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Relationship between Autumn Cold Hardiness and Field Performance in northern *Pinus sylvestris*

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Results from 3 artificial freezing tests (one-year-old seedlings) and 15 field trials (9- to 21-year old trees) of half-sib offspring from first generation Scots pine (*Pinus sylvestris* L.) plus-trees were used to estimate the amount of additive genetic variance for autumn cold hardiness and traits assessed in the field, and the genetic correlations between them. Cold hardiness of individual seedlings was scored visually, based on the discoloration of their needles after freezing in a climate chamber. The field traits analyzed were tree vitality, tree height, spike knot frequency, branch diameter, branch angle, stem straightness, and susceptibility to infection by the pathogenic fungi *Phacidium infestans* L., *Gremmeniella abietina* (Lagerb.) Morelet, *Melampsora pinitorqua* (Braun) Rostr. and *Lophodermella sulcigena* (Rostr.) Höhn. Narrow sense individual heritabilities varied between 0.30 and 0.54 for autumn cold hardiness, 0 and 0.18 for tree vitality, 0.07 and 0.41 for tree height, and 0.01 and 0.26 for the remaining traits. Based on the results of the artificial freeze tests, our estimates of additive genetic correlations indicate that while early selection for cold hardiness can improve seedling survival rates in the field, it may also reduce growth in mild environments. It also has minor effects on quality traits and attack by common fungal diseases. The results indicate that artificial freeze testing is an appropriate method for identifying suitable clones for establishing seed orchards to supply stock for the reforestation of regions with harsh environments.

Keywords cold hardiness, genetic coefficient of variation, genetic correlation, multivariate analysis, narrow-sense heritability, Scots pine
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1 Introduction

During the 1980s and 1990s six Scots pine (*Pinus sylvestris* L.) seed orchards were established to provide material for reforestation programmes in harsh environments across northern Sweden (Andersson 1985, Rosvall et al. 2001). The selection of clones for these orchards was based on the results of artificial freeze tests of juvenile progenies in climate chambers (Andersson 1985). The rationale for adopting this selection strategy was that available progeny field trials were still too young to evaluate, and strong correlations had been found between injuries in artificial autumn freezing tests on first-year seedlings and field mortality assessments at ages of 10–18 years (Andersson 1986, Nilsson and Eriksson 1986, Nilsson and Andersson 1987, Nilsson et al. 1991). The six seed orchards should provide reforestation material for around 50 percent of the productive forestland in northern Sweden (Rosvall 2003). However, it is important to assess how early selection, based on freeze tests, could influence reforestation efforts, particularly with respect to tree survival rates, tree height, stem quality, and the incidence of fungal diseases.

The survival of Scots pine in northern latitudes shows a positive clinal relationship with the latitude of seed origin (Persson 1994), indicating an acclimation rhythm that is adapted to the photoperiod. Strong clinal correlations at the population level between autumn cold acclimation and seed origin have also been found in several artificial freeze test studies (Andersson 1986, Andersson 1992, Aho 1994, Sundblad and Andersson 1995, Nilsson 2001). Furthermore, considerable variation has been reported in field survival rates among different families within northern Scots pine populations (Eriksson et al. 1976, Persson and Andersson 2003), and in the degree of injury in artificial freeze tests during autumn cold acclimation among first-year seedlings representing different Scots pine families from narrow geographical areas in northern Sweden and Finland (Norell et al. 1986, Andersson 1992, Aho 1994).

As for field survival rates, large among- and within-population variations in tree growth have been reported in northern Scots pine material (Eriksson et al. 1976, Persson and Andersson 2003). In field trials of 11 to 13-year-old relatives Nilsson et al. (1991) found significant positive correlations between the freeze damage suffered by first-year seedlings and tree height, suggesting that selection for progeny with early cold acclimation may adversely affect growth.

Stem quality characters, including bole straightness, spike knot number, branch diameter, branch number and branch angle are also under genetic control in Scots pine (Remröd 1976, Eriksson et al. 1987, Haapanen et al. 1997, Hannrup et al. 2000), and in the northern part of the distribution range of Scots pine, the southward transfer of trees has been shown to result in a reduction in the number of spike knots and stem bends (Persson and Ståhl 1993).

