GENOTYPE ENVIRONMENT INTERACTIONS IN FOUR FULL-SIB PROGENY TRIALS OF *PINUS SYLVESTRIS* (L.) WITH VARYING SITE INDICES

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ABSTRACT

The importance of genotype× environment interactions for the breeding strategy of *Pinus sylvestris* in southern Sweden was investigated in 144 full-sib families (12 × 12 factorial cross) located at four test sites with contrasting site conditions and in two different climate zones (range of 1.5 degrees latitude and 205 m altitude). The traits assessed were height at 12 and 16 years in the field, height increment between 12 and 16 years, and diameter and volume at 16 years in the field. Performance across sites showed significant site effects for all traits. Also the female × site and male × site effects were significant for all traits but did not exceed 40 % of the total additive genetic effects, thus of minor importance compared to the additive effects. Type B genetic correlation estimates between the same trait at different test sites were moderate to high (range 0.38 to 0.97) and in most cases significant. Within sites, the female and male effects were significant for all traits. Estimated female × male variances reached at most 77 % of the estimated total additive genetic variances. Both age-age genetic correlations and trait-trait genetic correlations were generally high and significant ($p < 0.05$) for the time period 12–16 years in the field. The main implications for breeding are: that genotype × environment interactions are of little importance suggesting that a single breeding zone should be sufficient for this region; and that the major genetic effects are additive, so there is no need to consider the non-additive genetic effects in the current breeding programme.

Key words: *Pinus sylvestris* L., factorial mating design, additive genetic correlation, type B genetic correlation, heritability, additive genetic coefficient of variation, genotype × site interaction.

INTRODUCTION

Scots pine occupies a large area in Sweden with a broad span of site conditions, where especially soil characteristics can vary considerably even within a climate zone. In Sweden, the long-term breeding strategy of Scots pine is based on the Multiple Population Breeding System concept (NAMKOONG *et al.* 1980, BURDON & NAMKOONG 1983). This implies that the breeding efforts to maximise the genetic gain per time unit are combined with dynamic gene conservation to safeguard the potential for adaptation to future changes in climate and forest ecosystems (ERIKSSON *et al.* 1993, ROSVALL 1999). It further implies that the breeding population in each generation is divided into 20–24 sub-populations distributed at sites with differing photoperiodic and temperature climate (DANELL 1993). Within the climate zone of a sub-population, genotype × environment (G × E) interactions should be low and relatively unimportant for breeding. However, soil conditions within a climate zone can vary considerably from very fertile to poor soils. It is therefore of great interest for the design of the breeding strategy to know whether this variation in soil conditions can generate G × E interactions within a climate zone.

Genetically, Scots pine is one of the two most studied Swedish forest tree species, owing to its importance as a main timber tree. Genetic parameters have been estimated on different levels of genetic entries: provenances, half-sib families, full-sib families and clones in seed orchards, aiming at a better understanding of the genetic variation and the inheritance of traits responsible for wood production and wood quality (*eg.* EICHE 1966, ERIKSSON *et al.* 1980, STÅHL 1984, JANSSON 1998).

However, there is a lack of studies, in which the main objective is to test genotype × environment (G × E) interactions under strongly varying local site

conditions. Thus, HAAPANEN (1996) pointed out that G × E interaction "has received surprisingly little attention in the forestry literature". G × E interactions were shown to be of importance for some species in particular experimental series (SHELBOURNE 1972, OWINO *et al.* 1977, MORGENSTERN 1978, KLEINSCHMIT *et al.* 1979, SKRØPPA 1984, GREGORIUS & NAMKOONG 1987, JOHNSON & BURDON (1990), HAAPANEN 1996, 2001). But in other studies they were considered to be of little importance in the field-test experiments (SHELBOURNE 1972, LI & MCKEAND 1989, MATHESON & COTTERILL 1990, PSWARAYI *et al.* 1997). It is often pointed out, that one of the difficulties in studying the G × E interactions is that in many cases the environments at the sites of the forestry experiments are hardly predictable. This is true especially for the year-to-year fluctuations in weather conditions. Therefore, many studies reporting G × E interactions were not designed especially for this purpose. An exception is the study by JOHNSON & BURDON (1990) for *Pinus radiata*, which was designed to investigate G × E interactions between extreme soil types - clay and pumice. In this study, strong G × E interactions between soil types for stem volume were found. However, G × E studies in controlled (*i.e.* predictable) environments have been performed in which such factors as nutrient supply, water availability and temperature were varied (JAHROMI *et al.* 1976, MULLIN 1985, NAMKOONG *et al.* 1992, JONSSON *et al.* 1997, SONESSON & ERIKSSON 2000). Also these studies indicate that G × E interactions exist in forest trees. Important questions are (1) how to design the trials to test whether G × E interactions exist and (2) whether the magnitude of the interactions is of practical importance for forest tree breeding. The importance of G × E interactions may also vary depending on the type of genetic entry such as provenances, half-sib families, full-sibs families, or clones (*e.g.* MORGENSTERN 1978).

The prime objective of our study was to estimate G × E interactions and, if any, elucidate their implications for forest tree breeding. To do so we studied a series of full-sib progeny trials planted in contrasting site conditions and in two different climate zones. An additional objective was to estimate genetic parameters of significance for breeding from individual trials. In agreement with HOULE (1992), we consider estimates of additive genetic coefficient of variation (CV_A) as important in this context.

MATERIALS AND METHODS

Materials, experimental design, traits assessed

The material used in the study included 144 full-sib families of *Pinus sylvestris*, resulting from a 12 × 12 complete factorial mating design. The male and female parents are plus trees originating from southern Sweden and southern Finland. The crosses were performed in 1978 in a seed orchard in southern Sweden. The seeds were sown in the nursery in spring 1980 and the seedlings were outplanted in April 1981 at four experimental test sites.

