Genetic Expression of
Scots Pine Growth and Survival
in Varying Environments

Torgny Persson

Faculty of Forest Sciences
Department of Forest Genetics and Plant Physiology
Umeå

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Abstract

The aim of the studies underlying this thesis was to quantify the genetic variability of important traits used for ranking candidate trees in northern Swedish Scots pine (*Pinus sylvestris* L.) breeding populations, with special focus on growth and survival and the genetic association between these traits.

The thesis reports studies based on simulated data, field data from 28 progeny trials, and early test data from four artificial freezing experiments. The field and freezing experiments comprised half-sib progenies of Swedish and Finnish Scots pine plus-trees. The field trials (9–21 years old) were established in a wide range of environmental conditions. The traits analyzed were survival, tree height, spike knot frequency, branch diameter, branch angle, stem straightness, and susceptibility to infections of the fungi *Phacidium infestans*, *Gremmeniella abietina*, *Melampsora pinitorqua* and *Lophodermella sulcigena*. In the freezing experiments cold hardiness of 1-year-old seedlings was assessed after freezing in a climate chamber.

In the simulation study the accuracy of single- and multiple-trait REML procedures was examined by studying estimates of within-individual genetic correlations between a categorical trait and a continuous trait with selectively deleted records. The average bias generated by multiple-trait REML was generally low, whereas single-trait REML systematically provided too moderate estimates. The variation among the correlations was generally high, showing that single-site estimates might be seriously misleading.

The average within-site genetic correlation between tree height and field survival was generally positive, whereas corresponding between-site estimates were positive when the tree heights were assessed in harsh environments, but negative if the tree heights were assessed in mild environments (0.05 and –0.25, respectively). The genetic correlation between cold hardiness and field survival was on average positive (0.30), while the average correlation between cold hardiness and tree height was negative (–0.23). For the quality characters and susceptibility to infections of the pathogens, genetic associations with cold hardiness could not be verified.

The most notable result was the contrasting correlation patterns across environments between tree height and field survival in the material sampled. The results show that tree heights from young trials located in harsh areas may reflect tree health and survival ability to a greater extent than growth capacity.

Keywords: Genetic coefficient of variation, Genetic correlation, Monte Carlo simulation, Multiple-trait analysis, Narrow-sense heritability, *Pinus sylvestris*, REML.

Author's address: Torgny Persson, Skogforsk, P.O. Box 3, S-918 21 SÄVAR, Sweden.

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Appendix

Papers I-IV

The present thesis is based on the following papers, which will be referred to by their Roman numerals:

I. Persson, T. & Andersson, B. 2004. Accuracy of single- and multiple-trait REML evaluation of data including non-random missing records. *Silvae Genetica* 53, 135-139.

II. Persson, T. & Andersson, B. 2003. Genetic variance and covariance patterns of growth and survival in northern *Pinus sylvestris*. *Scandinavian Journal of Forest Research* 18, 332-343.

III. Persson, T., Ericsson, T. & Andersson, B. Contrasting covariance patterns between growth and survival in northern *Pinus sylvestris*. (Manuscript).

IV. Persson, T., Andersson, B. & Ericsson, T. Relationship between autumn cold hardiness and field performance in northern *Pinus sylvestris*. (Manuscript).

Papers I and II are reproduced by permission of the journals concerned.

Introduction

The focus of the investigations this thesis is based upon was the genetic variability of important traits used for ranking candidate trees in northern Swedish Scots pine (*Pinus sylvestris* L.) breeding populations, with special emphasis on genetic characterization of growth and survival, and the genetic association between the traits. The thesis starts with a description of major climatic features of northern Sweden, then reviews aspects of growth, cold hardiness and mortality in Scots pine regenerations. These reviews are followed by a description of the material studied and methodology used, a synthesis and discussion of the results, main conclusions and possible applications of the findings. The thesis concludes with suggestions for further research.

