Longitudinal Differences in Scots pine Frost Hardiness

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Abstract

The autumn frost hardiness of Scots pine (*Pinus sylvestris* L.) populations from Scandinavia (57°28'–68°54' N, 13°00'–27°00' E) and the Komi Republic in Russia (61°30'–64°20' N, 49°10'–54°50' E), and open pollinated families from a population in Komi (61°43' N, 51°07' E) were examined in artificial freezing tests with one-year-old seedlings. The aims were to estimate genetic variation in hardiness between families of Russian origin and to compare populations of Russian (continental) and Scandinavian (maritime) origins. The longitudinal distance between the Scandinavian and Russian seed sources was associated with a significant difference in climatic conditions. At latitude 63°N the degree of continentality (the difference between July and January monthly mean temperatures) was 23.7°C for longitude 15°E in Sweden and 35.2°C for longitude 54°E in Komi. The narrow-sense heritability of frost hardiness calculated for the Russian families was 0.22. This indicates relatively high genetic control of the trait, of similar magnitude as earlier shown for populations of Scandinavian origin. Both Scandinavian and Russian populations showed a strong clinal variation in frost hardiness, northern populations being the hardest. In addition, Russian populations were more frost hardy than Scandinavian ones from corresponding latitudes and attained the same level of hardiness as Scandinavian populations from 4.1° latitude further north. The results indicate that the longitude or continentality of the origins of Scots pine populations is associated with adaptive pressures that have significant effects on hardiness and are distinct from photoperiodic effects. When enriching breeding or production populations by including populations from remote origins it is essential to recognize not only latitudinal origin, but also longitudinal origin or temperature regime, in order to match material to the planned utilization areas.

Key words: *Pinus sylvestris* (L.), adaptation, freezing tests, climatic change, continentality, heritability.

Introduction

Scots pine (*Pinus sylvestris* L.) is one of the most abundant and economically important forest tree species in northern parts of Europe. It is the subject of extensive breeding and seed orchard programs in both Scandinavia and Russia (DANELL, 1991; WILHELMSSON and ANDERSSON, 1993; NEKRASOV, 1995; ANTOLA, 1997). Abundant knowledge about provenance variation and transfer effects has been accumulated over a long time, providing the foundations for advanced breeding. In Scandinavia there has been a strong focus on latitudinal gradients, i.e. northward and southward transfers, and (to a lesser extent) altitudinal gradients (PERSSON and STAHL, 1990; PERSSON, 1994). Extensive transcontinental provenance experiments within the former USSR have also been established and evaluated (SHUTYAEV and GIERTYCH, 1997, 2000). In addition, genetic variation and genetic parameter estimates, including

genotype by environment (G x E) interactions, are now being gathered from progeny trials (e.g. HAAPANEN, 1996, 2001; JANS-SON et al., 2003; ROSVALL et al., 2002; PERSSON and ANDERSSON, 2003). The overall results show a potential to utilize both provenance transfer and selection of individual trees to improve survival and growth. Further, the G x E interaction appears to be too weak to cause major rank changes of families or provenances when they are grown within a limited geographical area (LINDGREN, 1982; GULLBERG and VEGERFORS, 1987; HAAPANEN, 1996; ZHELEV et al., 2003). Hence, their performance seems stable. The general explanation is that Scots pine, being a highly outcrossed species with extensive gene flow, has evolved a clinal adaptation to large-scale spatial and temporal variations in climatic factors, e.g. photoperiod and temperature, but no specific adaptations to more localised factors, such as particular soil conditions (SAVOLAINEN and HURME, 1997; ERIKSSON, 1998; ERIKSSON and EKBERG, 2001). However, very little is known about the effect of longitudinal origin of the seed source, at least with respect to the performance of continental provenances at maritime sites, and *vice versa*.

Information about the performance of material from remote origins should enlarge the potential pool from which suitable base material for breeding can be collected and, thus, could improve gain and diversity in future breeding and production populations. It should also provide valuable knowledge about the genetics of the species. Further, information about the expression of traits in varying environments should improve our ability to predict the effects of possible global climate changes. So far, empirical observations of the effects of expected climatic change usually have been obtained from provenance studies, in which northern provenances are grown in southern experiments with a milder climate (e.g. HÄNNINEN et al., 2001; BEUKER, 1994; MATYAS, 1994). However, climatic changes are expected to cause more complex alterations in climatic conditions than merely to increase mean temperatures. For instance, one hypothesis predicts that the climate in Scandinavia will become more maritime with milder winters, and extended summers with high precipitation (KOSKI, 1996; RÄISÄNEN et al., 2003).