In order to provide appropriate data for comparison and for testing the G × E interactions, the sites were selected according to a 2 × 2 factorial design (Table 1). The trials were located at two climate zones. The southern zone is characterized by a milder climate and the northern zone by a harsher, more continental climate. In each climate zone two trials were established: one on poor and one on good site conditions. The four trials are denoted: Southern high site index (SHSI), southern low site index (SLSI), northern high site index (NHSI), northern low site index (NLSI). The SLSI trial was located at a sandy soil site, adjacent to a sand-pit. The two northern sites were located at the bottom (NHSI) and near the summit (NLSI) of a hill.

The planting design was single-tree plots with 10 individuals per full-sib family per block. The spacing was 1.7 × 1.7 m. In this study, 2 of 4 blocks per site were measured. Thus, nominally, there were 2 × 144 × 10 = 2880 trees at each site. However, after the first years at the sites, the numbers of remaining trees were 2820 (SHSI), 2866 (SLSI), 2849 (NHSI), and 2739

Table 1. Geographic data about the sites of the experimental trials. SHSI = Southern High Site Index, SLSI = Southern Low Site Index, NHSI = Northern High Site Index, NLSI = Northern Low Site Index. Site index = mean height of dominant trees at age 100.

Trial name	Climate	Site index	Latitude (N)	Longitude (E)	Altitude (m)
SHSI	Mild	T25	59° 01′	15° 52′	70
SLSI	Mild	T19	59° 01′	15° 52′	70
NHSI	Continental	T25	60° 29′	16° 05′	170
NLSI	Continental	T22	60° 29′	16° 05′	275

(NLSI). At age 16 in the field, the numbers of assessed trees were 2664 (SHSI), 2724 (SLSI), 2194 (NHSI), and 2298 (NLSI), so that 94.5 %, 95.0 %, 77.0 %, and 83.9 %, respectively, of the remaining trees after the establishment phase are included in the analysis. The higher proportions of dead and missing trees at NHSI and NLSI were caused by strong weed competition (especially at NHSI) and attacks of animals and insects.

Traits assessed or calculated: H12: Height (m) at the age of 12 in the field (13 years from seed), measured in 1992, H16: Height (m) at the age of 16 in the field (17 years from seed), measured in 1996, HINCR12–16: Height increment (m) in the period 1992 to 1996, DBH16: Diameter (cm) at the height of 1.3 m, at the age of 16 in the field, VOL16: Volume (dm^3) at the age of 16 in the field, estimated according to the formula of BRANDEL (1990):

$$VOL = 0.0442904\, D^{1.85469} (D+20)^{0.01896} H^{2.04781} (H-1.3)^{-1.00739}$$

where: H = H16 and D = DBH16.
$VOL16^{1/2}$: Square root of volume VOL16 (see below for the justification of the use of the transformed trait).

Statistical analysis

As the trait VOL16 showed different phenotypic distributions between sites the transformed trait $VOL16^{1/2}$ was used instead. This variable also showed a better correspondence with the models below based on random effects following normal distributions.

Analysis of variance and variance components

For the analysis of variance and the estimation of the variance components across all four sites the model used was:

$$y_{ijklr} = \mu + s_i + b_{j(i)} + f_k + m_l + (fm)_{kl} + (sf)_{ik} + (sm)_{il} + (sfm)_{ikl} + e_{ijklr}$$

where:

y_{ijklr} = value measured at site i, block j, family kl, and individual r;
μ = overall mean,
s_i = fixed effect of site i, i = 1, 2, 3, 4,
$b_{j(i)}$ = fixed effect of block j within site i, j = 1, 2,
$f_k \sim N(0,\sigma_f^2)$ random effect of female k, k = 1, ..., 12,
$m_l \sim N(0,\sigma_m^2)$ random effect of male l, l = 1, ..., 12,
$(fm)_{kl}$, $(sf)_{ik}$, $(sm)_{il}$, $(sfm)_{ikl}$ random interaction,
$e_{ijklr} \sim N(0,\sigma_e^2)$ residual error,
r = 1, ..., n_{ijkl},
$0 \le n_{ijkl} \le 10$.

The interactions are assumed to follow normal distributions with means 0 and variances σ_{fm}^2, σ_{sf}^2, σ_{sm}^2 and σ_{sfm}^2, respectively. All random effects are assumed independent.

For the analysis of variance and the estimation of variance components at the separate sites, the model was:

$$y_{jklr} = \mu + b_j + f_k + m_l + (fm)_{kl} + e_{jklr}$$

where the effects are defined in accordance with the previous model.

The importance of a random effect was expressed as the ratio of its variance to the sum of all random effect variances. A test of equal variances between females and males was based on the test statistic $(\hat{\sigma}_f^2 - \hat{\sigma}_m^2)/se(\hat{\sigma}_f^2 - \hat{\sigma}_m^2)$. The standard errors ($se$) of the estimates of the relative variance components and the differences were found from the asymptotic covariance matrix by means of the delta technique (BULMER 1980). The numerical computations were performed using the SAS statistical package (SAS 1999). The procedure GLM was used for the analysis of variance and the procedure Mixed was used for the variance components and the asymptotic covariance matrix of the estimates.