The climate

Forest production in northern Sweden is confined to an area approximately delineated by latitudes 60 and 68°N. The region has an unpredictable and variable climate with a short, cool growing season (Ångström, 1974; Odin, 1984; Alexandersson, Karlström & McCann-Larsson, 1991). Data collected between 1930 and 1990 from forest areas in the interior of northern Sweden (Lindgren, 1993) indicate that there are significant variations in average temperatures between growing seasons, comparable to variations in altitude of 300 m. The annual temperature range generally increases with latitude; summers being cooler and winters colder further north, while the diurnal temperature fluctuations generally decrease with latitude (Heide, 1985). There are wide variations in both photoperiod and total radiation over the year. A strong relationship between the climate and the growth of trees has been demonstrated by Morén & Perttu (1994). The cited authors showed that the annual average forest yield in Sweden was strongly correlated (r = 0.89) with the temperature sum in day-degrees (threshold value, +5°C).

Growth

Total vegetative growth of any plant species generally depends on both its growth rate and the duration of the growth period. The growth period of Scots pine can be separated into several different morphological phases, such as shoot elongation from bud burst until shoot growth cessation, elongation of needles and roots, and diameter growth. Another, more physiologically relevant, way to define the growth period is the duration of cell division.

First-year Scot pine seedlings have a free growth pattern, in which new needle primordia are formed and elongate as long as the environment is favourable. The cessation of growth is regulated by both temperature and photoperiod (Koski & Sievänen, 1985). After the first year seedlings have a predetermined shoot growth pattern, since all of the needle primordia have been formed in the previous year. The shoot elongation period is then mainly affected by the temperature, and usually

finishes by early mid-summer (Koski & Sievänen, 1985). After cessation of shoot elongation the remaining part of the growing season is used (*inter alia*) for needle elongation and maturation, growth of roots and stem diameter, and formation and maturation of bud tissue. Cessation of aboveground vegetative growth and dormancy induction are strongly influenced by the photoperiod, but are also affected by temperature (Koski & Sievänen, 1985; Dormling, 1986).

Many studies of northern Scots pine have reported large variations amongst provenances in growth and hardiness characters, which exhibit clinal trends associated with the latitude of seed origin (Langlet, 1936; Persson, 1994). The further north the origins, the earlier the growth cessation, the shorter the tree height and the greater the hardiness of the material. However, no significant effects of altitudinal origin on either field survival (Persson, 1994) or autumn cold hardiness, as evaluated in artificial freezing tests (Sundblad & Andersson, 1995), have been found. Thus, the latitude of the seed source, temperature and photoperiod seem to be the main factors that regulate the phenology of Scots pine seedlings, and thus the length of the active growth period.

Cold hardiness

In most woody plants, the ability to withstand cold is connected to the regulation of acclimation and de-acclimation, rather than to absolute low temperature tolerance. The cold hardiness of perennial plants growing under northern conditions is mainly dependent on the synchronicity of the local climate and the plant's phenology during transitional periods in spring and autumn (Junttila, 1996).

The weather conditions of the late winter significantly influence the survival of Scots pine seedlings and young trees. Fluctuating temperatures (Nilsson & Walfridsson, 1995; Nilsson, 2001) and winter desiccation (Christersson & von Fircks, 1988), combined with photoinhibition and subsequent photooxidation (Öquist, 1983), may cause severe injuries. During spring, damaged photosynthetic apparatus may recover, but only if temperature conditions are suitable (Lundmark, Hällgren & Hedén, 1988).

Unhardened Scots pine plants of Scandinavian origin can normally withstand temperatures during the growing season of between –4° and –6 °C, depending on age, stage of development and the type of tissue (Christersson & von Fircks, 1988; Repo, 1992; for an extensive review, see Repo *et al.*, 2001). However, exposure to temperatures between zero and –6 °C during the growing season may cause visual symptoms, such as abnormally shaped or brown needles, and disturbance of apical dominance (Rikala & Repo, 1987; Ryyppö *et al.*, 1997). It has been proposed that night frosts followed by clear days, with high levels of solar radiation, increase the plants' susceptibility to photoinhibition and subsequent photooxidation (Lundmark & Hällgren, 1987; Strand & Lundmark, 1987; Hällgren, Lundmark & Strand, 1990). A cool, short growing season may result in incomplete physiological maturation of tissues during the autumn. Consequently, cambial freezing injury and dieback of terminal shoots may occur in the subsequent growing season (Venn, 1970).