Scots pine regenerations in northern regions can be affected by high incidences of disease caused by the pathogenic fungi *Phacidium infestans* L., *Gremmeniella abietina* (Lagerb.) Morelet, *Melampsora pinitorqua* (Braun) Rostr., and *Lophodermella sulcigena* (Rostr.) Höhn., attacks by *P. infestans* being the most frequent (Karlman 1986, Jalkanen 1986, Roll-Hansen et al. 1992, Mattila 2005, Ranta and Saloniemi 2005). The extent of injuries caused by *P. infestans* and *G. abietina* are generally correlated with the geographical origin of the trees; those with a more northerly origin tend to have higher levels of resistance (Stefansson and Sinko 1967, Dietrichson and Solheim 1987).

The aim of this study was to investigate the genetic relationship between the early autumn cold hardiness of one-year-old Scots pine seedlings, and the field performance under varying environmental conditions, of older, related individuals in terms of tree vitality, tree height, branch and stem quality, and susceptibility to attack by common fungal diseases.

2 Materials and Methods

2.1 Genetic Material and Experimental Design

The data analyzed in the present study were obtained from artificial freeze tests of the autumn

Table 1. Summary of the progeny trials and the genetic material studied. The experiments were divided into three different test groups. Each test group included a separate set of unique half-sib families that were tested in one freeze test (prefix FRR) and five field trials (prefix F).

Experiment	Temp. sum.[a]	Survival 12[b]	Survival 20[b]	Mean height 12[c]	Mean height 20[c]	No. blocks	No. stands	No. families	Total no. progenies
FRR833	.	.	.	.	.	9	33	284	15306
F356	514	55.0	13.4	101	.	14	33	305	7690
F357	496	52.8	21.5	117	334	11	33	305	7355
F422	794	66.9	56.7	195	526	15	33	303	6061
F423	628	24.3	12.7	158	370	10	33	303	7578
F429	606	66.3	.	125	.	18	33	291	6070
FRRT6	.	.	.	.	.	4	32	234	4917
F495	531	34.6	.	141	.	18	37	297	4168
F496	645	81.7	.	153	.	11	38	303	4116
F497	839	79.5	.	221	.	14	40	308	4187
F498	721	92.3	.	158	.	16	39	304	4207
F499	835	94.8	.	176	.	16	39	305	4116
FRR894R	.	.	.	.	.	6	34	271	10894
F506	1062	68.7	.	267	.	24	38	360	6160
F507	858	91.1	.	244	.	19	38	360	6212
F508	626	57.7	.	.	.	28	38	358	6512
F509	935	90.6	.	319	.	18	38	360	7193
F510	531	32.9	.	216	.	24	38	359	8116

[a] Expected temperature sum in day-degrees, threshold temperature +5ºC (Morén and Perttu 1994).
[b] Survival 12 and Survival 20 = Percentage of individuals surviving in age groups 11–13 and 19–21 years, respectively.
[c] Mean height 12 and Mean height 20 = Least square mean heights (cm) in age groups 11–13 and 19–21 years, respectively.

cold hardiness of one-year-old seedlings, and field measurements of 9- to 21-year-old relatives. In both cases, the plants were open-pollinated half-sib progenies of first-generation Scots pine (*Pinus sylvestris* L.) plus-trees. The field traits analyzed were tree vitality, tree height, spike knot frequency, branch diameter, branch angle, stem straightness, and susceptibility to infection by the pathogenic fungi *Phacidium infestans* L., *Gremmeniella abietina* (Lagerb.) Morelet, *Melampsora pinitorqua* (Braun) Rostr., and *Lophodermella sulcigena* (Rostr.) Höhn. The test material originated from three unrelated genetic groups, each of which comprised a separate set of half-sib families. One freeze test and five field trials were conducted for each test group (Table 1). The total number of families included in each test group ranged from 305 to 360 and the majority of the families within a test group were represented in all six experiments. The mother plus-trees were selected from 33 to 40 forest stands, depending on the test group. Each stand was assumed to represent a separate population located between approximately 65º and 68ºN in Sweden. The number of plus-trees in each stand varied from two to 30. A detailed overview of the origin of the genetic material and the locations of field trials is presented by Persson et al. (2006).