Heritability estimates

Assuming equal additive variance components for females and males, the narrow-sense heritability on a single-tree basis within a site was defined as:

$$h^2 = 2(\sigma_f^2 + \sigma_m^2)/\sigma_p^2 = 4\sigma_A^2/\sigma_p^2$$

where σ_A^2 denotes the common value of the additive female and male variances, and where the phenotypic variance $\sigma_p^2 = \sigma_f^2 + \sigma_m^2 + \sigma_{fm}^2 + \sigma_e^2 = 2\sigma_A^2 + \sigma_{fm}^2 + \sigma_e^2$. The heritability was numerically determined by insertion of the estimated variance components. Using the delta technique (BULMER 1980) for the standard error, a confidence interval for h^2 was obtained by first calculating the interval using the logarithmic scale and afterwards retransforming it to the original scale. The logarithmic scale was used as it made the distribution of the estimates more symmetrical and thus is more suitable for the calculation of confidence intervals using techniques based on normally distributed estimates.

The across-site heritability was estimated by also including the variance components for genotype x site interaction in the phenotypic variance.

Coefficients of variation

Additive genetic coefficients of variation (%) were estimated as:

$$\hat{CV}_A = 100\sqrt{2(\hat{\sigma}_m^2 + \hat{\sigma}_f^2)}/\hat{\mu} = 100\sqrt{4\hat{\sigma}_A^2}/\hat{\mu}$$

where $\hat{\mu}$ is the estimated mean of the site.

Genetic correlations

Additive genetic correlations were estimated between the different traits at each test site, separately. Type B genetic correlations according to BURDON (1977), were also estimated between the same trait at two test sites.

Using the earlier univariate models simultaneously for two traits, x and y, the female effects were assumed to follow a bivariate normal distribution according to

$$\begin{bmatrix} f_k(x) \\ f_k(y) \end{bmatrix} \sim N\left(\begin{bmatrix} 0 \\ 0 \end{bmatrix}, \begin{bmatrix} \sigma_f^2(x) & \sigma_f(x,y) \\ \sigma_f(x,y) & \sigma_f^2(y) \end{bmatrix} \right)$$

where $\sigma_f(x,y)$ is the covariance. Similar bivariate models were assumed for the male and female × male effects, and also the residual effects when x and y correspond to different traits at the same site. Arranging the data in a special manner and using the traits also as effects in the Mixed procedure of SAS, estimates of the variances and covariances were obtained. Assuming equal variances and covariances for the female and male effects, the additive genetic correlation was calculated as

$$\varrho_A = \frac{\sigma_f(x,y) + \sigma_m(x,y)}{\sqrt{[\sigma_f^2(x) + \sigma_m^2(x)]\ [\sigma_f^2(y) + \sigma_m^2(y)]}} = \frac{\sigma_A(x,y)}{\sqrt{\sigma_A^2(x)\ \sigma_A^2(y)}}$$

The confidence intervals for ϱ_A were found in the same way as for the heritabilities except that the Fisher z-transform (inverse of tangent hyperbolic function) and modifications of it were used for the confidence intervals. The modified z-transformation was needed for the type B genetic correlations.

RESULTS

Performance at individual sites

At the southern trial with low site index (SLSI), the growth was much slower than at any of the other trial sites (Table 2). This was particularly evident for VOL16.

The female and male effects for all growth traits at all sites were strongly significant ($p < 0.001$ in all cases but one at 0.01, details not shown). The tests of equal variance components for females and males never showed any significant results and assuming equal variance components, the heritability estimates varied between 0.05 and 0.24 for the individual traits (Table

Table 2. Trait means, estimates and 95 % confidence intervals (italics) for heritabilities (bold), and estimated coefficients of additive variation (%) based on separate ANOVAs from the four field trials. SLSI = Southern Low site Index, NLSI = Northern Low Site Index, NHSI = Northern High Site Index, SHSI = Southern High Site Index.

Trait	SLSI			NLSI		
	Mean	h^2	CV_A	Mean	h^2	CV_A
H12 (m)	2.8	**0.08** *0.04-0.17*	6.5	4.1	**0.05** *0.02-0.12*	3.9
H16 (m)	4.0	**0.13** *0.07-0.25*	7.8	6.5	**0.08** *0.04-0.17*	3.8
HINCR 12-16 (m)	1.2	**0.19** *0.10-0.34*	11.9	2.3	**0.13** *0.07-0.25*	4.8
DBH16 (cm)	5.0	**0.15** *0.08-0.27*	12.2	10.0	**0.07** *0.03-0.16*	7.2
VOL16 (dm^3)[1]	6.8	**0.14** 0.08-0.27	12.9	32.5	**0.08** *0.04-0.17*	7.9

Trait	NHSI			SHSI		
	Mean	h^2	CV_A	Mean	h^2	CV_A
H12 (m)	4.9	**0.08** *0.04-0.17*	4.5	5.2	**0.21** *0.12-0.38*	5.9
H16 (m)	7.5	**0.12** *0.06-0.23*	4.3	7.7	**0.24** *0.14-0.43*	5.5
HINCR 12-16 (m)	2.5	**0.12** *0.06-0.23*	4.7	2.4	**0.12** *0.06-0.23*	5.3
DBH16 (cm)	11.3	**0.07** *0.03-0.16*	6.9	10.4	**0.19** *0.10-0.35*	9.3
VOL16 (dm^3)	44.9	**0.08** *0.04-0.18*	7.8	38.7	**0.21** *0.12-0.39*	10.5

[1] The estimates of h^2 and CV_A are based on Vol $16^{1/2}$

Table 3. Estimated non-additive genetic variation, $4\hat{\sigma}^2_{mf}$ as a percentage of the additive genetic variation, $2(\hat{\sigma}^2_f + \hat{\sigma}^2_m)$. All significant female x male effects are indicated. – = female x male estimate was 0. SLSI = Southern Low Site Index, NLSI = Northern Low Site Index, NHSI = Northern High Site Index, SHSI = Southern High Site Index.