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Mortality in Scots pine regenerations

In northern Sweden, the growing season becomes shorter and its harshness increases at higher latitudes and altitudes (Alexandersson, Karlström & McCann-Larsson, 1991; Morén & Perttu, 1994). The mortality in Scots pine regenerations increases in harsher areas (Eriksson *et al.*, 1980; Persson, 1994) and is usually the result of repeated injuries occurring over several years (Eiche, 1966; Stefansson & Sinko, 1967).

Tolerance of harsh/adverse conditions seems to depend, partly, on the tree size. Mortality in Scots pine regenerations occurs predominately before the trees reach a height of 2 m, corresponding to approximately 12–16 years after planting (Persson & Ståhl, 1993). Mortality, at least in harsh areas, usually decreases considerably in trees more than 20 years old (Persson & Ståhl, 1993). The reduced mortality associated with tree height and age may be partially explained by selection, *i.e.* most of the trees with low tolerance to cold die at a young age (Ståhl & Andersson, 1985), and partly to sensitivity to environmental disturbances decreasing with tree size.

Objectives

The objective of the work underlying this thesis was to gain more knowledge about the genetic variability of important traits used for ranking candidate trees in northern Swedish Scots pine breeding populations. The following main questions were addressed:

- How large is the additive genetic and environmental (co)variation for tree height and field survival in northern Swedish Scots pine progeny trials? Is there any genetic association between the traits? Does the genetic expression and thus the genetic association between the traits vary among environments?

- How will selection of Scots pine seed orchard clones based on the results of artificial autumn freezing tests on first year progenies influence the performance of new forests originating from these seed orchards?

Attempts to address these questions began with a methodological simulation of the effects of varying degrees of non-random missing records and different estimation procedures on estimates of (co)variance components and associated genetic correlations.

Materials and Methods

This research involved studies based on both simulated data and assessments made in field trials and artificial freezing test experiments. All experiments examined in Papers II-IV constitute part of the northern Swedish tree improvement program of Skogforsk, the Forestry Research Institute of Sweden.

Simulation study (Paper I)

In the study described in Paper I a stochastic model was designed to generate data records for two correlated traits with known (co)variances. The data were intended to resemble the results of tree height and field survival in northern Swedish Scots pine (*Pinus sylvestris* L.) half-sib progeny trials, *i.e.* the within-individual correlation between a selectively purged continuous trait and an ordered categorical trait. The accuracy of single- and multiple-trait REML estimation procedures was examined by studying the influence of different levels of selectively deleted records on average bias and variation of derived correlation estimates. Ten thousand data sets were generated for each of a number of partially factorial combinations of additive genetic and environmental correlations, narrow sense individual heritabilities and mortality levels.

Field material (Papers II–IV)

Paper II was based on 9–13-year height and survival data from 18 field trials with open-pollinated or polycross progenies of 703 Swedish, and 185 Finnish, Scots pine trees. The trials were part of four test groups of field experiments, with different genetic material within each test group. Each test group comprised four or five trials, including between 68 to 305 half-sib families. The parent trees originated from naturally or artificially regenerated forest stands. The number of stands in each test group varied between eight and 33, from each of which two to 29 trees were selected. The trials were established over a broad latitudinal and climatic range (61°00' to 67°30'N, and 496 to 1003 day-degrees, respectively). Survival across the trials averaged 62%.

In Paper III 9–13-year height and survival data were derived from three test groups of field progeny trials, each consisting of an independent set of open-pollinated families of Scots pine trees. Each test group comprised five field trials with between 305 and 360 half-sib families, in total 15 trials and 976 families. The material examined in Papers II and III included five trials common to both studies. The parent trees were selected from 30–50-year-old artificially regenerated forest stands. The number of stands varied between 33 and 40 in each test group and the number of trees that were selected in each stand varied from two to 30. The latitudinal range of the trials varied from approximately 62° to 67°30'N. Survival across the trials averaged 66%.