All experiments were established by the Forestry Research Institute of Sweden (Skogforsk). The open-pollinated seeds were collected from the plus-trees in the forest stands. In the field trials one-year-old potted seedlings were used in a randomized single-tree plot design. The freezing experiments were designed as complete blocks with 4–9 replications (Table 1), in which the seedlings were grown in a heated greenhouse with additional artificial light. To reduce systematic greenhouse effects, the location of the seedlings was changed weekly. For the first 9–10 weeks after germination, the seedlings were subjected to day/night cycles of 20/4 hours with 20–25º/12–15º C temperatures. In order to initiate cold acclimation in the seedlings, night length was successively increased by one hour per week, from 10 to 18 weeks after sowing, while the day

and night temperature was decreased to 15º–20º and 5º C, respectively. When the night length reached 10–14 hours the seedlings were exposed to low temperatures in a freezing chamber, one complete replicate at a time. The temperature in the chamber was initially set to +10º C and then gradually reduced by 4º C per hour. The minimum temperature varied between –10º C and –15º C for the different replicates and the chamber was maintained at that minimum temperature for two hours. Thawing was then initiated at a rate of 5º C per hour. The seedlings were kept in darkness during the cooling and thawing treatments, after which they were returned to the greenhouse.

2.2 Trait Assessment

Tree vitality was scored in four classes: healthy (3), slightly damaged (2), severely damaged but still alive (1), and dead (0). The height of living trees was also measured. Spike knots were assessed as the number of whorls where spike knots could be observed. Branch diameter and angle were visually assessed and classified into one of nine classes: class 5 was considered the 'standard' against which other classes were defined, and was taken as an 'average' example from a representative sample of similar-sized nearby trees; class 1 = extremely thin branches or straight angles and class 9 = the thickest possible branches or very sharp angles. Each tree was assessed relative to the trees in its neighbourhood. Stem straightness was visually graded in three classes: class 3 = stems with a straight bole and class 1 = stems with a severely crooked bole. The extent of visible infections of the fungi *P. infestans*, *G. abietina*, *M. pinitorqua* and *L. sulcigena* was judged by grouping trees into five classes based on the severity of the infection, according to guidelines described by Karlman et al. (1982). For each disease agent, class 0 = undamaged tree, class 1 a slightly damaged tree, and class 4 a severely damaged or dead tree. Between two and three weeks after freezing in the artificial freezing experiments, the cold hardiness of individual seedlings was assessed according to the extent of needle discoloration. This was visually scored in seven classes: 1 = all needles discoloured; 2–6 = the proportion of discoloured needles, decreasing in 20% intervals (99% to 81%, 80% to 61% etc.), and 7 = no visible discoloration of needles.

2.3 Statistical Analyses

The existence in northern Scots pine of a clinal variation associated with the latitude of seed origin has been thoroughly verified (Persson and Ståhl 1993, Persson 1994), thus justifying the inclusion of the 'stand' as a genetic effect in the model.

Macro-environmental variation in the field trials was accounted for by clustering observations from adjacent single-tree plots into blocks in the statistical model (Ericsson 1997). The number of blocks across the trials ranged from 10–28 (Table 1). Categorical data were transformed separately within each block to normal linearized score values (Gianola and Norton 1981).

Multivariate REML (Restricted Maximum Likelihood) analyses were performed to estimate the additive genetic and environmental variances for all traits, and the additive genetic correlations between cold hardiness and field traits. The analyses were carried out separately within each test group, using data from one freeze test and one field trial at a time. Bivariate analyses were conducted for cold hardiness and tree vitality. Trivariate analyses were conducted in order to reduce bias in derived correlation estimates between cold hardiness and the other traits, due to non-random mortality in the field (Persson and Andersson 2004). Tree vitality (the trait describing mortality in the field) was included as the third trait.

For all data, the fitted mixed linear model was:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Ws} + \mathbf{Zf} + \mathbf{e}$$

with

$$\mathbf{y} = \left[\mathbf{y}_1' \; \mathbf{y}_2' \; \mathbf{y}_3'\right]', \; \mathbf{b} = \left[\mathbf{b}_1' \; \mathbf{b}_2' \; \mathbf{b}_3'\right]', \; \mathbf{s} = \left[\mathbf{s}_1' \; \mathbf{s}_2' \; \mathbf{s}_3'\right]',$$

$$\mathbf{f} = \left[\mathbf{f}_1' \; \mathbf{f}_2' \; \mathbf{f}_3'\right]' \text{ and } \mathbf{e} = \left[\mathbf{e}_1' \; \mathbf{e}_2' \; \mathbf{e}_3'\right]'$$

