

## GENETIC PARAMETER ESTIMATES FOR GROWTH TRAITS AND STEM STRAIGHTNESS IN A BREEDING SEEDLING ORCHARD OF *EUCALYPTUS GRANDIS*

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**GAPARE, W. J., GWAZE, D. P. & MUSOKONYI, C. 2003. Genetic parameter estimates for growth traits and stem straightness in a breeding seedling orchard of *Eucalyptus grandis*.** Genetic parameters for growth and stem straightness were determined for a fourth generation breeding seedling orchard (BSO) of *Eucalyptus grandis* in Zimbabwe. Data were from 30 half-sib open pollinated families assessed at two, five and six years of age. Growth traits had low to moderate heritability estimates (0.04 to 0.20). Age-age genetic correlations were large and positive for all traits ( $r_A = 0.80$ ). Both heritability estimates and genetic correlations were unaffected by systematic thinning. However, selective thinning inflated heritability estimates at age of thinning and reduced them at subsequent ages after selective thinning. The latter was attributed to compensatory growth. Selective thinning reduced genetic correlations. Thus for unbiased estimates of genetic parameters from BSOs, analysis should be done on data collected prior to thinning or from systematically thinned tests.

Key words: Heritability - genetic correlation - selective thinning - systematic thinning - tree breeding

**GAPARE, W. J., GWAZE, D. P. & MUSOKONYI, C. 2003. Anggaran parameter genetik bagi ciri-ciri tumbesaran dan kelurusan batang di dalam kebun pembiakbakaan anak benih *Eucalyptus grandis*.** Parameter genetik untuk tumbesaran dan kelurusan batang ditentukan untuk generasi keempat kebun pembiakbakaan anak benih *Eucalyptus grandis* di Zimbabwe. Data diambil daripada 30 famili separuh sib yang didebungakan secara bebas dan dinilai pada umur dua tahun, lima tahun dan enam tahun. Ciri-ciri tumbesaran mempunyai anggaran keterwarisan yang rendah atau sederhana (0.04 hingga 0.20). Korelasi genetik antara umur dengan umur tinggi dan positif untuk

semua ciri ( $r_A = 0.80$ ). Kedua-dua anggaran keterwarisan dan korelasi genetik tidak dipengaruhi oleh penjarangan teratur. Namun, penjarangan pilihan menaikkan nilai anggaran keterwarisan pada umur penjarangan dan menurunkan nilai ini selepas penjarangan. Penurunan anggaran keterwarisan selepas penjarangan adalah disebabkan oleh tumbesaran kompensatori. Penjarangan pilihan mengurangkan korelasi genetik. Justeru, untuk mengelakkan daripada anggaran parameter genetik kebun pembiakbakaan anak benih yang serong, analisis perlu dilakukan terhadap data yang diperoleh sebelum penjarangan ataupun daripada penjarangan teratur.

## Introduction

*Eucalyptus grandis* is one of the most widely utilised tree species for afforestation in the warmer parts of the world. Zimbabwe is no exception and 20% (approximately 24 000 ha) of the commercial forestry land is planted with this species (Timber Producers Federation 1999). The species has been grown in commercial plantations for over three decades. *Eucalyptus grandis* remains the fastest growing eucalypts species in Zimbabwe. The species is extensively used for poles, mining timber, pulp and furniture.