Trial name	H12	H16	HINCR 12–16	DBH 16	VOL $16^{1/2}$
SLSI	19.5	1.0	0.1	7.7	6.8
NLSI	71.2*	56.0*	9.0	77.2*	71.2*
NHSI	6.9	9.9	–	31.9	28.4
SHSI	20.8*	20.0*	18.7	57.6***	50.7***

Significance levels: * = $p \leq 0.05$, *** = $p \leq 0.001$.

Table 4. Summary of the estimated pairwise genetic correlation coefficients between different traits within the individual field trials. The number of significant correlation coefficients ($p < 0.05$) are given in brackets. The maximum number is 4, implying that for all 4 field trials the estimated correlation coefficients were significant.

Trait	H 16	HINCR 12–16	DBH 16	VOL $16^{1/2}$
H 12	high (4)	moderate – high (4)	high (4)	high (4)
H 16		high (3)	moderate – high (3)	moderate – high (3)
HINCR 12 – 16			low – high (2)	low – high (3)
DBH 16				high (4)

2). The estimated heritabilities were, on the whole, higher at the southern trials than at the northern trials. At the southern trial with high site index (SHSI), the estimates of heritability were consistently highest followed by the southern trial with low site index (SLSI) except for HINC12–16. In contrast, the estimated CV_A was larger or much larger at SLSI, ranging from 6.5 % to 12.9 %, than at any of the other trials.

The non-additive female x male effect was statistically significant for all traits at SHSI and NLSI, except for height increment (HINCR12–16, Table 3). In the other two trials no significant non-additive effect was noted for any trait. The estimated non-additive variance components, $4\hat{\sigma}^2_{mf}$, were consistently smaller than the total additive genetic variation and reached at most 77 % (DBH16 at NLSI) (Table 3).

Most of the within-site (type A) genetic correlations were high and significant (summarized in Table 4). The highest correlations were estimated for diameter – volume (DBH16–VOL$16^{1/2}$) and for height (H12 –H16) at all trial sites. The lowest, non-significant ones were found at the two northern trials for the trait – pairs height increment – diameter (HINCR12–16–DBH16).

Performance across sites

For individual traits, the estimated heritabilities across sites varied from 0.07 (DBH16, VOL$16^{1/2}$) to 0.12 (H16). The female x site and male x site interactions were significant for all traits. None of the three-factor interactions, female x male x site was significant. The ratio between the summed two- and three-factor interactions and the total additive genetic variance component, expressed as percentage, varied between 16 (H16) and 41 (DBH16). No details in this paragraph are tabulated.

The estimated type B genetic correlations between the same trait assessed at two different trial sites at a time, were moderate to high (range 0.38 to 0.97), and in most cases (26 of 30) significant (Table 5). It is noteworthy that for four out of the six site-pair correlations, all correlation estimates were significant and varied between 0.48 (confidence interval *0.01–0.80*) and 0.97 (confidence interval *0.77–1.00*). In contrast, the site pair SLSI–NLSI showed only two out of five possible significant correlation estimates. The two sites with low site indices had on average lower correlation estimates than the two sites with high site indices. The highest and lowest between-site correlation estimates involved NHSI and SLSI, respectively.

DISCUSSION

Genotype x environment interactions

Since the site effect was strongly significant for all traits studied, this experimental series should be ideal

Table 5. Estimates and 95% confidence intervals (*italics*) for pairwise genetic correlation coefficients between the same traits studied at the four field trials. Correlation coefficients significantly different from zero ($p < 0.05$) are in bold. SLSI = Southern Low Site Index, NLSI = Northern Low Site Index, NHSI = Northern High Site Index, SHSI = Southern High Site Index.

Trial combination	H12	H16	HINCR 12–16	DBH 16	VOL $16^{1/2}$
SLSI – NLSI	0.50 *–0.07–0.89*	0.52 *–0.03–0.87*	0.38 *–0.13–0.73*	**0.64** *0.19–0.94*	**0.61** *0.15–0.91*
SLSI – NHSI	**0.91** *0.65–1.00*	**0.77** *0.47–0.99*	**0.48** *0.01–0.83*	**0.83** *0.55–1.00*	**0.79** *0.48–1.00*
SLSI – SHSI	**0.83** *0.58–1.00*	**0.74** *0.42–0.96*	**0.58** *0.18–0.86*	**0.68** *0.34–0.92*	**0.69** *0.36–0.92*
NLSI – NHSI	**0.90** *0.18–1.00*	**0.96** *0.64–1.00*	**0.91** *0.67–1.00*	**0.92** *0.61–1.00*	**0.91** *0.61–1.00*
NLSI – SHSI	**0.67** *0.26–0.94*	**0.86** *0.64–1.00*	**0.95** *0.82–1.00*	0.49 *0.00–0.83*	**0.55** *0.10–0.85*
NHSI – SHSI	**0.92** *0.76–1.00*	**0.94** *0.74–1.00*	**0.97** *0.77–1.00*	**0.56** *0.09–0.88*	**0.68** *0.31–0.93*

for a study of the relative importance of G × E interactions. However, the limited number of general combining ability effects constitutes a serious constraint. The significant site effect stemmed mainly from the poor growth at SLSI trial located at a sandy soil site, adjacent to a sand-tip.