All field trials were planted with one-year-old potted seedlings in single-tree plot designs, randomized without restrictions. The seedlings were grown from seed, collected from the parent trees in the forest stands (open-pollinated), or produced by controlled crosses in clonal archives and seed orchards using pollen mixtures (polycrosses). Prior to the analyses, each trial was uniformly sub-divided into blocks, in order to reduce the influence of environmental variation (Ericsson, 1997). Families originating from the same forest stand were considered to represent a distinct population. Most of the half-sib families within a test group were represented in all experiments of that group. Tree condition, which reflects survival ability, was scored for each individual tree in four ordered classes:

healthy, slightly damaged, severely damaged but still alive, and dead. In addition, the height of the living trees was measured.

Freezing tests (Paper IV)

In Paper IV the results of artificial freezing tests of the autumn cold hardiness of 1-year-old Scots pine seedlings were compared with measurements on relatives in the field. The experiments were part of the same test groups of half-sib families as in Paper III. Each test group was replicated in one freezing test and five field trials (the trials assessed in Paper III). Freezing injury was assessed 2 – 3 weeks after freezing in a climate chamber and visually scored on individual seedlings based on discoloration of needles. The field traits analyzed included the height and tree condition records assessed in Paper III, extended with measurements of spike knot frequency, branch diameter, branch angle, stem straightness, and susceptibility to infections of the pathogenic fungi *Phacidium infestans* L., *Gremmeniella abietina* (Lagerb.) Morelet, *Melampsora pinitorqua* (Braun) Rostr. and *Lophodermella sulcigena* (Rostr.) Höhn. The total age of the trees at the time of measurement in the field ranged from nine to 21 years.

Statistical analyses and genetic parameter estimation

Die-back of trees due to non-random genetic factors is not an uncommon feature in forest-genetic field trials. This implies that the assumptions of independent and random sampling required in standard univariate genetic evaluations, cannot usually be fulfilled. Hence, applying univariate statistical methods to field data containing non-random missing records does not take account of all available information, and produces genetic variance estimates that are likely to be biased (Meyer & Thompson, 1984; Meyer, 1991). In contrast, multivariate mixed-model analyses (Hendersson, 1984) can simultaneously utilize information from all evaluated traits, the genetic and environmental correlation between traits, and the genetic relationships between individuals. In addition, the genetic relationships may take account of selective mortality and, thus, yield more accurate estimates (see reviews by Shaw, 1987; Schaeffer, Schenkel & Fries, 1998; and Hofer, 1998). Ideally, to derive unbiased (co)variance estimates in cases where the selection criteria are correlated to the analyzed trait(s), complete pedigree information back to the unselected base population and comprehensive data on the selection process (*e.g.* survival data for all trees) should be available, and the selection criteria should be translation invariant (*i.e.* unaffected by fixed effects).

In the past, the use of multivariate methods has been limited due to the need for large computer capacity. However, recent advances in computer hardware and software have enabled the analysis of large data sets, including data on several traits, with readily available tools. A newly developed software package, ASReml (Gilmour *et al.*, 2001), has become a popular evaluation tool among breeders worldwide. ASReml estimates variance components under a general linear mixed model by restricted maximum likelihood, iterating an average information algorithm (Gilmour, Thompson & Cullis, 1995). It supports genetic, multivariate,

repeated measures, and spatial and multi-environment analyses. ASReml was the evaluation tool in all of the studies underlying this thesis (Papers I–IV).

All data were analyzed using single- or multiple-trait linear mixed models of the general form, in matrix notation:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Z}_1\mathbf{s} + \mathbf{Z}_2\mathbf{f} + \mathbf{e},$$

where $\mathbf{y}$ is the observation vector of individual phenotypic values, $\mathbf{b}$ is a vector of fixed effects (overall mean and block effects), $\mathbf{s}$ and $\mathbf{f}$ are vectors of random stand and family effects, respectively, and $\mathbf{e}$ is the vector of individual residual deviations. $\mathbf{X}$, $\mathbf{Z}_1$ and $\mathbf{Z}_2$ are the corresponding incidence matrices. For multiple traits, $\mathbf{y}$ is the vector of joint trait values with the other equation elements assembled correspondingly.