Since the 1960s, there has been sustained work on the genetic improvement of *E. grandis* in Zimbabwe (Mullin *et al.* 1981). In this context, there has been an increasing interest on the part of the Zimbabwe Forestry Commission to invest in *E. grandis* breeding in order to enhance plantation productivity and uniformity. Throughout the past 40 years, *E. grandis* has been the subject of intensive tree improvement activities in Zimbabwe. Changes in the intensity of the programme reflected the commercial importance of the species. Key aspects of the programme were described in Barnes *et al.* (1997). Briefly, the Multiple Population Breeding Strategy (MPBS) was implemented in 1981 and the concept of the breeding seedling orchard (BSO) became central to the MPBS in Zimbabwe. The concept of the BSO has been summarised by Barnes (1995). At the inception of the MPBS concept, the breeding population of *E. grandis* was structured into five main sub-populations based on differences in environmental conditions at the place of selection of plus trees that provided seed for the various sub-populations (Barnes *et al.* 1997). In addition, there were an additional five sub-populations of exotic origin that were hypothesised to have special attributes, i.e. high productivity, cold tolerant and canker resistant. The overall strategy for *E. grandis* breeding was to test whether there was any genotype by environment worth exploiting in the five main sub-populations that had been assembled and to establish whether or not the special attributes of the exotic sub-populations were expressed in the Zimbabwe environment. A single BSO constitutes the selected genetic material for each of the sub-populations.

There is one BSO per sub-population per generation and it performs the combined functions of the selection base, progeny test, seed production and breeding populations of the conventional strategy. Several limitations exist which make the management of the BSO problematic. For example, management for seed production functions would compromise precision of selection (Barnes 1995). In breeding programmes, accurate genetic parameters such as heritabilities and

juvenile-mature correlations are important because they enable selection to be done early, reducing the length of the breeding cycle, thereby maximising gains realised per unit time and yet in the management of BSOs, they can only be accurate up to the age of first selective thinning (Barnes 1995). Where correlations are inaccurate and or weak, selection has to be delayed until the trees are mature. This is not only economically expensive but also delays the availability of genetically improved seed. On the other hand, if genetic parameters are unaffected by thinning, selective thinning could be carried out early without compromising availability of improved seed. The effect of selective thinning in *E. grandis* BSOs has not been ascertained. This paper reports on genetic parameter estimates (heritabilities, genetic correlations) and determines the effects of selective thinning on genetic parameter estimates. The information will be critical for the evaluation of the effectiveness of the BSO concept in a MPBS.

## Materials and methods

### *Location and field design*

BSO comprised 30 half-sib families (seedlots) of *E. grandis*. These half-sib families constituted the fourth generation BSO (EB50) that originated from third generation selections in EB3 planted at John Meikle Research Station. The families in EB3 were from plus trees selected from progeny tests in the Eastern Highlands. The seed was sown in August 1991 and the trial established in January 1992 at John Meikle Forest Research Station (latitude: 18° 3' S, longitude: 32° 51' E, altitude: 1268 m above sea level). The site receives a mean annual rainfall of 1725 mm and the soils are granite in origin. No fertilisers were used but the site was kept clear of weeds for several months after planting. The BSO was established in randomised complete block design replicated six times with nine-tree family square plots. Spacing was approximately 3 × 3 m.

### *Assessments*

The BSO was measured at two, five and six years for the following traits:

- height (HT) and diameter at breast height (DBH). Height and diameter at two, five and six years are hereafter referred to as HT2, DBH2, HT5, DBH5, HT6 and DBH6 respectively
- stem straightness (ST) was assessed using a 7-point absolute scale (1 = crooked to 7 = very straight) as outlined by Barrett and Mullin (1968) at two, five and six years (ST2, ST5 and ST6 respectively).

Stem straightness scores were tested for normality and found to be normally distributed and was therefore treated as a continuous variable.

Estimates of volume (VOL) in m<sup>3</sup> were derived following *E. grandis* volume equation by Bredekamp (1982)

$$\text{Log VOL} = -4.2328 + 1.7154 \log \text{DBH} + 1.1070 \log \text{HT} \quad (1)$$

where

DBH = diameter at breast height (cm)

HT = height (m)

The BSO was thinned from below at five years according to the BSO concept (Barnes 1995).

