysjön	17	62°57'	17°38'	120	1017
Meselberget	23	64°20'	16°42'	410	680	Mosjölund	12	62°41'	16°57'	350	853
Länsgränsen	27	65°15'	20°35'	345	699	Oppbodarna	6	62°33'	14°18'	510	696
Isliden	28	65°52'	20°47'	250	745	Mattismyran	32	66°03'	22°14'	120	841
Åsarna	30	66°16'	21°32'	170	790	Bredsele	22	64°32'	15°58'	410	681
Högländet	29	66°11'	20°08'	370	633	Länsgränsen	26	65°15'	20°35'	350	695

the containers at the beginning of May 1996. Some of the cells of the containers were double sown so that the empty cells could be filled with these spare seedlings later on. The greenhouse was provided with 19-hour uninterrupted fluorescent light at intensity of 39,880 lux, and day/night temperatures and day/night temperatures approximately +20°C/15°C. In each replication with 11 containers, one container included 1 origin, 6 stands, 2 families per site and 7 seedlings per families. Therefore, there were 924 seedlings in each replicate and 3696 seedlings totally. In the middle of July, the seedlings were moved to "the Møllehouse" – a greenhouse with a roof but without walls to allow natural cold acclimation.

#### Freezing Test and Height Growth

All seedlings stopped growing before freeze testing, and therefore the freezing treatment imposed no effect on height growth. The freezing test procedure was similar to that used by NILSSON and ERIKSSON (1986). During the period of September 20 to October 1, 1996, four freezing tests with respective temperatures -14°C, -16°C, -20°C and -23°C were applied to one-fourth of the materials (i.e. 11 containers with 924 seedlings), respectively. The freezing test was performed in a dark freezing chamber by gradually cooling down the air temperature from +15°C during 6.5 hours. The rates of temperature drop for four freezing tests were approximately 4.46°C/hr, 4.77°C/hr, 5.38°C/hr and 5.85°C/hr, respectively. The predetermined freezing temperature was maintained for 3 hours, and then followed by 6.5 hours thawing back to normal temperature (+15°C). Then, the freezing chamber was exposed to fluorescent light at normal temperature (+15°C) for 15 hours. Finally, the seedlings were moved to the greenhouse with the conditions of 16-hour fluorescent light at +18°C and 8-hour darkness at +12°C.

Freezing damage was assessed about two weeks after the treatment. Freezing damage was closely correlated with cold acclimation (NILSSON and ERIKSSON, 1986). According to the proportion of discolored part of the needles, freezing damage was scored for each seedling:

Score	Symptom description	Proportion of discolored plant
0	no damage,	0%
1	very slight damage,	<10%
2	slight damage,	10% to 20%
3	intermediate damage,	20% to 70%
4	serious damage,	>70%
5	dead,	100%

Seedlings with a low score were less damaged or more resistant to low temperature. Besides assessment of freezing damage, height growth after one growing season was also measured on each seedling. From the damage assessment, mortality that was score 5, was also obtained for studying cold acclimation.

#### Statistical Analysis

Because the conditions in greenhouses and freezing chambers were very uniform, the greenhouse and freezing chamber layout of the materials were not considered as major experimental factors in the statistical analysis. According to the structure of the materials and freezing test temperature, a mixed model was used for freezing damage and mortality:

$$[1] Y_{ijklm} = \mu + T_i + O_j + S(O_j)_k + F(S(O_j)_k)_l + e_{ijklm},$$

where  $Y_{ijklm}$  = the damage score or mortality of the  $m$ th individual,  $l$ th half-sib family,  $k$ th site,  $j$ th origin and  $i$ th freezing temperature,

$T_i$  = the fixed freezing temperature effect (T),

$O_j$  = the fixed origin effect (O),

$S(O_j)_k$  = the random site effect (S) within origins,

$F(S(O_j)_k)_l$  = the random half-sib family effect (F) nested within sites that in return are nested within origins,

$e_{ijklm}$  = the residual (E).