To attempt to obtain an explanation of a G × E interaction, pairwise type B genetic correlations according to BURDON (1977) between the same trait at each pair of the four trial sites were estimated. Most of these genetic correlations were fairly strong and significant (Table 5). However, the two sites with low site indices, NLSI and SLSI, gave four (NLSI) or three (SLSI) non-significant correlations out of 15 possible, while the two high site-index trials had one (SHSI) or none (NHSI). This suggests that the two sites with low site indices contributed most to the otherwise limited G × E interaction. This was expected for the SLSI site, since the growth data from this site deviated most from the corresponding data at the three other sites. As regards the genetic correlations involving the SLSI data, the poor growth at this test locality could reduce the strength of these genetic correlations. To test this, correlations were estimated between SLSI height at age 16 (H16) with heights at age 12 (H12) at the other test localities. These correlation estimates showed the same pattern as the estimates at the same age. Moreover, the site-pair correlation SLSI – NLSI between the two sites with almost identical mean heights at different ages, 4.0 m (H16, SLSI) and 4.1 m (H12, NLSI), had a low correlation coefficient, 0.38, confidence interval (–0.24, 0.78). Thus, the estimated correlations at the same stage of development did not improve the strength of the relationships. The genetic correlations estimated for the two most extreme pairs of sites, SLSI – SHSI and SLSI – NHSI, were moderate to high and significant, indicating that the difference in edaphic and climate conditions between these two trial – site pairs did not generate any important G × E interactions.

The volume growth at age 16, $VOL16^{1/2}$, proved to be the trait least sensitive to variations in environmental conditions, since all the six correlations were significant. For the other traits, this figure was five out of six correlations. This may be a random effect. Diameter growth is probably the trait that will be affected first by increasing competition. However, this trait did not give more non-significant correlations than the other traits. Therefore, the results do not indicate any time trends for type B genetic correlations. On the other hand, we cannot exclude that the G × E interactions may be more important with age, if the variation in magnitude of competition increases among the trials. Also HAAPANEN (2001) failed to prove any time trends for type B genetic correlations for height growth in his Scots pine progeny trials where ages ranged from 5 to 18 years. In *Pinus elliottii*, DIETERS *et al.* (1995) observed a decreasing impact of additive G × E interactions for volume between the ages 5 to 14 years. Furthermore, in our study even though the interactions female × site and male × site were significant for all traits, the summed variance components of these two-factor interactions and the three-factor interaction did not exceed 41 % of the total additive variances for any of the traits. This further indicates the minor importance of G × E interactions. SHELBOURNE (1972) proposed that if this ratio equals or exceeds one half (*i.e.* type B correlation ≤ 0.67, see DIETERS *et al.* 1995), the interaction is considered as being important for breeding.

The results indicate that the differences in the site conditions influenced most of the families in a similar way. This contrasts with results from other studies with Scots pine in Scandinavia. GULLBERG & VEGERFORS (1987) reported for the region of South-central Sweden, that G × E interactions should be considered at least for the growth traits (height, diameter and volume). HAAPANEN (1996) found "at least moderate", in his words, family-by-trial interactions in Finnish Scots pine studied across different site series. He found no significant family by field test design interactions. Recently, HAAPANEN (2001) reported that G × E interaction

inflated the additive genetic variances and heritabilites estimated from within trial sites analyses by 60 %. In our study, the corresponding figures for single-site h^2 varied from 14 % (H16) to 46 % ($VOL16^{1/2}$). However, HAAPANEN (2001) could not find any clear pattern of association between the magnitude of the G x E interactions and the trial site environments although they differed strongly in height growth. Also DIETERS *et al.* (1995) failed to prove any such relationship with site quality for the interactive behaviour of volume in 171 full-sib progeny trials of *P. elliottii*. In a growth-chamber study of open-pollinated families from two Swedish populations of Scots pine, significant family x temperature interactions were found, but no family x water interactions for growth traits in the first growth period (SONESSON & ERIKSSON 2000). It should be remembered that both temperature and water availability differences were large in their study. Their results partly agree with our results of minor G x E interactions in spite of the very large differences in site index.

The growth conditions in the areas from which the plus trees were selected vary in a mosaic pattern reflecting site index. Since *P. sylvestris* is a wind-pollinated species, there is probably a strong gene flow among stands growing under a broad span of growth conditions. Under such conditions, trees that give rise to offspring that grow well under a broad range of conditions are expected to have the highest fitness. This means that specific adaptation to the growth conditions is less likely. This in turn means that interactions will be limited; rather, it is expected that the species will have a high phenotypic plasticity with stable ranking from site to site (ERIKSSON 1998).

There are different reports and opinions as regards the importance of G x E interactions in other species. SHELBOURNE (1972) pointed out that G x E interactions are often detectable, but of little importance. He concluded that for *P. radiata* and the "southern pines" such as *P. taeda* and *P. elliottii*, G x E interactions were mostly associated with edaphic rather than with climatic factors. A case in point is the strong G x E interactions between soil types found for *P. radiata* by JOHNSON & BURDON (1990). Similar results were obtained by BURDON *et al.* (1997) for progeny performance across several countries. This is in contrast to some other studies in *P. radiata* where no coherent patterns of G x E interactions were observed (MATHESON & RAYMOND 1984, MATHESON & COTTERILL 1990). Also other studies involving the same species showed different results concerning G x E phenomena. For example, in *P. taeda*, OWINO *et al.* (1977) found that G x E interactions could significantly bias upward the heritabilities and gain prediction, while OWINO (1977) and MCKEAND *et al.* (1990), for example, estimated the G x E interactions to be of little importance for most traits of this species. However, when traits were combined into composite traits, the G x E interaction was important only if the two components were negatively correlated with each other (MCKEAND *et al.* 1997).

Further, in their study of G x E interactions involving soil types in *P. radiata*, JOHNSON & BURDON (1990) found that it was possible to select a single set of genotypes for a group of sites with very little sacrifice in genetic gain, compared with selecting for specific site categories. But failure to evaluate candidate genotypes on certain of those sites could lead to substantial losses of genetic gain. Also MATHESON & COTTERILL (1990) discussed the possibilities of matching genotypes to environment, *i.e.* of exploiting existing interactions. They concluded, however, that to obtain additional genetic gain by making use of G x E interactions 'is highly questionable as additional genetic gains to be had through using the interactions are very small in relation to the overall gains themselves'.