, where **y** is the observation vector of the individual tree observations of traits 1, 2 and 3 (reduced to two traits in the bivariate analyses), and **b**, **s**, **f** and **e** are the corresponding vectors of the fixed effects (*i.e.* overall mean and block effects),

random stand effects, random family effects, and random residual deviations, respectively. **X**, **W** and **Z** are the corresponding incidence matrices, connecting the observations to the fixed, random stand, and random family effects, respectively. The random effects were assumed to follow independent multivariate normal distributions with zero means and (co)variances

$$V\begin{bmatrix}\mathbf{s}\\ \mathbf{f}\\ \mathbf{e}\end{bmatrix}=\begin{bmatrix}\mathbf{G}_s\otimes\mathbf{I} & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{G}_f\otimes\mathbf{I} & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{R}\otimes\mathbf{I}\end{bmatrix}$$

, where **0** is a null matrix, **I** are identity matrices (with the order corresponding to **W**, **Z**, and the number of records, respectively), $\mathbf{G}_s = \{\sigma_{s_i s_j}\}$, $\mathbf{G}_f = \{\sigma_{f_i f_j}\}$ and $\mathbf{R} = \{\sigma_{e_i e_j}\}$ are the stand, family and residual variance-covariance matrices, respectively (i, j = 1 to trait n, denoting the variance when $i = j$, *e.g.* $\sigma_{s_i s_i} = \sigma^2_{s_i}$), and $\otimes$ is the direct product. In the trivariate analyses, the covariance between cold hardiness and tree vitality was set to zero in $\mathbf{G}_s$ and $\mathbf{G}_f$. In **R**, all off-diagonal elements were assumed to be zero for the combination of traits that were measured in different trials.

REML estimates of (co)variance components were derived using the average information algorithm (Gilmour et al. 1995) implemented in the ASReml program (Gilmour et al. 2001). The variance components were restricted to be positive, while individual correlation estimates were allowed to exceed the boundaries of 1 and –1.

The estimated additive genetic variances and covariances, environmental variances, narrow-sense individual heritabilities, and additive genetic correlations, were calculated at the overall level as

$$\hat{\sigma}^2_A = \hat{\sigma}^2_s + 4\hat{\sigma}^2_f, \hat{\sigma}_{A_{12}} = \hat{\sigma}_{s_1 s_2} + 4\hat{\sigma}_{f_1 f_2}, \hat{\sigma}^2_E = \hat{\sigma}^2_e + 3\hat{\sigma}^2_f,$$

$$\hat{h}^2 = \hat{\sigma}^2_A / (\hat{\sigma}^2_A + \hat{\sigma}^2_E) \text{ and } \hat{r}_A = \hat{\sigma}_{A_{12}} / \sqrt{\hat{\sigma}^2_{A_1}\hat{\sigma}^2_{A_2}}$$

, respectively (*i.e.* assuming common stand effects and true half-sibs). Approximate standard errors of the parameters were calculated using Taylor series expansion as implemented in the ASReml program. The additive genetic and environmental coefficients of variation (CV_A and CV_E, respectively) were defined as $100\sqrt{\hat{\sigma}^2} / \bar{x}$ for tree height and $100\left[\left[\Phi(\sqrt{\hat{\sigma}^2}) - 0.5\right] / 0.5\right]$ for the categorical variables at the 50% incidence level, where $\hat{\sigma}^2$ pertains to $\hat{\sigma}^2_A$ and $\hat{\sigma}^2_E$ for CV_A and CV_E, respectively, $\bar{x}$ is the least square mean for tree height and Φ is the standard normal probability distribution function. Weighted average estimates of $\hat{r}_A$ were calculated as $\bar{r}_A = \sum(\hat{r}_{A_i} / SE^2_i) / \sum(1 / SE^2_i)$, where $\hat{r}_{A_i}$ and SE_i refer to the estimates of the ith $\hat{r}_A$ and its standard error, respectively.

3 Results

The lowest survival rates and mean heights were mostly found in trials at sites with a low temperature sum (Table 1). In test group F356–F429, the average survival rate declined from 53.1% to 26.1% between 11–13 and 19–21-years of age. The proportion of individuals with spike knots varied from 13.95 to 87.55, with an average value across all trials of 49.0% (data not shown). Of the monitored fungi, attacks by *P. infestans* and *G. abietina* were most frequently detected, with the highest infection levels generally recorded at sites with a low temperature sum.