In the analysis, the freezing damage (FD) score was used for freezing damage, but 0 was given to dead seedlings for mortality (MP). These measures were interpreted as measures of cold acclimation. Let MS denote the mean squares for different effects. The error term for testing site effect was 0.9641 MS(F)+0.0359 MS(E) with the degrees of freedom 122.22 for FD and 124.26 for MP. The error term for testing origin effect was 0.9835 MS(S)+0.0165 MS(E), with the degrees of freedom 10.042 and 10.18 for FD and MP, respectively. Other effects (T and F) are tested using the residual as the error term.

It should be noted that the different low temperature tests were performed separately over a period of 11 days rather than at the same time. Therefore, temperature effect might be confounded with time-scale cold acclimation process. However, our main concern is stand site effect.

Similarly a mixed model without fixed temperature effect was used for height growth

$$[2] Y_{jklm} = \mu + O_j + S(O_j)_k + F(S(O_j)_k)_l + e_{jklm},$$

where  $Y_{ijklm}$  = the height of the  $m$ th individual,  $l$ th half-sib family,  $k$ th site, and  $j$ th origin,

$O_j$  = the fixed origin effect (O),

$S(O_j)_k$  = the random site effect (S),

$F(S(O_j)_k)_l$  = the random half-sib family effect (F),

$e_{ijklm}$  = the random error (E).

Site effect was tested against MS(F) while origin effect was tested against MS(S).

PROC GLM of SAS software (SAS Institute Inc., 1992) was used to perform the significance test for different effects and characters. In both models, Type III mean squares were used to calculate all effects involved. PROC MIXED was used to estimate freezing damage and height growth for each test stand site, and to calculate the variance components of site and family for both traits. Linear regression was performed to analyze the relationship of the estimated freezing damage and height, and of both characters with geographic variables, site index (LINDGREN et al., 1994), GDD and seed weight associated with the stand sites.

#### Results

The effect of test sites was significant on the freezing damage score ( $P = 0.037$ ) and height ( $P = 0.011$ ), but was not significant for mortality. Family variation was large in all three characters ( $P < 0.0001$ ). Temperature in freezing tests had significant effects on mortality and freezing damage ( $P < 0.0001$ ). The two Canadian seed sources were significantly different in mortality ( $P = 0.033$ ), similar in height ( $P = 0.064$ ), but differed in freezing damage. Only the aftereffects (sites effects) on height and freezing damage were considered in the following, unless otherwise stated.

Although seed production environments significantly influenced seedling height growth and freezing damage, its variance component was small relative to within-site family variance and total variance. The site component accounted for 1.2% and

Table 2. – Estimated height and freezing damage and their standard errors (in brackets) for six test stand sites of each of two seed origins.

Toad River				Fireside			
Stand site	Site code	Height (mm)	Freezing damage	Stand site	Site code	Height (mm)	Freezing damage
Pausele	24	84.12(2.117)	2.95(0.078)	Sjöbysjön	17	89.61(2.106)	2.86(0.077)
Meselberget	23	81.10(2.140)	3.03(0.079)	Mosjölund	12	88.71(2.105)	2.83(0.077)
Länsgränsen	27	83.17(2.125)	3.12(0.078)	Oppbodarna	6	84.69(2.110)	2.96(0.077)
Isliden	28	83.97(2.128)	3.12(0.078)	Mattismyran	32	89.53(2.106)	2.86(0.077)
Åsarna	30	84.15(2.111)	3.08(0.077)	Bredsele	22	83.24(2.112)	2.99(0.077)
Höglandet	29	79.67(2.116)	2.96(0.077)	Länsgränsen	26	88.77(2.111)	2.94(0.077)

3.3% of the total variations for freezing damage and height, respectively, whereas the within-site family component accounted for 10.6% and 23.7% of the variation, respectively. Estimated height and freezing damage using mixed model were presented in table 2.