### Statistical analyses

Variance components were estimated using the method of restricted maximum likelihood (REML), available in the MIXED procedure of SAS/STAT package (SAS 1992, Littell *et al.* 1996). Family effects were estimated for all traits using SAS PROC MIXED (Littell *et al.* 1996) to calculate the generalised least square estimates. The statistical model used for the analyses was

$$\gamma_{jkl} = \mu + B_j + F_k + FB_{jk} + W_{jkl} \quad (2)$$

where

$$\begin{aligned} \gamma_{jkl} &= \text{observation of the } l \text{ th tree in the } j \text{ th block and the } k \text{ th family} \\ E(\gamma_{jkl}) &= \mu + B_j \\ \text{Var}(\gamma_{jkl}) &= \sigma_F^2 + \sigma_{BF}^2 + \sigma_w^2 \\ \mu &= \text{general mean} \\ B_j &= \text{fixed effect of the } j \text{ th block} \\ F_k &= \text{random effect of the } k \text{ th family} \\ E(F_k) &= 0 \\ \text{Var}(F_k) &= \sigma_F^2 \\ FB_{jk} &= \text{random plot error due to interaction between } j \text{ th block} \\ &\quad \text{and } k \text{ th family} \\ E(FB_{jk}) &= 0 \\ \text{Var}(FB_{jk}) &= \sigma_{FB}^2 \\ w_{jkl} &= \text{random tree error of the } l \text{ th tree in the } jk \text{ th plot} \\ E(w_{jkl}) &= 0 \\ \text{Var}(w_{jkl}) &= \sigma_w^2 \end{aligned}$$

Total phenotypic variance ( $\sigma_T^2$ ) was estimated as

$$\sigma_T^2 = \sigma_F^2 + \sigma_{FB}^2 + \sigma_w^2 \quad (3)$$

Heritability estimates reported in this study could be biased upwards because the data were based on only one site and because the genotype-environment interaction effect that was not separated from the family component in the linear model applied.

Biased individual tree heritability ( $h^2_b$ ) was estimated using variance components in the following manner:

$$h^2_b = \sigma^2_A / \sigma^2_T \quad (4)$$

where

$$\begin{aligned} \sigma^2_A &= \text{within population additive genetic variance} \\ \sigma^2_T &= \text{corresponding phenotypic variance} \end{aligned}$$

The covariance among offspring of true half-sib families is  $\frac{1}{4}$  of additive genetic variance (i.e. the coefficient of relationship is 0.25). The coefficient of relationship of open-pollinated (OP) families will often be higher than 0.25. This could result from selfing, inbreeding and or a smaller number of effective male pollinators leading to the presence of some percentage of full-sibs within the OP family (Squillace 1974). An assumption of a coefficient of 0.25 will generally result in an overestimate of heritability. Thus, instead of multiplying family variance by 4 in the calculation of heritability, family variance was multiplied by 3. In other words, the coefficient for relationship for the OP families was assumed to be 0.33.

Age-age genetic correlations and trait-trait correlation were obtained using the following formula:

$$r_A = \sigma_{Axy} / (\sigma_{Ax} \sigma_{Ay}) \quad (5)$$

where

$$\begin{aligned} r_A &= \text{additive genetic correlation between traits } x \text{ and } y \\ \sigma_{Axy} &= \text{additive genetic covariance between traits } x \text{ and } y \\ \sigma_{Ax} &= \text{additive genetic variance component for trait } x \\ \sigma_{Ay} &= \text{additive genetic variance component for trait } y \end{aligned}$$

Covariance components were calculated using a dummy variable approach (Searle *et al.* 1992).

Variances are not independent of the scale and the mean of the respective traits (Sokal & Rohlf 1995). Therefore, to relatively compare the genetic variances of the different traits across ages, a parameter measuring the genetic coefficient of variation was calculated as:

$$CV_A = 100\% \times \sigma_A / \bar{x} \quad (6)$$

where

- $CV_A$  = coefficient of additive genetic variation  
 $\sigma_A$  = square root of additive genetic variance for a trait  
 $\bar{x}$  = population mean for the trait

The higher the values of  $CV_A$ , the higher is their relative variation. The  $GCV$  expresses the genetic variance relative to the mean of the trait of interest and gives a standardised measure of the genetic variance relative to the mean of the trait. It provides an indication of how much genetic gain that may be obtained from selection of a specified number of standard deviations above the mean.