Narrow sense individual heritabilities varied from 0.30 to 0.54 for cold hardiness, 0 to 0.18 for tree vitality, 0.07 to 0.41 for tree height, and 0 to 0.26 for the remaining traits (Table 2). Standard errors were generally below 0.1 and frequently in the range 0–0.04. In test group F356–F429 the $\hat{h}^2$ for tree height at 19–21 years of age was larger than corresponding 9–13-year-old estimates. Among the quality traits, branch angle showed the highest $\hat{h}^2$ values while stem straightness had the lowest values. CV_A estimates (Table 3) varied from 2.1 to 53.8%, with pooled estimates across trials ranging between 10.8% and 44.3% for the different traits. In test group F356–F429, the CV_A for tree vitality at 19–21 years of age was smaller than the corresponding estimates for the 9–13-year-old trees.

The arithmetic mean CV_E values across trials for tree vitality in the trials F356, F357, F422 and F423, were 56.9% and 49.4% at tree ages 11–13 and 19–21 years, respectively (data not shown). For tree height, the pooled CV_E values in trials F357, F422 and F423 decreased from 28.4% to 16.6% for trees between 11–13 and 19–21 years of age.

Table 2. Multivariate estimates of narrow-sense individual heritabilities (with standard errors in parenthesis) for the traits evaluated[a].

Experiment	V12	V20	H12	H20	SK	BD	BA	SS	PI	GA	MP	LS	CH
FRR833	.	.	.	.	.	.	.	.	.	.	.	.	0.50 (0.04)
F356	0.17 (0.03)	0.10 (0.02)	0.15 (0.04)	.	0.06 (0.04)	.	.	.	0.11 (0.03)	0.21 (0.03)	.	.	.
F357	0.15 (0.02)	0.14 (0.02)	0.15 (0.03)	0.27 (0.08)	*n.e.*	.	.	.	0.12 (0.03)	0.20 (0.03)	.	.	.
F422	0.01 (0.00)	0.00 (0.00)	0.07 (0.02)	0.22 (0.05)	0.07 (0.03)	.	.	.	0.02 (0.01)	.	.	.	.
F423	0.14 (0.02)	0.14 (0.02)	0.18 (0.04)	0.41 (0.13)	0.08 (0.06)	.	.	.	*n.e.*	0.02 (0.01)	.	.	.
F429	0.10 (0.02)	.	0.14 (0.03)	.	0.04 (0.03)	.	.	.	0.09 (0.02)	0.01 (0.00)	.	.	.
FRRT6	.	.	.	.	.	.	.	.	.	.	.	.	0.54 (0.06)
F495	0.18 (0.04)	.	0.08 (0.04)	.	0.03 (0.07)	.	.	.	0.09 (0.07)	0.26 (0.05)	.	.	.
F496	0.06 (0.03)	.	0.17 (0.04)	.	0.00 (0.00)	.	.	.	0.11 (0.03)	.	.	0.12 (0.04)	.
F497	0.06 (0.03)	.	0.19 (0.04)	.	0.10 (0.04)	.	.	.	0.05 (0.03)	0.02 (0.03)	0.13 (0.04)	0.25 (0.05)	.
F498	0.02 (0.02)	.	0.26 (0.04)	.	0.09 (0.03)	.	.	.	*n.e.*	.	0.14 (0.03)	.	.
F499	0.00 (0.00)	.	0.28 (0.04)	.	0.09 (0.03)	.	.	.	.	.	.	.	.
FRR894R	.	.	.	.	.	.	.	.	.	.	.	.	0.30 (0.03)
F506	0.03 (0.02)	.	0.17 (0.04)	.	0.02 (0.02)	0.16 (0.04)	0.20 (0.04)	0.04 (0.03)	.	.	0.00 (0.00)	.	.
F507	0.02 (0.02)	.	0.15 (0.03)	.	0.07 (0.02)	0.07 (0.02)	0.14 (0.03)	*n.e.*	.	.	.	.	.
F508	0.10 (0.02)	.	.	.	.	.	.	.	.	0.08 (0.03)	0.05 (0.03)	.	.
F509	0.00 (0.00)	.	0.14 (0.02)	.	0.05 (0.02)	0.11 (0.02)	0.15 (0.03)	0.04 (0.02)	.	.	0.07 (0.02)	.	.
F510	0.11 (0.02)	.	0.10 (0.02)	.	0.13 (0.03)	.	.	.	0.12 (0.03)	0.05 (0.01)	.	.	.
Mean[b]	0.08	0.10	0.16	0.30	0.06	0.11	0.17	0.04	0.09	0.11	0.08	0.19	0.45

[a] V12 and V20 = Tree vitality in age groups 11–13 and 19–21-years, respectively; H12 and H20 = tree height at ages of 9–13 and 19–21 years, respectively; SK = spike knots; BD = branch diameter; BA = branch angle; SS = stem straightness; PI, GA, MP and LS = infections by the fungi *P. infestans*, *G. abietina*, *M. pinitorqua* and *L. sulcigena*, respectively; CH = cold hardiness. SK, BD, BA, SS, PI, GA, MP, LS were all assessed in the field from trees in the age group of 11–13 years.