Table 3 showed that linear correlations were significant between height and stand site environment's GDD and site index in the Toad River origin, and between freezing damage and GDD in the Fireside origin. Low elevation sites favored fast growth in both origins as expected, although the correlation between height and elevation in both origins, was not significant (Table 3). The correlation of freezing damage with site elevation was opposite in direction, but not significant for any seed source. High elevation sites tended to increase cold resistance in the Toad River material, but tended to reduce cold resistance in the Fireside material. Stand environments with high GDD produced fast-growing seedlings in both origins, although the effect was not significant in the Fireside origin. High GDD significantly lowered freezing damage in the Fireside material but tended to increase non-significant freezing damage in the Toad River material. Site index effect on freezing damage and height was generally similar to GDD, but the former was smaller.

Table 3. – Correlations and significance levels (in brackets) of freezing damage (FD) and height (HT) with stand site locations, site index, growing degree-day (GDD) and seed weight (SW).

	Toad River			Fireside		
	SW	FD	HT	SW	FD	HT
Latitude	0.136 (0.798)	0.234 (0.656)	0.050 (0.925)	-0.410 (0.419)	0.134 (0.800)	0.185 (0.726)
Longitude	0.427 (0.399)	0.584 (0.224)	0.295 (0.571)	0.132 (0.803)	-0.391 (0.443)	0.712 (0.112)
Elevation	-0.696 (0.125)	-0.460 (0.358)	-0.721 (0.106)	-0.609 (0.199)	0.683 (0.135)	-0.774 (0.071)
Site index <sup>1</sup>	0.717 (0.109)	0.312 (0.547)	0.846 (0.034)	0.910 (0.012)	-0.737 (0.095)	0.543 (0.265)
GDD	0.841 (0.036)	0.440 (0.382)	0.920 (0.009)	0.900 (0.015)	-0.817 (0.047)	0.702 (0.120)
SW		0.490 (0.324)	0.963 (0.002)		-0.744 (0.090)	0.755 (0.083)
FD			0.459 (0.360)			-0.836 (0.038)

<sup>1</sup>) Predicted using  $99.78 - 1.226 * \text{Latitude} - 0.01205 * \text{Elevation}$  (LINDGREN et al., 1994).

Seed weight was associated with GDD and site index in both origins (Table 3). Higher GDD and site index yielded significantly heavier seeds in both origins. GDD and site index were correlated with elevation (LINDGREN et al., 1994). Higher elevation sites consistently tended to yield lighter seeds as expected, seedlings were taller for sites with heavier seeds in both origins. Seed weight and freezing damage had no apparent correlation in the Toad River origin but had a weak correlation in the Fireside origin.

Height growth had a strong negative correlation with freezing damage in the Fireside origin (Table 3), that is, taller seedlings were more resistant to cold treatment. There was, however, no significant relationship between height and freezing damage in the Toad River origin. The Fireside origin generally performed better than the Toad River origin. The overall means of mortality, freezing damage and height were 3.6%, 2.90 and 87.7 mm, respectively, for the Fireside origin, compared with that of 5.9%, 3.05 and 83.3 mm, respectively, for the Toad River origin.

## Discussion

The maternal growing environment can influence the offspring's adaptive performance, particularly at early age (SCHMIDTLING, 1987; DORMLING and JOHNSEN, 1992; ANDERSSON, 1994; LINDGREN and WEI, 1994; STOEHR et al., 1998). Changes in adaptive performance caused by seed production environment can play an important role in the success of forest operations and management. Low cold tolerance due to aftereffects on cold acclimatization may lead to high mortality. On the other hand, mild conditions may directly or indirectly enhance seedling growth rate, thus influencing their ability to compete with weeds at young ages. Aftereffects can therefore be beneficial.

Aftereffect studies have been carried out mostly on genetically identical grafts (clones) in seed orchards or clonal archives (BJØRNSTAD, 1981; JOHNSEN, 1989a and b; DORMLING and JOHNSEN, 1992; LINDGREN and WEI, 1994; STOEHR et al., 1998). Seed orchards or clonal archives are usually located in milder climates outside of the natural habitats where the parental clones originated, or the reforestation areas where seed from seed orchards will be planted. In the present study real forests at sites where the origins were commercially planted, are compared. All sites investigated were located within the range of forest environments suitable for planting lodgepole pine (Table 1).