Genetic parameters within trial sites

Since *Pinus sylvestris* is an exclusively seed-propagated species, and a large fraction of the seeds for reforestation comes from seed orchards (ERIKSSON *et al.* 1994), we are most interested in the magnitude of the additive genetic variances compared with the non-additive variances. The non-additive variance, estimated as female x male interaction, was smaller than the total additive variance for all traits and sites (Table 3). The ratio non-additive to additive genetic variance varied from 0 % to 77 % among traits. The non-additive effects were not significant for any trait at SLSI and NHSI. Four of the five traits were significant at NLSI and SHSI. The increment trait, HINCR12–16, did not show any significant non-additive effects at any site, while the other traits showed significant non-additive effects at two of the sites. The strongly significant non-additive effects for DBH16 and $VOL16^{1/2}$ at SHSI could be due to stronger competition in this trial as it is located at a site with the most favourable site conditions (cf. YANCHUK 1996). The minor non-additive variances for most traits are in line with results based on more than 100 progeny trials of *P. sylvestris* in Sweden where the ratio dominance variance to additive variance for height (6–15 yr) was estimated at 25 % (ROSVALL *et al.* 2001). However, for individual trials it was not unusual that the non-additive variance exceeded the additive variance (Dr. Gunnar Jansson, pers. comm.). For full-sib families of *P. taeda*, the corresponding ratio for height increased from 20 % at age 1 to its greatest value of 440 % at age 6 and then decreased to 90 % at

age 13 and to 20 % at age 26 (BALOCCHI *et al.* 1993). This decrease was due to a levelling off of the dominance effect after age 12 simultaneously as the additive effect continued to increase. Also in earlier studies of *P. taeda* it was reported that the non-additive variance constituted a major part of the genetic variation (*e.g.* FOSTER & BRIDGWATER 1986). The average dominance variance to additive variance over age classes and years was 60 % for volume in *P. elliottii* (DIETERS *et al.* 1995). In a four diallel series of *Pseudotsuga menziesii*, YANCHUK (1996) estimated the average ratios of specific combining ability variance to general combining ability variance at 34 %, 32 % and 47 % for height at age 7 and 12, and volume at age 12, respectively. In conclusion, there is a trend of a more important role for the non-additive effects in *P. taeda*, *P. elliottii* and *Pseudotsuga menziesii* than observed in *P. sylvestris*.

Although our single-site heritability estimates were low and varied between 0.05 and 0.24 (Table 2) and across-site heritabilities varied between 0.07 and 0.12, the additive genetic effects were all strongly significant. Low heritabilities were also reported in most of the published heritability estimates for height and diameter in pine species. For example, CORNELIUS (1994) compiled the individual tree heritabilities for seven different traits from 67 published studies of conifers, mostly pine species, and broadleaved trees. For height, diameter and volume, the heritabilities commonly fall within the lower part of the range 0–0.5. In *P. sylvestris*, a median heritability value of 0.18 for height (6–15 years of age) was estimated by ROSVALL *et al.* (2001), based on 70 progeny trials in southern Sweden. The estimates of CV_A obtained in our study also fall within the corresponding range reported by CORNELIUS (1994) except for mean volume which was lower in our study. For height in *P. sylvestris*, ROSVALL *et al.* (2001) estimated a median CV_A of 8 % compared to a mean value of 5 % found in our study. Similar CV_A estimates for height in *P. sylvestris* were also found by HANNRUP *et al.* (1998) and HAAPANEN (2001).

Age – age genetic correlations (H12–H16) were high and significant (0.93–0.98) at all trial sites (data not shown). Similarly, in *P. elliottii*, correlations between heights at different ages varied between 0.79–0.99 (HODGE & WHITE 1992) and for volume between 0.57–0.98 (DIETERS *et al.* 1995). Also the trait–trait genetic correlations estimated in our study were generally high and significant. For instance, the genetic correlations between height and diameter, both at the same and different ages, exceeded 0.60 at all sites. In *P. elliottii*, genetic correlations between height and diameter at the same age were as a rule positive. But both high and low correlations were found depending on site (HODGE & WHITE 1992). In the same study, height – diameter correlations for different time periods varied between 0.17 and 0.82. Additional examples of high genetic correlations between height and diameter have been reported for Douglas-fir (0.81) (YEH & HEAMAN 1982) and *P. banksiana* (0.69) (KLEIN 1995). At all four test sites in our study, the strongest correlations with the most limited confidence intervals (*0.98 –1.00*) were those influenced by autocorrelations, such as DBH16–VOL16$^{1/2}$. Similar high genetic correlations between diameter and volume at the same ages (0.97 –1.00) have been reported for *P. elliottii* (HODGE & WHITE 1992). In the present study, weak and non-significant correlations were found only between the pairs HINCR12–16–DBH16 and HINCR12–16–VOL16$^{1/2}$ at the two northern test sites. One reason for this might be the lower heritabilities for DBH16 and VOL16$^{1/2}$ at these sites. Another reason might be that there were more trees missing at these sites. This may also be the reason why the correlations between H12 and HINCR12–16 were weaker at the two northern sites. With a few exceptions, the correlations between volume at age 16 and the other growth traits exceeded 0.80. Also in *P. elliottii* there were fairly high trait–trait genetic correlations for the time period 10–15 years (HODGE & WHITE 1992). As both the age–age correlations and the trait–trait correlations for the time period 12–16 were generally high, this suggests that an optimum selection age would be around 12 years provided that the correlations do not decrease much between 16 years and rotation age. This is supported by the data presented by ROSVALL *et al.* (2001) who estimated the correlation at 0.7 between height at 10–15 years and volume production at a rotation age of 70 years based on progeny trials and old provenance trials.