[b] Arithmetic mean across trials.

n.e. – not estimated: the genetic variance could not be estimated.

Table 3. Multivariate estimates of additive genetic coefficients of variation (%) for the traits evaluated. The trait codes are presented in Table 2.

Experiment	V12	V20	H12	H20	SK	BD	BA	SS	PI	GA	MP	LS	CH
FRR833	.	.	.	.	.	.	.	.	.	.	.	.	46.4
F356	28.8	16.1	9.2	.	17.6	.	.	.	23.2	36.7	.	.	.
F357	26.8	21.2	13.8	12.1	*n.e.*	.	.	.	30.0	41.5	.	.	.
F422	6.2	4.5	7.5	7.9	18.4	.	.	.	11.7	.	.	.	.
F423	22.3	18.8	11.0	12.6	18.1	.	.	.	*n.e.*	14.4	.	.	.
F429	21.2	.	9.5	.	12.1	.	.	.	29.4	2.9	.	.	.
FRRT6	.	.	.	.	.	.	.	.	.	.	.	.	49.0
F495	26.8	.	11.3	.	9.2	.	.	.	20.3	53.8	.	.	.
F496	14.6	.	12.6	.	2.5	.	.	.	31.0	.	.	12.6	.
F497	16.3	.	11.2	.	24.2	.	.	.	9.9	6.7	27.8	23.0	.
F498	7.3	.	12.5	.	22.6	.	.	.	*n.e.*	.	26.1	.	.
F499	2.1	.	15.2	.	23.3	.	.	.	.	.	.	.	.
FRR894R	.	.	.	.	.	.	.	.	.	.	.	.	37.4
F506	10.6	.	11.5	.	10.6	21.0	25.6	15.0	.	.	2.6	.	.
F507	7.0	.	11.5	.	19.7	12.7	20.1	*n.e.*	.	.	.	.	.
F508	21.0	.	.	.	.	.	.	.	.	26.3	11.5	.	.
F509	2.1	.	9.6	.	16.6	17.6	21.9	13.4	.	.	16.6	.	.
F510	20.2	.	13.3	.	33.1	.	.	.	40.6	20.0	.	.	.
Mean[a]	15.6	15.1	11.4	10.8	17.5	17.1	22.5	14.2	24.5	25.3	16.9	17.8	44.3

[a] Arithmetic mean across trials.
n.e. – not estimated: it was not possible to estimate the genetic variance.

The $\hat{r}_A$ values between cold hardiness and 11–13-year-old tree vitality ranged between –0.64 and 0.65, although some estimates (including all of the negative values) were not significantly distinguishable from zero because of large standard errors (Table 4). The weighted average $\hat{r}_A$ across all trials was 0.30, indicating that good performance in freeze tests is positively correlated with higher survival rates in the field. The $\hat{r}_A$ values with the largest standard errors were generally from trials with low mortality and small values of $\hat{h}^2$ and CV_A, which significantly increases the probability of obtaining highly misleading correlation estimates (Persson and Andersson 2004). Aggregating $\hat{r}_A$ values solely from trials with an $\hat{h}^2$ equal to or greater than 0.03 resulted in 10 estimates with a weighted average of 0.39. For 19–21-year-old trees in test groups F356–F429, all $\hat{r}_A$ values between vitality and cold hardiness were positive, with a weighted average of 0.26, while the weighted average of the corresponding 11–13-year estimates was 0.25.

Large variation was observed in sign and reliability among the $\hat{r}_A$ values between cold hardiness and height of 9–13-year-old trees, with values ranging between –0.57 and 0.19, and with a weighted average across all trials of –0.17 (Table 4). Most of the negative $\hat{r}_A$ values were derived from tree heights assessed in trials with the highest temperature sums, while the positive $\hat{r}_A$ values were all derived from sites with harsher environments. The height of a young tree located in a harsh environment may reflect aspects of a tree's health more than its growth capacity (Persson et al. 2006). When the harshest sites (defined here as sites with a temperature sum below 700) were excluded, the weighted average for the remaining seven $\hat{r}_A$ values was –0.33. The $\hat{r}_A$ values between cold hardiness and height of 19–21-year-old trees in test groups F356–F429 varied from –0.15 to –0.01, with standard errors of the same magnitude as the parameter estimates.