Aftereffects are evident in freezing damage because the correlation between seed weight and freezing damage was not significant and the tendency of the correlation was opposite in the two seed sources. For height growth, however, the aftereffects observed may be an indirect consequence of stand environment effect on seed weight (*Table 3*; MAZER and GORCHOV, 1996). Even effects caused by seed weight can be regarded as aftereffects, however, the material in this study is too limited to separate seed weight from other aftereffects. In many of the other studies on aftereffects, particularly for growth, the differences could not be completely explained by seed weight (e.g. JOHNSEN, 1989b; LINDGREN and WEI, 1994; STOEHR et al., 1998).

The magnitude of aftereffects associated with the environments of stands is relatively small in comparison with other main effects such as within site family and within family variation. However, the benefit of taking both of them into account in forest operations should not be neglected because large difference may occur between different environments. In the Toad River origin, for instance, seedlings from site 30 were 5.5% taller than from site 29, and freezing damage for site 28 was 5.7% greater than for site 24. In the Fireside material, seedlings from site 17 were 7.5% taller than from site 22, and freezing damage for site 22 was 5.7% greater than for site 12.

Locating seed production populations (clonal or family/provenance seedlings) in the proper environments can be a strategy to create plants with desirable adaptive performance, at least at early stage (JOHNSEN, 1989a and b; LINDGREN and WEI, 1994; STOEHR et al., 1998). The area where seed material is planned to be used could be affected by the site and year of seed collection. If seed production is in an indoor seed orchard it may be possible to intentionally or unintentionally change the performance of the forest regeneration material produced. The justification for testing individual seed lots to determine their use in practical forestry now increases because aftereffects have an important role. The plant production regime in nurseries can also be adjusted to manage aftereffects.

Early studies have generally concluded that a warmer or more southern environment selects for height growth and a longer growing season while a colder environment selects for a shorter growing season and earlier cold acclimation in the autumn (JOHNSEN, 1989a and b; LINDGREN and WEI, 1994; JOHNSEN and SKRØPPA, 1996), suggesting that height growth and cold acclimation may be a trade-off in the development of aftereffects. In addition, the negative relationship between height growth and early cold acclimation has also been consistently found among natural populations of lodgepole pine (REHFELDT et al., 1999). Our results showed no such trade-off; height and cold acclimation were not correlated in the Toad River origin and strongly positively correlated in the Fireside origin (*Table 3*), but this is based on very limited data. The physiological and genetic mechanism of aftereffects may involve complex interactions of seed production environments and genotypes. Sites for both origins in this study are located within a relatively small geographic range (*Table 1*). Aftereffects may have different relationships with different origins or genotypes within small ranges than from those found over a wide range. When two compared sites are far away, aftereffects may favor desirable characters at one site but not at another (LINDGREN and WEI, 1994; and STOEHR et al., 1998). It may therefore be possible to improve both height and cold acclimation simultaneously by properly choosing sites for seed orchard or seed production locations.

Geographic variables like latitude, longitude and elevation can be good descriptors of environmental conditions in some situations (LINDGREN et al., 1994). Moving parents from north

to south or from high to low elevations is expected to generate offspring with longer shoot elongation periods and lower frost resistance (JOHNSEN, 1989a and b; LINDGREN and WEI, 1994; JOHNSEN and SKRØPPA, 1996). A weak negative correlation between height growth and elevation in the present study is consistent with the above reports as well as the provenance testing results in lodgepole pine (e.g. REHFELDT et al., 1999). However, we found no significant correlation of latitude and longitude with height growth and freezing damage, and in the Fireside origin freezing damage tended to increase with increasing elevation, which may again be explained by the variation of aftereffects within a relatively small range of elevations involved (*Table 1*).