The aims of this investigation were to estimate autumn cold hardiness of Scots pine populations from eastern (continental) and western (maritime) origins, and to estimate genetic variation between families. This was expected to yield information about the large scale spatial genetic variation of the species, and to enhance the possibility of enriching breeding populations through long-distance exchange of material. Further, knowledge about adaptation in diverse climates was expected to substantially improve predictions about performance under climate change scenarios.

Material and Methods

We used three different categories of Scots pine (*Pinus sylvestris* L.) material, i.e. Scandinavian populations (natural stand seed from northern Sweden and Finland), Russian populations (natural stand seed from the Komi Republic), and Russian families (open pollinated seed from single plus trees in a natural stand in Komi), (Table 1). The Russian seed were all

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Table 1. – Geographical origin of investigated seed sources.

Designation	Latitude (N)	Longitude (E)	Altitude a.s.l. (m)
<i>Natural stand seed from Russia</i>			
Ust-Kulom	61°30'	54°00'	< 200
Pomozdino	62°05'	54°20'	< 200
Megdurechensk	63°05'	50°50'	< 200
Sosnogorsk	63°50'	54°50'	< 200
Mechura	63°50'	51°10'	< 200
Udora	64°20'	49°10'	< 200
<i>Natural stand seed from Sweden/Finland^{a)}</i>			
Hultsfred	57°28'	15°50'	145
Mariannelund	57°35'	15°25'	220
Dampetorp	58°15'	13°00'	-
Laxå	59°00'	14°40'	120
Malung, Lima	60°30'	13°45'	450
Harkonberget	60°54'	14°20'	(350)
537-97	61°30'	15°30'	400
Y997	62°00'	15°55'	325
Stöde	62°25'	16°40'	200
791-98	63°00'	17°00'	200
Ramsele	63°30'	16°25'	400
1133-97	64°15'	19°30'	200
Aborrträskliden	64°45'	18°45'	295
S23A9810117	65°00'	20°30'	150
Malå	65°30'	18°45'	400
Arvidsjaur	65°35'	19°10'	400
Harads	66°10'	18°50'	200
Skellefteå	65°30'	20°00'	250
Isopuolamajärvi	66°53'	22°40'	150
Tärendö	67°05'	22°40'	250
Kaunisvaara	67°30'	23°20'	210
Lainio	67°40'	22°20'	350
Särkijärvi	68°00'	23°30'	200
Almajärvi	68°02'	23°10'	320
Inari	68°54'	27°00'	100
<i>Open pollinated progenies from 20 plus trees</i>			
Plus-tree 1-20	61°43'	51°07'	< 100

^{a)}longitudes are approximate

Figure 1. – Approximate origins of tested Scots pine seedlings. Scandinavian and Russian origins are indicated by filled and open circles, respectively. The Russian plus tree stand is indicated by the asterisk.

from seed that matured in 1999, while the Scandinavian seed matured in various years. The longitudinal distance between the Swedish and Russian seed sources was around 40° (or approximately 2000 km), Fig. 1, and is assumed to be associated with a significant difference in climatic conditions (maritime vs. continental, respectively). Continental climates characteristically have lower winter temperatures and higher summer temperatures than maritime climates (LOCKWOOD, 1985). In

Figure 2. – Monthly mean temperatures (upper panel) and number of days with ground frost (lower panel) at latitude 63°N in Sweden (longitude 17°E – filled circles) and Russia (longitude 54°E – open circles) from the CRU CL 2.0 data-set for the period 1961–1990, available at www.cru.uea.ac.uk (NEW et al., 2002).

Fig. 2 the monthly mean temperature and annual number of days with ground frost are shown for areas representative of the population origins in Scandinavia and Russia, respectively. The degree of continentality is here defined as the difference in monthly mean temperatures between the coldest (January) and warmest (July) month, according to LOCKWOOD (1985). The Swedish seed sources could be regarded as maritime and the Russian as continental.