For the quality characters (spike knot, branch diameter, branch angle and stem straightness) and the susceptibility to infection by each of the pathogens, the $\hat{r}_A$ values for cold hardiness varied considerably (Table 4). The correlation estimates generally had high standard errors and no strong

Table 4. Multivariate estimated additive genetic correlations (with standard errors in parenthesis) between cold hardiness in the freeze experiment and the different field traits. The trait codes are presented in Table 2.

Experiment	V12	V20	H12	H20	SK	BD	BA	SS	PI	GA	MP	LS
F356	0.25 (0.08)	0.27 (0.10)	–0.06 (0.12)	.	–0.14 (0.18)	.	.	.	–0.19 (0.10)	–0.03 (0.04)	.	.
F357	0.28 (0.09)	0.35 (0.09)	0.19 (0.08)	–0.01 (0.13)	*n.e.*	.	.	.	0.03 (0.09)	0.04 (0.04)	.	.
F422	0.18 (0.05)	0.17 (0.06)	–0.17 (0.11)	–0.15 (0.11)	0.07 (0.15)	.	.	.	–0.01 (0.12)	.	.	.
F423	0.44 (0.08)	0.37 (0.09)	0.02 (0.08)	–0.15 (0.14)	–0.28 (0.21)	.	.	.	*n.e.*	0.00 (0.02)	.	.
F429	0.54 (0.10)	.	0.16 (0.10)	.	–0.09 (0.19)	.	.	.	–0.07 (0.03)	–0.01 (0.05)	.	.
F495	0.55 (0.10)	.	–0.10 (0.13)	.	–0.11 (0.40)	.	.	.	0.11 (0.22)	–0.05 (0.06)	.	.
F496	0.49 (0.19)	.	–0.14 (0.09)	.	–0.02 (0.14)	.	.	.	–0.39 (0.10)	.	.	0.12 (0.14)
F497	–0.16 (0.18)	.	–0.30 (0.11)	.	–0.04 (0.13)	.	.	.	–0.52 (0.24)	–0.04 (0.27)	0.32 (0.13)	0.08 (0.11)
F498	–0.64 (0.46)	.	–0.43 (0.09)	.	–0.03 (0.15)	.	.	.	*n.e.*	.	0.07 (0.12)	.
F499	–0.06 (0.11)	.	–0.57 (0.08)	.	–0.03 (0.14)	.	.	.	.	.	.	.
F506	0.19 (0.21)	.	–0.33 (0.11)	.	–0.16 (0.11)	–0.22 (0.12)	–0.05 (0.11)	–0.04 (0.18)	.	.	0.11 (0.13)	.
F507	0.45 (0.30)	.	–0.30 (0.10)	.	0.20 (0.14)	–0.28 (0.15)	–0.04 (0.11)	*n.e.*	.	.	.	.
F508	0.20 (0.12)	.	.	.	.	.	.	.	.	–0.04 (0.09)	–0.37 (0.23)	.
F509	0.28 (0.15)	.	–0.33 (0.09)	.	0.09 (0.14)	–0.11 (0.11)	–0.08 (0.11)	–0.04 (0.16)	.	.	0.18 (0.13)	.
F510	0.65 (0.09)	.	0.00 (0.08)	.	0.09 (0.10)	.	.	.	–0.09 (0.09)	0.05 (0.02)	.	.
Mean[a]	0.30	0.26	–0.17	–0.11	–0.01	–0.19	–0.06	–0.04	–0.09	0.01	0.13	0.09

[a] Weighted average estimates across trials of additive genetic correlations.
n.e. – not estimated: it was not possible to estimate the genetic (co)variance.

associations were observed. However, if estimates that were clearly non-significant were excluded, there were tendencies for branch diameter and damage by *P. infestans* to be negatively correlated with cold hardiness.

4 Discussion

The aim of this investigation was to examine correlations between cold hardiness and field performance in Scots pine across a range of environments. Therefore, the statistical analyses of the field performance were carried out on a single-site basis. However, it should be noted that these values may be influenced by genotype by environment interactions.

The generally moderate, positive correlations between autumn cold hardiness and tree vitality illustrate that survival is a complex trait, reflecting the combined effects of all the events causing injuries and die-back in Scots pine regenerations, and that autumn cold acclimation is only one of several important factors. Nevertheless, the positive genetic correlation demonstrates that early selection, based on artificial freeze tests during autumn cold acclimation, should improve the ability of selected material to survive in harsh environments.