The combination of many factors determines a forest environment. Geographic coordinates may not be the most effective descriptors of environments to define aftereffects. Site index obviously improves the description of the stand site environments. Climatic variables may even better describe the differences in the environment conditions between stand sites. For instance, the results from this study show that GDD were generally more effective than the geographic coordinates and site index in relating aftereffects to growth and cold acclimation (*Table 3*).

Aftereffects may be part of population adaptation process in nature, or may be just type of physiological response of parents to specific environments. In the first situation, aftereffects will always accompany the evolution of a population subject to migration and gene flow (JOHNSEN and SKRØPPA, 1996). Aftereffects modify natural selection processes imposed on new gene combinations in their native niches. Therefore, aftereffects may gradually be fixed over time, and play a role in development and formation of local races. In the second situation, difference in height may be a transient phenomenon caused by the products of physiological responses such as differences in seed weight (*Table 3*). If so, aftereffects may vanish sooner or later. STOEHR et al. (1998) showed that aftereffects on height in the second growing season are much smaller than in the first growing season.

Aftereffects could be evolutionarily valuable. Perhaps it is more efficient if parents can transfer instructions relevant to the current climate in directly to their offspring rather than depending only on natural selection for adaptation. Climate changes and aftereffects may make trees more adapted to a variable climate. When trees re-colonize after glaciations, the winners are those which can adapt rapidly to a new niche with no competing trees, and aftereffects would give an advantage in invading such a new niche.

We assumed that differences in selection or pollination did not cause major differences between stands. There were, however, mortality differences, even if mortality was never high in the investigated stands. In a few stands only a few trees bore a sufficient number of cones, so selection of those trees may have an influence. Families with poor quality seeds were avoided. The fertilizing pollen may be dominated by a rather small number of trees and selection may have some importance here. There may also be some pollen from outside the stand in the air. It is difficult to completely exclude that such factors could matter, but it does not seem likely. Eleven trees from each stand were sampled, which is rather low to form a reliable stand average, but this should be adjusted for by the statistical analysis.

Aftereffects may influence tree breeding through several ways. Firstly, difference between native and parental environments of genetic material may determine the influence of after-

effects on the adaptive performance of the material. In most tree breeding programs, parental environments of testing/breeding stock differ from their origins. Material from different origins may be collected from a test trial, breeding population or seed orchard within the same environment. Even if the site of seed production is the same, annual variations in such things as the nutritional state or sun exposure of the cone or seed treatments may be important. Aftereffects may therefore be confounded with other components of variation and individual genotype's performance (provenance, family, etc), at least at an early age. The possible scale of aftereffects depends on difference between native and parental environment of a genotype (seed source, provenance, family, or clone). Aftereffects may not be of long-term significance, but may be a factor to consider, especially because early testing results are so attractive, and because much of the performance of a forest or a test material may be phenotypically correlated with the state of the trees at a young age. Secondly, selection from a test population (provenance and progeny trial) may result in aftereffects in the next generation. A breeding program can start from selection of superior provenance and individuals from a provenance trial. In advanced generation breeding, selection from breeding/test population is always an essential step. Aftereffects are probably a source of reducing the estimation of individual/family's breeding value as well as decreasing selection efficiency. Finally, the location of a seed orchard may affect some characters in the offspring such as growth and cold resistance. More knowledge needs to be gained before breeders are able to solve or mitigate the problem caused by aftereffects, and to use aftereffects as a useful tool in their programs.

Both natural selection and aftereffects can direct the biological adaptation processes (JOHNSEN and SKRØPPA, 1996). It has been shown that the growth rhythm and hardiness of *Picea abies* native to cold areas but raised in warm environments perform similar to those native to warm areas (SKRØPPA, 1994; JOHNSEN, 1989a). Seeds from introduced, well-performing plantations or orchards may therefore be expected to perform better than those collected from originally distributed areas, mainly for two reasons: 1) potential favorable aftereffects, and 2) proved genetic adaptation to target planting environments by seed sources selection and testing.

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