Seeds were sown, raised and tested in Styrofoam containers (9 x 6 cells/container) with a cell size of 95 cm³. Twelve complete replicates, each containing six individual seeds per test entry in a row, were used. The position of test entries was randomly allocated to rows for the first replication and then shifted by one row for each replication to reduce systematic environmental variance. Further, container positions within the greenhouse were changed weekly. Seedlings were grown in a greenhouse with controlled heating and additional artificial light (providing 175 $\mu\text{mol m}^{-2}\text{s}^{-1}$ incident light). For the first ten weeks the day/night length was 20/4 h with a day/night temperature regime of 20/12°C. After that the conditions were changed to induce frost hardiness in the seedlings, by reducing the day/night temperature to 12/5°C and increasing the night length by 1 h per week to 16 h (week 22). The experiment was terminated after two additional weeks with 16 h nights (week 24). Seedlings were given a mixed fertilizer (N:P:K 100:13:65, 4 g N/m² and week) from the fourth to the fourteenth week.

Starting at week 18, night length 12 h, the first replications were moved from the greenhouse to a freezing chamber to test frost hardiness. Such tests were subsequently performed on complete replicates every 1–3 days. The test temperature was initially +10°C, then decreased at 5°C h⁻¹ to a preset minimum temperature (varying from –10 to –20°C for different replications), maintained at this level for two hours, and then returned to +10°C at a rate of 5°C h⁻¹. The selected preset minimum level was intended, in each case, to induce around 50% mortality in the material tested, and thus, gradually decreased during the hardening period. Freezing was applied in darkness, with root insulation of the containers (framed by Styrofoam plates) and without inoculating water. After freezing, seedlings were returned to greenhouse conditions to allow visible symptoms of damage to develop. The freezing damage was visually scored at week 24 using seven injury classes, mainly based on the amount of discoloured needles, according to ANDERSSON (1989).

Prior to the analyses the damage scores were linearized by transformation to normal score (NSC) values according to GIANOLA and NORTON (1981). Damage scores were thus first transformed to ranks, which were transformed to the expected values of the order statistics of the normal distribution, expressed in standard deviation units. We then used separate models for analysing stands and families. The stand data were analysed according to the fixed linear model:

$$y_{ijk} = b_i + c_j + d(L_{ijk} - \bar{L}) + e_{ijk} \quad (1)$$

where y_{ijk} is the NSC value for individual seedlings, b_i is the effect of replication, c_j is the effect of category (Scandinavian or Russian origin), d is a regression coefficient, L_{ijk} is latitudinal origin (°N) with mean $\bar{L}$, and e_{ijk} is the random residual, assuming IID (independent and identically distributed) with mean and variance (0, σ_e^2). The model was fitted by the GLM procedure of the SAS statistical package (SAS INSTITUTE INC., 1999). The interaction between categories and latitudinal origin was initially included in the model, but excluded due to lack of significance ($p > 0.975$ for type III sum of squares).

For the family analysis we fitted normal score transformed data to the following linear mixed model equation:

$$y_{ijk} = b_i + f_j + (bf)_{ij} + e_{ijk} \quad (2)$$

where y_{ijk} is the NSC value for individual seedlings, b_i is the fixed effect of replication, f_j is the random effect of family, assuming IID (0, σ_f^2), $(bf)_{ij}$ is the random interaction between replication and family, assuming IID (0, σ_{bf}^2), and e_{ijk} is the random residual, assuming IID (0, σ_e^2). The analysis was performed using the Mixed procedure of the SAS statistical package and REML method for variance estimation (SAS INSTITUTE INC., 1999).

Narrow sense heritability (h^2) was calculated as $4\sigma_f^2/(\sigma_f^2 + \sigma_{bf}^2 + \sigma_e^2)$ with standard error (SE) estimated according to the delta (Taylor series expansion) method.

Results

The latitudinal interval (span) of the populations tested was large enough for them to exhibit a clinal variation in frost hardiness (Table 2, Fig. 2). Each shift northward in latitude of origin reduced the damage score by 0.127 NSC units per degree, on average. As expected, northern populations were the hardest. Further, a distinct difference between the two population categories (Scandinavian and Russian) was revealed. Since there was no interaction effect between categories and latitudinal origin they seemed to follow the same cline, although at different parallels. Russian populations were more frost hardy than Scandinavian ones from corresponding latitudes, and

Figure 3. – Damage after autumn freezing tests of Scots pine populations from Scandinavia (filled squares) and Russia (open squares), and Scots pine open pollinated half-sib families (cross-hair) from one Russian population, with parallel regression lines and 95% confidence intervals.