Biological parameters were derived from the REML estimates of (co)variance components within each test group and calculated according to standard formulae. The expected relationships between biological and statistical variances and covariances assumed that one-quarter of the stand and family variation were expressed in the polycross material, and in the open-pollinated material that the entire stand variation and a quarter of the family variation were expressed in the estimates.

The inclusion of a population (stand) effect in the model (not done in Paper I) was justified by the clinal among-population variation in northern Scots pine and the latitudinal range within the test groups studied, which implied that it was possible to sub-divide derived genetic parameters into among-population, within-population and overall estimates (*i.e.* including the genetic effects of both stand and parent). In Paper II parameter estimates for all three levels were presented. In Paper III among- and within-population parameter estimates were derived. However, to avoid possible spurious genetic associations due to gametic phase disequilibrium, which may have substantial effects on among-population correlation estimates, but relatively little effect on within-population estimates (Latta, 1998), only the results from the additive within-population correlation were calculated in Paper III. In Paper IV, on the other hand, the overall additive correlation was presented since the original selection of seed orchard clones included both the stand and family effects.

The additive genetic correlations were designated *inter-site* correlations if they were derived from multivariate analyses of, for instance, tree heights from different trials (using the data from the different trials as separate traits) and bi- or trivariate evaluated *within-* or *between-site* correlations for correlations between two different traits, *e.g.* the genetic correlation between tree height and tree condition measured on the same individuals (within-site) or on separate but related individuals located at two different sites (between-site). The evaluations always included data on the survival rate in a trial (the third trait in the trivariate analyses) if some of the data for an assessed trait were missing in order to reduce bias due to possible non-random mortality. For example, the evaluation of the correlation between tree condition in trial A and tree height in trial B also included tree condition in trial B. In addition, a variant of the within- and between-site

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correlations, designated bivariate *multi-site* correlation was also calculated, in which records from several trials (if available) were joined for each trait.

Combined estimates of additive genetic correlations across field trials were either calculated as arithmetic mean values (Paper II) or by weighting the estimates proportionally to the inverse of the estimated sampling variance (Papers III and IV). In Papers II–IV, correlation estimates associated with estimated narrow sense individual heritabilities of less than 0.03 were in some cases excluded from the averaging since results from simulation studies have shown that the sampling variance, and thus the number of possible unrealistic out-of-bound estimates, increases with decreasing heritabilities (Visscher, 1998; Paper I). The approach can be questioned, but the error introduced if such "unreliable" estimates are rejected should be compared with the clearly misleading averages that might be derived if ambiguous correlation estimates, some of which may be far outside theoretical boundaries, are included in a weighted mean.

Results and discussion

Comparison of single- and multiple-trait REML evaluations

Applying multiple-trait REML to the data including non-random missing records in Paper I provided average additive genetic within-site correlation estimates with low bias. The results were in agreement with theoretical expectations (Gianola *et al.*, 1989) and earlier simulation studies (Ouweltjes, Schaeffer & Kennedy, 1988; Jensen & Mao, 1991; Van Tassel, Casella & Pollak, 1995; Schenkel & Schaeffer, 1998). The single-trait REML analyses of the same data, using pairwise sums of trait records (Searle & Rousaville, 1974), systematically provided estimates of correlations that were too moderate, *i.e.* closer to zero than the true correlations (*cf.* Fig. 1). However, when the data were balanced (zero missing records), both single- and multiple-trait REML generated unbiased genetic correlation estimates, as expected. For both methods, the variation among derived correlation estimates was generally high, especially at low heritabilities. This implies that although multiple-trait REML must be recommended in situations where non-random mortality is present there is still a high probability that a single genetic correlation estimate will deviate considerably from the true value.