IMPLICATIONS FOR BREEDING

Our results suggest that G × E interactions do not play any significant role in the experimental series tested so far, which means that the differences in site conditions influenced most of the families in a similar way. Since the relative performance of the genetic entries did not change considerably across the different environments, our four trials fit reasonably well into one single breeding zone. As the northern high site index site, NHSI, had the highest average genetic correlation, this suggests that sites with similar climatic and edaphic conditions should be the best selection sites for volume. However, studies of G × E interactions, both in unselected populations and more advanced breeding populations, must be included in the breeding programmes, particularly in the cases of breeding zones with highly variable site conditions. Further, we observed that the

major genetic effects are additive, and therefore there is no need to consider the non-additive genetic effects in the current breeding programme. Our results also indicate that the same genes strongly influenced the growth traits during the time period 12–16 years, suggesting that early selection can improve growth at a more mature age if the findings by ROSVALL *et al.* (2001) are generally valid.

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REFERENCES

BALOCCHI, C. E., BRIDGWATER, F. E., ZOBEL, B. J. & JAHROMI, S. 1993: Age trends in genetic parameters for tree height in a nonselected population of loblolly pine. *For. Sci.* **39**: 231–251.

BRANDEL, G. 1990: Volume functions for individual trees. Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*) and birch (*Betula pendula & Betula pubescens*). Swedish Univ. of Agric. Sciences, Dep. of Forest Yield Research, Report No 26. 183 pp. (In Swedish with English summary).

BULMER, M. G. 1980: The Mathematical Theory of Quantitative Genetics. Clarendon Press, Oxford, 255 pp.

BURDON, R. D. 1977: Genetic correlation as a concept for studying genotype–environment interaction in forest tree breeding. *Silvae Genet.* **26**: 168–175.

BURDON, R. D. & NAMKOONG, G. 1983: Short Note: Multiple populations and sublines. *Silvae Genet.* **32**: 221–222.

BURDON, R. D., HONG S. O., SHELBOURNE, C. J. A., JOHNSON, I. G, BUTCHER, T. B., BOOMSMA, D. B., VERRYN, S. D., CAMERON, J. N. & APPLETON, R. 1997: International gene pool experiments in *Pinus radiata*: Patterns of genotype–site interaction. *New Zeal. J. For. Sci.* **27**(2): 101 –125.

CORNELIUS, J. 1994: Heritabilities and additive genetic coefficients of variation in forest trees. *Can. J. For. Res.* **24**: 372–379.

DANELL, Ö. 1993: Breeding programmes in Sweden — General approach. *In* Progeny testing and breeding strategies. Proceedings of the Nordic Group of Tree Breeding, Edinburgh, Scotland. 6–10 October. Supplement. (ed. S. J. Lee). Forestry Commission, Edinburgh, Scotland. pp.128 (i–v).

DIETERS, M. J., WHITE, T. L. & HODGE, G. R. 1995: Genetic parameter estimates for volume from full-sib tests of slash pine (*Pinus elliottii*). *Can. J. For. Res.* **25**: 1397 –1408.

EICHE, V. 1966: Cold damage and plant mortality in experimental provenance plantations with Scots pine in Northern Sweden. *Studia For. Suec.* **36**, 219 pp.

ERIKSSON, G. 1998: Evolutionary forces influencing variation among populations of *Pinus sylvestris*. *Silva Fennica* 32: 173–184.

ERIKSSON, G., ANDERSSON, S., EICHE V., IFVER, J. & PERSSON, A. 1980: Severity index and transfer effects on survival and volume production of *Pinus sylvestris* in northern Sweden. *Studia For. Suec.* **156**, 32 pp.

ERIKSSON, G., NAMKOONG, G. & ROBERDS, J. H. 1993: Dynamic gene conservation for uncertain futures. *For. Ecol. Manage.* **62**:15–37.

ERIKSSON, U., YAZDANI, R., WILHELMSSON, L. & DANELL, Ö. 1994: Success rate of a supplemental mass pollination in a seed orchard of *Pinus sylvestris* L. *Scand. J. For. Res.* **9**: 60–67.

FOSTER, G. S. & BRIDGWATER, F. E. 1986: Genetic analysis of fifth-year data from a seventeen parent partial diallel of loblolly pine. *Silvae Genet.* **35**: 118–122.

GREGORIUS, H.-R. & NAMKOONG, G. 1987: Resolving the dilemmas of interaction, separability and additivity. *Math. Biosci.* **85**: 51–69.

GULLBERG, U. & VEGERFORS, B. 1987: Genotype – environment interaction in Swedish material of *Pinus sylvestris*. *Scand. J. For. Res.* **2**: 417–432.

HAAPANEN, M. 1996: Impact of family-by-trial interaction on the utility of progeny testing methods for Scots pine. *Silvae Genet.* **45**: 130–135.

HAAPANEN, M. 2001: Time trends in genetic parameter estimates and selection efficiency for Scots pine in relation to field testing method. *For. Genet.* **8**: 129–144.

HANNRUP, B., WILHELMSSON, L. & DANELL, Ö. 1998: Time trends for genetic parameters of wood density and growth traits in *Pinus sylvestris* L. *Silvae Genet.* **47**: 214–219.

HODGE, G. R. & WHITE, T. L. 1992: Genetic parameter estimates for growth traits at different ages in slash pine and some implications for breeding. *Silvae Genet.* **41**:252 –262.

HOULE D. 1992: Comparing evolvability and variability of quantitative traits. *Genetics* 130: 195–204.

JAHROMI, S. T., GODDARD, R. E & SMITH, W. H. 1976: Genotype × fertilizer interactions in slash pine: Growth and nutrient relations. *For. Sci.* **22**: 211–219.