Theoretical standard errors of heritability, age-age genetic correlations and trait-trait correlations were calculated according to Dickerson (1969) and Namkoong (1979).

### *Effect of thinning on genetic parameters*

To determine the effect of thinning regime on genetic parameters, computer simulations were used to impose two alternative thinning regimes on the five-year measurements. The first simulated thinning regime was systematic thinning, i.e. all even number trees in the plot were removed. This is essentially random with respect to the traits under the study. The second simulated thinning regime was selective thinning, i.e. all trees in the plot that were marked for thinning during the assessments were deleted from the data. Also, analysis was carried out on assessments at six years of age on trees selectively thinned at five years.

## **Results**

### *Growth traits*

Mean tree heights at ages two, five and six years were 10.8, 20.9 and 26.7 m respectively (Table 1). Mean single-tree volume at six years was 0.33 m<sup>3</sup>, which is double the volume estimated at five years (0.16 m<sup>3</sup>). Families were not significantly different in height, diameter and volume at two years but were statistically significant ( $p < 0.05$ ) at five years except in stem straightness. At six years, families differed significantly in diameter and volume ( $p < 0.05$ ).

**Table 1** Least squares means and standard errors for height, diameter, volume and stem form for a fourth generation *Eucalyptus grandis* breeding seedling orchard in Zimbabwe at two, five and six years

Age (years)	No. of trees	Height (m)	DBH (cm)	VOL (m <sup>3</sup> )	straightness (score)
2	1615	10.83 ± 0.67	8.97 ± 0.59	0.029 ± 0.004	4.48 ± 0.21
5	1615	20.89 ± 1.01	15.69 ± 1.03	0.161 ± 0.02	4.76 ± 0.42
6	883	26.68 ± 0.79	20.67 ± 0.89	0.336 ± 0.04	4.99 ± 0.18

*Genetic variances and heritability estimates*

Genetic coefficients of variation (GCV) for growth traits ranged from 6–12% for height, 6–16% for diameter, and 7–35% for volume between ages two and five years (Table 2). Estimates of  $h^2_b$  for height, diameter and volume at age two years were 0.06, 0.04 and 0.03 respectively. Estimates of  $h^2_b$  prior to thinning for height, diameter and volume at age five years were 0.20, 0.16 and 0.12 respectively. Heritability estimates after selective thinning were 0.51, 0.45 and 0.37 at five years for height, dbh and volume respectively. Heritability estimates after simulated systematic thinning for height, diameter and volume at five years of age were 0.16, 0.15 and 0.11 respectively.

**Table 2** Variance component and heritability estimates for growth in a breeding seedling orchard of *Eucalyptus grandis*

Trait	Thinning regime <sup>a</sup>	$\sigma^2_A$	$\sigma^2_T$	$h^2_b \pm \text{s.e.}$	GCV (%)
HT2	0	0.404	7.250	0.06 ± 0.03	6
DBH2	0	0.308	6.856	0.04 ± 0.02	6
VOL2	0	0.00007	0.00432	0.03 ± 0.02	7
STR2	0	0.056	0.505	0.11 ± 0.04	16
HT5	0	1.976	9.925	0.20 ± 0.08	7
HT5	1	6.265	12.206	0.51 ± 0.19	12
HT5	2	1.428	9.212	0.16 ± 0.12	6
DBH5	0	2.142	13.415	0.16 ± 0.10	9
DBH5	1	6.222	13.934	0.45 ± 0.31	16
DBH5	2	1.937	13.197	0.15 ± 0.18	8
VOL5	0	0.012	0.097	0.12 ± 0.08	17
VOL5	1	0.027	0.073	0.37 ± 0.09	35
VOL5	2	0.011	0.098	0.11 ± 0.09	16
STR5	0	0.143	1.4375	0.10 ± 0.07	8
STR5	1	0.193	1.235	0.16 ± 0.12	9
STR5	2	0.083	1.3813	0.06 ± 0.03	6
HT6	1	0.336	8.285	0.04 ± 0.02	2
DBH6	1	1.018	9.430	0.11 ± 0.09	5
VOL6	1	0.025	0.193	0.13 ± 0.09	11
STR6	1	0	0.533	0	-