Genetic characterization of growth and survival

In the material assessed in Papers II–IV, the mean tree height across trials generally ranged from 100 to 300 cm, and the survival rate from 20 to 90%. The lowest survival rates and tree heights were commonly found at sites with a low temperature sum. Consequently, wide variations were observed in the estimates of additive genetic and environmental variances across trials, for both tree height and tree condition. Narrow-sense individual heritability estimates at the within-population or overall levels were moderate to low, and commonly varied between
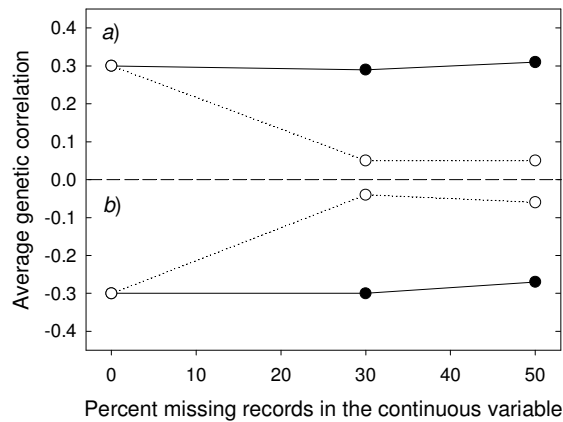
Fig. 1. Average additive genetic correlations, obtained from simulated data, between an ordered categorical variable (exemplifying tree condition) and a continuous variable with selectively deleted records (exemplifying height measurements that were missing for dead trees), calculated from single-trait REML estimates (○), utilizing the sum of two variables to derive the covariance between them, and multiple-trait REML (●). Narrow sense heritability and environmental correlation were set to 0.15 and 0, respectively. Genetic correlation was set to either (*a*) 0.3 or (*b*) –0.3.

0.1 to 0.3 and 0 to 0.1, for tree height and tree condition, respectively (Papers II–IV). The among-population heritabilities were in general small, varying between 0 to 0.03, for both tree height and tree condition (Papers II and III). Estimates of the additive genetic coefficient of variation, disregarding level of calculation, generally ranged from 5 to 15% and from 0 to 25%, for tree height and tree condition, respectively. Thus, when expressed, the genetic variance was largest for tree condition, but higher residual variation resulted in lower heritability estimates for tree condition than for tree height.

Significant heterogeneity among the additive genetic inter-site correlations at the within-population level for both tree height and tree condition was found in some of the material studied (Paper III). The fact that the inter-site correlations between tree heights from harsh and mild environments was observed to be lower than average in one of the test groups indicates that the tree heights in the different environments represented partly different traits. For tree condition, the variable inter-site correlations demonstrated the complex nature of the trait, which reflects the cumulative effects of all events causing injuries and die-back. In addition, the moderate but positive correlation with autumn cold hardiness, as assessed in freezing tests (Paper IV), shows that the cold acclimation rhythm in the autumn is an important, but not sole, contributor to the trait.

The bivariate within- and trivariate between-site additive genetic correlations between 9–13-year tree height and tree condition also varied considerably, both in sign and magnitude, but no clear trends were detected in the overall data (Papers II and III). However, when the correlations were separated into within- and between-site estimates, and the between-site correlations were further sub-divided into two groups depending on the harshness of the site (depending on the temperature sum),

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a pattern was detected. Following this sub-division, within-site correlations between tree height and tree condition were generally positive (Papers II and III), while the between-site correlations were generally positive when the tree heights were assessed in a harsh environment and negative when they were assessed in a milder environment (Paper III; illustrated in Fig. 2). A plausible reason for the divergence in these patterns is that families with low survival ability are likely to be most stressed in the harshest sites, and thus their growth will be more inhibited than that of hardier and healthier families. The positive correlations indicate that height measurements of 9–13-year-old trees in harsh environments strongly reflect their health and survival ability, while the negative estimates, generally obtained from material growing in environments where both traits were satisfactorily expressed, probably represent the 'true' genetic relationship between undisturbed growth and survival. Estimates of phenotypic and genetic correlations are often similar in both sign and magnitude (Lynch & Walsh, 1998). The negative associations at the provenance level between growth and survival found in numerous common-garden experiments of northern Scots pine populations (Persson & Ståhl, 1993; Persson, 1994) strengthen the hypothesis that there is a negative association between the traits.
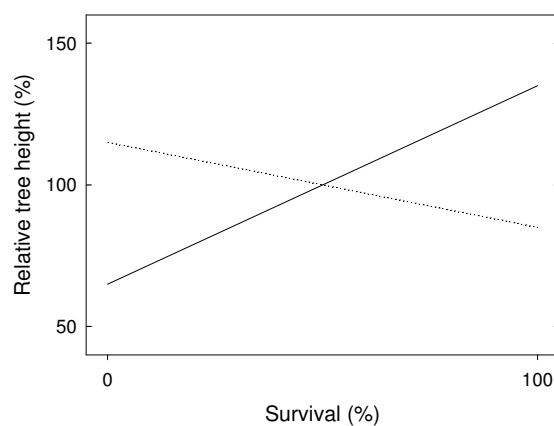