Table 2. – Frost hardiness (NSC transformed damage levels) parameter estimates from model (1) with p -levels.

Source	Parameter	Estimate	Std. error	p level
Replication	b_i			<0.001
Category	c_j	-0.5260	0.0419	<0.001
Regression coefficient for latitude	d	-0.1272	0.0050	<0.001

Table 3. – Frost hardiness (NSC transformed damage levels) variance parameter estimates from model (2) with p -levels.

Source	Parameter	Estimate	Std. error	p level
Family	σ_f^2	0.0203	0.0097	0.018
Replication $\times$ Family	σ_{bf}^2	0.0595	0.0114	<0.001
Residual	σ_e^2	0.2960	0.01283	<0.001
Replication	b_i			<0.001

tended to attain the same level of frost hardiness as Scandinavian populations from 4.1° latitude further north, according to the regression analyses (c_j/d , see Table 2).

Open pollinated families varied significantly in frost hardiness (Table 3). Narrow sense heritability was calculated to be 0.22 (SE = 0.10), indicating relatively high genetic control of the trait. The most hardy half sib family performed as an average Swedish population from 67.5°N, whereas the least hardy was comparable to a Swedish population from 62°N. The results reveal large genetic variation in autumn frost hardiness. There were also indications that the Russian plus tree progenies were somewhat more damaged in the freezing tests, on average, than progenies from entire natural stands of the same latitudinal origin.

Discussion

The heritability of frost hardiness among open pollinated families was 0.22 in the Russian populations studied here. This is in good agreement with the heritabilities for Scandinavian populations that would be derived using data provided by NILSSON (1990). Heritabilities of this magnitude, along with pronounced additive genetic variation, clearly show potential for improving frost hardiness by breeding.

The mean hardiness of plus tree progenies were lower than the average hardiness of populations with corresponding latitudinal origins. The phenotypic plus tree selection, favouring trees with good growth, might have affected hardiness negatively due to correlated responses. However, the negative relationship between growth and survival normally found when selecting among provenances has not been found for individuals selected within populations (ANDERSSON et al., 2003). Thus, given the close relationship between frost hardiness and survival in northern Scots pine (NILSSON and ANDERSSON, 1987), the lower average hardiness of plus tree progenies found here is probably due to normal random variation between populations rather than to correlated responses. Sources of random variation include temporal variations in pollination parameters, and pollen clouds of more generally southerly origins than normal may have prevailed during the particular year of plus tree pollination.

Latitudinal clines were evident in both categories of material, since trees with northern origins showed relatively little damage. However, populations from Komi in Russia were harder than populations from Scandinavia of the same latitudinal origin. Since the Russian seed tested all matured in the same year (1999), the pollination conditions may have been unrepresentative, favouring more northern and harder pollen. However, it is unlikely that all populations systematically experienced conditions favouring hardy pollen since the populations are widely geographically separated and are thus exposed to different weather conditions. Overall, given the large number of populations tested, the results should have a reasonably high confidence level.

To our knowledge, this is the first report of significant longitudinal differentiation in Scots pine hardiness. In fact, SHUTYAEV and GIERTYCH (2000) found large scale regional differences in survival and other characters within the former USSR, but no evident longitudinal effects. Populations from the northwest had superior survival, but these populations were also by far the most northerly. Furthermore, western seed sources from Scandinavia with a more maritime origin were not included in their study. We interpret the longitudinal differences in frost hardiness as being mainly due to differences in temperature regime, because of the selective power of low temperatures for Scots pine cold hardiness (EICHE, 1966; HEIDE, 1985; TIGERSTEDT, 1994; JUNTILA, 1996). The climate in Scandinavia is considerably milder than in Komi at corresponding latitudes, due to the impact of the Gulf stream. In October at latitude 63°N (a critical period for attaining winter hardiness, when mean temperatures begin to drop below zero), the mean temperature is 3.8°C lower at longitude 54°E compared to longitude 17°E according to the CRU CL 2.0 data-set (NEW et al., 2002). The same difference in October mean temperature within Sweden requires a shift of 4° latitude further north (from lat 63°, long 17°E to lat 67°, long 23°E). This corresponds quite well with the freezing test results, showing that Swedish populations needed a 4.1° more northerly origin than populations from Komi in Russia to attain equivalent levels of frost hardiness. The results reveal interesting differences amongst Scots pine populations indicating that the longitude or continentality of their origin is associated with adaptive pressures that have significant effects on hardiness and are distinct from photoperiodic effects. Analogous differences in hardiness of similar magnitude associated with differences in longitudinal origin have been reported earlier by NILSSON (2001), but his comparison applied to different species – *P. contorta* from Canada and *P. sylvestris* from Sweden. The inland *P. contorta* had a cold acclimation rhythm comparable to that of Scots pine from 5–9° more northerly origins.