Contrasting correlation patterns were observed among $\hat{r}_A$ values between autumn cold hardiness and tree height, with a negative association if the tree heights were assessed in relatively mild environments, and a positive association if the heights were assessed in harsh environments. These findings are consistent with the results of Persson et al. (2006), who found that the sign of the genetic correlation between tree height and tree vitality changed from negative to positive as the harshness of the field site increased. The results of the present study clearly strengthen the hypothesis proposed by Persson et al. (2006) that the heights of 9–13-year-old trees, measured in harsh and mild environments, to some extent represent different traits. The generally negative correlations between cold hardiness and tree height indicate that selection, based on the performance of juvenile progenies in artificial freeze tests during autumn cold acclimation, can have a negative influence on height growth in mild environments.

The large variability among the $\hat{r}_A$ values across trials for cold hardiness, and the traits spike knot, branch diameter, branch angle, stem straightness, and resistance to infections by *P. infestans*, *G. abietina*, *M. pinitorqua* and *L. sulcigena*, together with their large standard errors, suggest that trends of genetic association may have been masked. These results demonstrate that there are probably low levels of consistent genetic association between cold hardiness and these traits. However, the tendency for cold hardiness and infection by *P. infestans* to be negatively genetically correlated supports earlier Scots pine provenance studies (Stefansson and Sinko 1967), indicating that hardy families are less susceptible to this pathogen.

The generally large CV_A of susceptibility to the fungal diseases considered in this study, despite the low average $\hat{h}^2$, indicates that enough additive genetic variance is present to make breeding for resistance beneficial. However, parameter estimates for threshold characters are dependent on the incidence of the specific trait in the population (Gianola 1982), with the optimum incidence level being approximately 50%. Thus, selection efficiency would vary in practice, depending on the prevailing conditions (incidence level).

Since both stand and family effects were considered during the selection of seed orchard clones based on progeny freeze tests, we chose to infer genetic relationships from overall correlation estimates, despite the fact that between-population covariance estimates may be influenced by both pleiotropic and built-up genetic associations (Latta 1998). Persson and Andersson (2003) provided support for this approach as they found close agreement among additive genetic correlations between tree height and tree vitality that were estimated at both the family level and at overall levels, in a study of northern Swedish and Finnish Scots pine populations.

The ranges of $\hat{h}^2$ and CV_A values for tree vitality, tree height, quality traits and *M. pinitorqua* damage are consistent with earlier investigations of northern Scots pine populations (Andersson and Danell 1997, Haapanen et al. 1997, Hannrup et al. 2000, Olsson and Ericsson 2002, Persson and Andersson 2003, Zhelev et al. 2003), demon-

strating the expression of the traits in the present study to be representative of this species. In a survey of 13 Scots pine progeny trials (5–39 years old) in southern Sweden, Jansson et al. (2003) found that individual tree heritability for height increased slightly over time, whereas in a study of 26 Scots pine progeny trials in Finland Haapanen (2001) found no systematic time trends in tree height heritability for trees between the ages of 5 and 18 years. However, both Jansson et al. (2003) and Haapanen (2001) reported that CV_A values for tree height decreased with age. We found that $\hat{h}^2$ values for tree height clearly increased with age, but we observed no clear trend for the corresponding CV_A values. Since the CV_E for tree height declined with age, the increase in $\hat{h}^2$ for tree height between the ages of 9–13 and 19–21-years was mainly due to reduced environmental variability. The reductions in CV_E with age, for both tree vitality and tree height are presumably due to a decrease in the susceptibility of trees to environmental disturbance as they become older and taller. The $\hat{r}_A$ values between cold hardiness and tree vitality did not change markedly with age, while the $\hat{r}_A$ values between cold hardiness and the height of 19–21-year-old trees were insignificant and hence may have masked possible time trends. Thus, the $\hat{r}_A$ between cold hardiness and tree vitality seems to be accurately expressed by trees between 11 and 13 years old, whereas later assessments, from a larger number of trials, are needed to verify age trends in the $\hat{r}_A$ between cold hardiness and tree height.

In conclusion, the selection of seed orchard clones based on juvenile freeze test results would probably improve tree vitality. However, it would also reduce tree height in mild environments and have minor effects on quality traits and attack by common fungal diseases in any new forests originating from these seed orchards.

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