<sup>a</sup>0 = no thinning, 1 = selective thinning, 2 = systematic thinning  
GCV = genetic coefficient variation

*Genetic correlations*

Age-age correlations for height, diameter, volume and stem straightness (Table 3) were highly correlated ( $r_A = 1.00$ ). Height was strongly correlated with diameter with  $r_A$  values above 0.67, except the poor correlation between two-year height and two-year volume ( $r_A = 0.35$ ) (Table 3). Volume was poorly correlated with stem straightness ( $r_A = 0.13$  to 0.53), while diameter and height were moderately to highly correlated with stem straightness ( $r_A = 0.37$  to 0.80) (Table 3).

**Table 3** Genetic correlation estimates and associated standard errors in a breeding seedling orchard of *Eucalyptus grandis* prior to thinning

	HT2	HT5	DBH2	DBH5	VOL2	VOL5	ST2
HT5	1.00*						
DBH2	0.82 ± 0.05	0.68 ± 0.08					
DBH5	0.87 ± 0.04	0.92 ± 0.03	1.00*				
VOL2	0.35 ± 0.03	1.00*	1.00*	1.00*			
VOL5	0.81 ± 0.05	0.97 ± 0.01	0.99 ± 0.01	1.00*	1.00*		
ST2	0.80 ± 0.04	0.37 ± 0.04	0.64 ± 0.06	0.50 ± 0.09	0.53 ± 0.07	0.39 ± 0.14	
ST5	0.60 ± 0.03	0.68 ± 0.05	0.47 ± 0.11	0.62 ± 0.08	0.29 ± 0.13	0.13 ± 0.09	1.00*

\* Absolute values greater than one are arithmetically possible but are meaningless and in the table they have been set to unit

Effect of thinning on genetic correlation estimates is presented in Table 4. Genetic correlations between heights at two and five years were 0.87 and 0.86 for systematic and selective thinning respectively. Genetic correlation between height at ages two and six years after selective thinning was 0.48. Genetic correlations between diameter at age two and six years were 1.00 and 0.97 for systematic and selective thinning respectively. However, genetic correlations for stem straightness between ages two and five years were of much lower magnitude than other traits for both systematic and selective thinning (0.48 and 0.51 respectively). Weaker correlations were observed between traits before thinning and after selective thinning at six years. For example, correlations between diameter before thinning and after selective thinning were 0.98 and 0.47 respectively. Similar trends were observed for stem straightness (0.50 and 0.08 respectively).

**Table 4** Effect of thinning on genetic correlation estimates and associated standard errors in an *Eucalyptus grandis* BSO

Trait 1-Trait 2*	Before thinning		Systematic thinning		Selective thinning	
	$r_A$	SE	$r_A$	SE	$r_A$	SE
HT2-HT5	1	0	0.87	0.03	0.86	0.06
HT2-HT6	-	-	-	-	0.48	0.11
DBH2-DBH5	1	0	1.00	0	0.97	0.02
DBH2-DBH6	-	-	-	-	0.54	0.12
VOL2-VOL5	1	0	0.82	0.03	0.81	0.08
VOL2-VOL6	-	-	-	-	0.45	0.13
ST2-ST5	1	0	0.48	0.12	0.51	0.21
ST2-ST6	-	-	-	-	0.46	0.22
HT5-HT5	1	0	0.74	0.05	1	0
HT5-HT6	-	-	-	-	0.65	0.08
DBH5-DBH5	1	0	0.70	0.09	0.98	0.01
DBH5-DBH6	-	-	-	-	0.47	0.15
VOL5-VOL5	1	0	0.68	0.09	0.58	0.11
VOL5-VOL6	-	-	-	-	0.43	0.11
ST5-ST5	1	0	0.89	0.05	0.50	0.11
ST5-ST6	-	-	-	-	0.08	0.32

\*Trait 1 is before thinning and trait 2 is after thinning. HT is height, DBH is diameter, number is age. Thinning was carried out at the older age in each trait-trait combination



## Discussion

### *Growth traits*

Estimates of genetic parameters for growth and stem straightness are limited in *E. grandis* and those reported here suggest that these traits are under weak to moderate genetic control. Genetic coefficients of variation for all traits increased with age. This shows that there was a moderate increase in genetic variance between ages two and five years for height, diameter and volume. The GCV is a convenient way to express the size of the additive variance controlling a trait or the potential gain that can be made in a trait.