JANSSON, G. 1998: Approaches to genetic testing and evaluation in forest tree breeding. PhD Thesis. Swedish University of Agricultural Sciences. *Acta Universitatis Agriculturae Sueciae. Silvestria* **56**: 24 pp.

JOHNSON, G. R. & BURDON, R. D. 1990: Family-site interactions in *Pinus radiata*: Implications for progeny testing strategy and regionalised breeding in New Zealand. *Silvae Genet.* **39**: 55-62.

JONSSON, A., ERICSSON, T., ERIKSSON, E., KÄHR, M., LUNDKVIST, K. & NORELL, L. 1997: Interfamily variation in nitrogen productivity of *Pinus sylvestris* seedlings. *Scand. J. For. Res.* **12**: 1–10.

KLEIN, J. I. 1995: Multiple-trait combined selection in jack pine family-test plantations using best linear prediction.

Silvae Genet. **44**: 362–375.

KLEINSCHMIT, J., SVOLBA L., WEISGERBER H., JESTAEDT, M., DUMPFLMEIER, R., RUETZ W. & DIETRICH H. 1979: Ergebnisse aus dem internationalen Douglasien-Herkunftsversuch von 1970 in der Bundesrepublik Deutschland. II. Ergebnisse der Feldversuche im Alter 6. *Silvae Genet.* **28**: 226–244.

LI, B. & MCKEAND, S. E. 1989: Stability of loblolly pine families in the southeastern U.S. *Silvae Genet.* **38**: 96–101.

MATHESON, A. C. & COTTERILL, P. P. 1990: Utility of genotype × environment interactions. *For. Ecol Manage.* **30**: 159–174.

MATHESON, A. C. & RAYMOND, C. A. 1984: The impact of genotype × environment interactions on Australian *Pinus radiata* breeding programs. *Aust. For. Res.* **14**: 11–25.

MCKEAND, S. E., LI, B., HATCHER, A. V. & WEIR, R. J. 1990: Stability parameter estimates for stem volume for loblolly pine families growing in different regions in the southeastern United States. *For. Sci.* **36**: 10–17.

MCKEAND, S. E., ERIKSSON, G. & ROBERDS, J. H. 1997: Genotype by environment interaction for index traits that combine growth and wood density in loblolly pine. *Theor. Appl. Genet.* **94**: 1015–1022.

MORGENSTERN, E. K. 1978: The interaction between genotype, site and silvicultural treatment. *In*: Proc. VIIIth World Forestry Congress. Jakarta, 16–28 Oct. 1978, 20 pp.

MULLIN, T. J. 1985: Genotype – nitrogen interactions in full-sib seedlings of black spruce. *Can. J. For. Res.* **15**: 1031 –1038.

NAMKOONG, G., BARNES, R .D. & BURLEY, J. 1980: A Philosophy of Breeding Strategy for Tropical Forest Trees. *Tropical Forestry Papers* No. **16**. Commonwealth Forestry Institute. University of Oxford, Oxford. 67 pp.

NAMKOONG, G., JONSSON, A. & ERIKSSON, G. 1992: Genetic variation in nutrient response functions. *Theor. Appl. Genet.* **85**: 165–172.

OWINO, F. 1977: Genotype × environment interaction and genotypic stability in loblolly pine. II. Genotypic stability comparisons. *Silvae Genet.* **26**: 21–26.

OWINO, F., KELLISON, R. C. & ZOBEL, B. J. 1977: Genotype × environment interaction and genotypic stability in loblolly pine. V. Effects of genotype × environment interaction on genetic variance component estimates and gain predictions. *Silvae Genet.* **26**: 131–134.

PSWARAYI, I. Z., BARNES, R. D., BIRKS, J. S. & KANOWSKI, P. J. 1997: Genotype – environment interaction in a population of *Pinus elliottii* Engelm. var. *elliottii*. *Silvae Genet.* **46**: 35–40.

ROSVALL, O. 1999: Enhancing gain from long-term forest tree breeding while conserving genetic diversity. PhD Thesis. Swedish University of Agricultural Sciences. *Acta Universitatis Agriculturae Sueciae. Silvestria* **109**. 65 pp.

ROSWALL, O., JANSSON, G., ANDERSSON, B., ERICSSON, T., KARLSSON, B., SONESSON, J. & STENER, L-G. 2001: Genetic gain from present and future seed orchards and clone mixes. *SkogForsk. Redogörelse* nr **1**. 2001. (In Swedish with English summary). 41 pp.

SAS INSTITUTE INC. 1999: *SAS/STAT® User's Guide, Version 8*, Cary, NC: SAS Institute Inc.

SHELBOURNE, C. J. A. 1972: Genotype – environment interaction: Its study and its implications in forest tree improvement. Proc. IUFRO Genetics–SABRAO Joint Symposia. Tokyo, Oct. 1972. B–1(I): 1–28.

SKRØPPA, T. 1984: A critical evaluation of methods available to estimate the genotype × environment interaction. *Studia. For. Suec.* **166**: 3–14.

SONESSON J. & ERIKSSON, G. 2000: Genotypic stability and genetic parameters for growth and biomass traits in a water × temperature factorial experiment with *Pinus sylvestris* L. seedlings. *For. Sci.* **46**: 487–495.

STÅHL, E. G. 1984: Variation in shoot growth phenology among clones and populations of *Pinus sylvestris*. PhD Thesis, Swedish University of Agricultural Sciences, Department of Forest Yield Research, 103 pp.

YANCHUK, A. D. 1996: General and specific combing ability from disconnected partial diallels of coastal Douglas-fir. *Silvae Genet.* **45**: 37–45.

YEH, F. C. & HEAMAN, C. 1982: Heritabilities and genetic and phenotypic correlations for height and diameter in coastal Douglas-fir. *Can. J. For. Res.* **12**: 181–185.