Fig 2. Principal genetic relationships between survival in a harsh environment and tree height in a harsh environment (solid line) and a mild environment (dotted line).

Early selection of seed orchard clones based on freezing test results

The most striking findings from Paper IV were the generally positive, but moderate, genetic correlations between autumn cold hardiness assessed in freezing tests and tree condition, and the negative correlations between cold hardiness and tree heights (for which most of the estimates were derived from plants growing in mild environments). The results indicate that selection of seed orchard clones based on the performance of juvenile progenies in artificial freezing tests in climate chambers will improve the survival ability of the selected clones, but reduce their height growth in mild environments.

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Among the quality traits branch angle showed the highest, and stem straightness the lowest, heritabilities. The fungal species that most frequently caused detected infections were *P. infestans* and *G. abietina*, and the highest infection levels of the fungi were generally found at harsh sites with low temperature sums. The genetic correlations between cold hardiness and both the quality characters and susceptibility to the different pathogens varied considerably. However, a tendency towards a negative genetic association between cold hardiness and infection by *P. infestans* was observed, indicating that good performance in freezing tests is associated with high resistance to this pathogen.

The repeated measurements of tree height and tree condition performed in four trials (Paper IV), at ages of 9–13 and 19–21 years, made it possible to study age trends in derived parameter estimates. The narrow-sense heritability estimates for tree height were found to clearly increase with age, in accordance with results presented by Jansson, Li & Hannrup (2003). The genetic correlation between autumn cold hardiness and tree condition was constant over age, while the variability of the genetic correlation between autumn cold hardiness and tree heights masked possible time trends. Thus, the genetic association between cold hardiness and tree condition seems to be satisfactorily expressed by the time the material is 11–13 years old, but future assessments and data from more trials are needed to verify age trends in height growth parameters.

Conclusions, applications and suggested research

Multiple-trait REML estimation of (co)variance components is recommended for field data affected by non-random mortality. For such data, the use of single-trait REML evaluations often generates a heavy bias. For both approaches, especially at low heritabilities, there is a substantial probability of obtaining seriously misleading genetic correlation estimates if the analysis is based on data from a single environment.

Selection of seed orchard clones based only on juvenile freezing test results will probably improve field survival, reduce height growth expressed in mild environments and have minor effects on quality traits and the incidence of common fungal diseases in the new forests originating from the resulting seed orchards.

The most notable result was the contrasting correlation patterns across environments between tree height and tree condition in the material sampled. The results indicate that caution should be applied involving 9–13-year tree height measurements in genetic evaluations from Scots pine trials located in harsh environments, since the growth potential of individuals with relatively low hardiness may have been suppressed. However, the age at evaluation of tree heights in these studies may have been too young, since the trees in the field were at early stages of development at the time of assessment, with mean heights in the trials varying between 1 and 3 m. The mortality of trees in harsh areas usually decreases considerably after they are 20 years old (Persson & Ståhl, 1993),

probably due to the combined effects of susceptibility to environmental disturbances declining with increasing age and tree size, and early die-back of less well-adapted trees. That is, the ability of surviving trees to express their true growth potential will probably increase with time. Therefore, further information on older, more fully developed trees needs to be collected, and collated with the results of this study to assess the consistency of the detected patterns. Ideally, the trials in this study should be re-assessed at a later age.

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