### *Genetic variances and heritability estimates*

Genetic parameters reported in this study appear to be less than those reported previously for the same species. Reddy and Rockwood (1989) reported individual tree heritability of 0.39 for height and diameter for half-sib *E. grandis*. Kedharnath (1983) reported constant heritability of about 0.20 for height of *E. grandis* at 3 years, increasing to 0.34 at 4.5 years. Those estimated for *E. globulus* in Portugal were also slightly higher ( $h^2 = 0.18-0.34$ ) (Borrallho *et al.* 1992). Possible reasons for lower heritability estimates in this fourth generation material could be due to a decline in additive genetic variance and/or inbreeding effects which also resulted in a decline in genetic gain from 9.3% in the third generation BSO to 5.3% in the fourth generation BSO (Gapare *et al.* 2003). Additive genetic variance is likely to be improved by increasing the number of families and also by initiating controlled pollination programme in *E. grandis* in Zimbabwe.

The heritability of stem form is lower than that of growth traits. The low heritability estimates for stem form may be due to genetic advances made in the first three generations of selection in the *E. grandis* breeding population in Zimbabwe. The low heritability estimates for stem straightness could be attributed to the assessment absolute score used in this study. Gwaze *et al.* (1997) argued that the stem straightness assessment employed in the breeding programme in Zimbabwe that uses an absolute score rather than relative score results in low heritability. The assessment of stem straightness in the BSO employed an assessment method that uses an absolute score ranging from 1 to 7 (Barrett & Mullin 1968). The scale that has a mid-point of 4 may result in low heritability estimates since assessors may score most trees as 4 (average).

The estimates of single-site biased heritability in the absence of thinning were generally low to moderate for growth traits. Biased heritability estimates for growth traits increased from low values at two years to moderate values at five years of age. Biased heritability estimates for straightness were moderate and were unaffected by age ( $h^2_b = 0.10$ ). In such a study, the coefficient of relationship among OP offspring depends on the frequency of selfing, frequency of related matings and number of pollen parents (Squillace 1974). Squillace (1974)

demonstrated that between 5 and 10 local males acting as pollen parents and 5% selfing, the coefficient of relationship among OP offspring is 0.33. If selfing is more frequent and/or there are fewer males contributing pollen to the offspring, the coefficient of relationship can be 0.40 or higher. Authors working with *Eucalyptus* progeny test data have assumed coefficients of relationship ranging from 0.33 to 0.54 (Griffin & Cotterill 1988, Woolaston *et al.* 1991, Borralho *et al.* 1992, Hodge *et al.* 1996). These assumptions were considered justified because many eucalypts species have mixed mating system (both selfing and outcrossing) (Moran & Bell 1983), and in addition, OP progeny from native *Eucalyptus* stands will often exhibit “neighbourhood inbreeding” due to short pollen dispersal distances associated with insect-vectored pollen (Potts 1990).

### *Effect of thinning on heritability estimates*

Selective thinning increased the additive genetic variance but had little effect on the phenotypic variance for all growth traits. On the other hand, systematic thinning did not change the variances. The net result was that heritability estimates were highly inflated with selective thinning and remained unchanged with systematic thinning at age five. For example,  $h^2_b$  before thinning, for height at five years was 0.20 and was unaffected by simulated systematic thinning but increased to 0.51 after simulated selective thinning. Similar trends were observed for stem straightness, although to a lesser extent. Systematic thinning did not affect the estimate of variances themselves but increased the standard errors of the heritability estimates because the estimates were based on smaller number of trees. There was an appreciable difference in heritability estimates at ages five and six when selective thinning was carried out at five years for all traits. This was surprising given that both estimates were based on the same trees with only a difference of one year in age. The biased heritability estimate for diameter, for example, was 0.45 at 5 years and 0.11 at 6 years after selective thinning at 5 years.