The overall findings from extensive provenance experiments within Scandinavia indicate that altitudinal origin has only minor and non-significant effects on hardiness and survival, in contrast to latitudinal origin (PERSSON, 1994; SUNDBLAD and ANDERSSON, 1995). In Scandinavia, altitudinal gradients covary to a great extent with longitude and continentality, since the mountain ridge and coast line both have mainly north-south orientations. Thus, the lack of altitudinal impact also implies a lack of longitudinal and continental effects. These results appear to conflict with our findings of distinct longitudinal differences in hardiness amongst Scots pines of different origins, but we probably found stronger effects because our material was sampled from a larger area. A possible reason for the apparent absence of longitudinal effects within Scandinavia is that the climatic variation may not be large enough, despite pronounced differences in harshness measured as the accumulated temperature sum during the vegetation period (ODIN et al., 1983; MOREN and PERTTU, 1994). At latitude 63°N, the maximum difference in continentality is 4.2°C within the forested area in Sweden (20.7°C and 24.9°C for longitudes 13°E and 18°E, respectively), compared with a difference of 11.5°C between Sweden and Komi in Russia (23.7°C for longitude 15°E in Sweden and 35.2°C for longitude 54°E in Komi) according to the CRU CL 2.0 data-set (NEW et al., 2002). Another possible contributory factor is that extensive gene flow via pollen migration between lowland and highland populations may undermine the evolution of hardy high-altitude provenances in Sweden.

Indeed, the results show that there is potential to enrich breeding populations with respect to autumn frost hardiness by including populations from remote origins. When doing this it is important to recognize not only latitudinal origin, but also longitudinal origin or temperature regime, in order to match material to planned utilization areas. Using eastern seed sources on western sites may also provide a way to improve survival at sites with very severe conditions where the scope for southward transfer of western material is limited due to the northern distribution range. Correspondingly, western seed sources may be superior on eastern sites with a locally mild climate. However, other characters, such as dehardening during spring, growth capacity, and resistance have to be considered as well. The presented results also demonstrate that if the climate changes to more maritime conditions with delayed and less harsh winters the present seed sources should be less frost damaged in the autumn. On the other hand, winter and spring frost damage may increase if the climatic changes include mild spells in winter or postponed spring and early summer conditions.

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Inbreeding in *Pinus Radiata* – V. The Effects of Inbreeding on Fecundity

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Abstract

A successful inbreeding and hybrid breeding strategy in tree improvement requires that 1) inbreeding (selfing) can produce superior inbred lines (effective purging of deleterious alleles), 2) there is heterosis among crosses of inbred lines, 3) early selection between lines is effective, and 4) inbreeding will not substantially reduce reproductive ability. We have previously reported that inbreeding depression on growth was lower in radiata pine relative to other conifers and segregation in the first two-generations of selfs generated superior inbred trees.

In addition, we have observed that early selection among inbred trees (lines) was more effective than in out-crossed populations and there was an apparent heterosis in radiata pine. In this study, the effect of inbreeding on the reproductive ability in young and adult trees of radiata pine has been quantified from five populations of varied inbreeding levels ($F=0$, 0.125, 0.25, 0.5, and 0.75). It was observed that the effects of inbreeding depression on fecundity was higher at a young age than at older age and inbreeding depression at a young age is due to two factors: 1) a delay of reproductive age (about 8.3, and 8.5% of trees delayed for $F=0.5$ and $F=0.75$ populations, respectively) and 2) a true reduction of flowering trees (6.7 and 13.1% more trees having no flowers for $F=0.5$ and $F=0.75$ populations than $F=0$ population, respectively). Despite significant

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