The method of thinning materially affected the estimates of heritability estimates through its effects on the additive and phenotypic variances. Systematic thinning had no effect on additive and phenotypic variances and this resulted in similar heritability estimates in systematically thinned population and unthinned population. In contrast, selective thinning increased the additive genetic variance but had less effect on the phenotypic variance. This resulted in higher heritability estimates in selectively thinned population compared with unthinned population. The lack of reduction in phenotypic variance in the selectively thinned population could be attributed to the fact that trees were not only selected for diameter growth but also for stem form. Matheson and Raymond (1984) as well as Cotterill and Dean (1988) also found that selective thinning inflated the heritability estimates in *P. radiata*. However, the inflation of heritability estimates in their study was due to a higher reduction in phenotypic variance than additive variance. In this study, all the growth traits were similarly affected by selective thinning but stem straightness was less affected by selective thinning than the growth traits. Barnes *et al.* (1992) reported that heritability estimates are often inflated by selective thinning if there

are dominance effects present. Dominance variance is part of the total genetic variance but can only be estimated if the genetic material in the BSO were full sibs. In a *Pinus patula* study, Barnes *et al.* (1992) found no evidence of dominance effects and selective thinning had minimal effects on heritability estimates. In the present study, the inflated heritability estimates after selective thinning suggest the possible presence of dominance effects in the BSO, but the BSO does not inherently allow for estimation of dominance effects.

Selective thinning affected genetic parameters estimated at subsequent growth after one year. Heritability estimates were highly reduced one year after selective thinning. This was due to a higher reduction in additive compared with phenotypic variances. This is an important result as it reveals that the effects of selective thinning on genetic parameters manifest itself both at the age at which thinning was carried out and at post-thinning growth stages. Trees recovering from growth restriction such as those in the intermediate classes might exhibit more rapid (compensatory) growth than trees in the dominant and codominant classes after thinning, thereby reducing the additive and phenotypic variance. Therefore, compensatory growth is likely to explain the reduction in heritability a year after selective thinning. While the compensatory growth reported here occurs after only one year of growth, Kremer (1992) states that compensatory growth may occur at growth separated by 16 years in a slow growing species, maritime pine. The results of this study suggest that any assessment of the effect of thinning on genetic parameters should consider the growing period after selective thinning. However, it is likely that competition affected the results since trees were growing fast, but the competition effects were not quantified and hence were not discussed.

#### *Effect of thinning on genetic correlations*

Selective thinning reduced genetic correlations for growth traits, while systematic thinning did not affect the correlations substantially. While genetic correlations between heights at two and five years were high ( $r_A = 1.00$ ) prior to thinning at five years, they were little affected by systematic and selective thinning ( $r_A = 0.87$  and  $0.86$  respectively) at the age of thinning. However, genetic correlations were highly reduced a year after selective thinning at six years. For example, genetic correlations between heights at two and six years were  $0.48$  while those between heights at two and five were  $0.86$ . The same trend was observed for diameter and volume growth. In contrast, genetic correlations between stem straightness at two and five years ( $r_A = 0.51$ ) and those between stem straightness at two and six years ( $r_A = 0.46$ ) were similar. Five-year traits before thinning were poorly correlated with six-year traits after selective thinning at five years. For example, correlation between diameter before thinning and diameter at 5 years after selective thinning at 5 years was  $0.98$  and that between diameter before thinning at 5 years and diameter at 6 years was  $0.47$ . Similarly, correlation between straightness at 5 years before and after thinning was  $0.50$ , while correlation between straightness before thinning at 5 years and at 6 years after thinning was only  $0.08$ .