

status number) rather than census number should be addressed, considering relatedness and fertility variation, for the monitoring of gene diversity in orchard crops.

Acknowledgment

Authors thank to Prof. DAG LINDGREN at the Department of Forest Genetics and Plant Physiology in the Swedish University of Agricultural Sciences (SLU-Umeå) for valuable discussion. We thank Dr. ROWLAND BURDON from the New Zealand Forest Research Institute and anonymous referees for their reviewing and valuable comments.

References

ANONYMOUS: 2000 yili calisma raporu, 2001 yili calisma programi (Working report of 2000 and working plan of 2001). The Research Directorate of Forest Tree Seeds and Tree Breeding, No: 3 (132/7), Ankara, Turkey (2001). — BILA, A. D.: Fertility variation and its effects on gene diversity in forest tree populations. Ph. D Thesis. Swedish University of Agricultural Science, Umeå, Sweden. Acta Universitatis Agriculturae Sueciae, Silvestria **166** (2000). — BILA, A. D. and LINDGREN, D.: Fertility variation in *Milletia stuhlmanii*, *Brachystegia spiciliformis*, *Brachystegia bohemii* and *Leucaena leucocephala* and its effects on relatedness in seeds. For. Genet. **5**: 119–120 (1998). — BILA, A. D., LINDGREN, D. and MULLIN, T. J.: Fertility variation and its effect on diversity over generations in a Teak plantation (*Tectona grandis* L.f.). Silvae Genet. **48**: 109–114 (1999). — CALISKAN, T.: Hizli gelisen turlerle ilgili rapor (Report of fast growing species in Turkey). Workshop-Hizli Gelisen Turlerle Yapilan Agaclandirma Calismalarinin Degerlendirilmesi ve Yapilacak Calismalar, 8–9 Aralik, Ankara. (1998). — CROW, J. F. and KIMURA, M.: An introduction to population genetics theory. Harper and Row Publishers, London, pp. 591 (1970). — FRIES, A.: Development of flowering and the effect of pruning in a clonal seed orchard of lodgepole pine. Can. J. For. Res. **24**: 71–76 (1994). — GRIFFIN, A. R.: Clonal variation in radiata pine seed orchards. I. Some flowering, cone, and seed production traits. Aust. For. Res. **12**: 295–302 (1982). — HODGE, G. R. and WHITE, T. L.: Advanced-generation wind-pollination seed orchard design. New Forests **7**: 213–236 (1993). — KANG, K. S.: Clonal and annual variation of flower production and composition of gamete gene pool in a clonal seed orchard of *Pinus densiflora*. Can. J. For. Res. **30**: 1275–1280 (2000). — KANG, K. S.: Genetic gain and gene diversity of seed orchard crops. Ph. D Thesis. Swedish University of Agricultural Science, Umeå, Sweden. Acta Universitatis Agriculturae Sueciae, Silvestria **187**. pp. 75 (2001). — KANG,

K. S. and EL-KASSABY, Y. A.: Considerations of correlated fertility between genders on genetic diversity: *Pinus densiflora* seed orchard as a model. Theor. Appl. Genet. **000**: 000–000 (in press) (2002). — KANG, K. S. and LINDGREN, D.: Fertility variation and its effect on the relatedness of seeds in *Pinus densiflora*, *Pinus thunbergii* and *Pinus koraiensis* clonal seed orchards. Silvae Genet. **47**: 196–201 (1998). — KANG, K. S. and LINDGREN, D.: Fertility variation among clones of Korean pine (*Pinus koraiensis* S. et Z.) and its implications on seed orchard management. For. Genet. **6**: 191–200 (1999). — KANG, K. S., HARJU, A. M., LINDGREN, D., NIKKANEN, T., ALMQVIST, C. and SUH, G. U.: Variation in effective number of clones in seed orchards. New Forests **21**: 17–33 (2001). — KESKIN, S.: Clonal variation in flowering and cone characteristics in a *Pinus brutia* seed orchard. SAFRI Technical Bulletin No. 9, Antalya, pp. 96 (1999). — KJAER, E. D.: Estimation of effective population number in a *Picea abies* (KARST.) seed orchard based on flower assessment. Scand. J. For. Res. **11**: 111–121 (1996). — KJAER, E. D. and WELLENLORF, H.: Variation in flowering and reproductive success in a Danish *Picea abies* (KARST) seed orchard. For. Genet. **4**: 181–188 (1997). — KOSKI, V. and ANTOLA, J.: National Tree Breeding and Seed Production Programme for Turkey 1994–2003. The Research Directorate of Forest Tree Seeds and Tree Breeding, Ankara, Turkey. (1993). — LINDGREN, D., GEA, L. and JEFFERSON, P.: Loss of genetic diversity monitored by status number. Silvae Genet. **45**: 52–59 (1996). — LINDGREN, D. and MULLIN, T. J.: Relatedness and status number in seed orchard crops. Can. J. For. Res. **28**: 276–283 (1998). — MATZIRIS, D.: Variation in cone production in a clonal seed orchard of Black pine. Silvae Genet. **42**: 136–141 (1993). — MATZIRIS, D.: Variation in growth, flowering and cone production in a clonal seed orchard of Aleppo pine grown in Greece. Silvae Genet. **46**: 224–228 (1997). — MATZIRIS, D.: Genetic variation in cone and seed characteristics in a clonal seed orchard of Aleppo pine grown in Greece. Silvae Genet. **47**: 37–41 (1998). — NIKKANEN, T. and RUOTSALAINEN, S.: Variation in flowering abundance and its impact on the genetic diversity of the seed crop in a Norway spruce seed orchard. Silva Fenn. **34**: 205–222 (2000). — SAVOLINEN, O. and KÄRKKÄINEN, K.: Effect of forest management on gene pools. New Forests **6**: 326–345 (1992). — YAZDANI, R. and LINDGREN, D.: Variation of pollen contamination in a Scots pine seed orchard. Silvae Genet. **40**: 243–246 (1991). — YAZDANI, R., LINDGREN, D., YAZDANI, F. S., PASCUAL, L. and ERIKSSON, U.: Flowering, phenology, empty seeds and pollen contamination in a clonal seed orchard of *Pinus sylvestris* in northern Sweden. In: Population genetics and genetic conservation of forest trees. SPB Academic Publishing, Amsterdam, p. 309–319 (1995).

Inbreeding in *Pinus Radiata*

III. The Effect of Inbreeding on Age-age Correlation and Early Selection Efficiency

By A. C. MATHESON¹), H. X. WU^{1*}), D. J. SPENCER¹), C. A. RAYMOND²) and A. R. GRIFFIN³)

(Received 17th December 2001)

Abstract

A breeding strategy involving inbreeding followed by cross-breeding of inbreds requires that the production of superior inbred lines must be possible, but crosses between lines should exhibit heterosis, inbreeding should not substantially delay reproduction, and early selection between lines to be effective. Age-age correlation and the effectiveness of early selection have been extensively reported for outcrossed populations of different species, but there are no reports for inbred populations. In this study, age-age correlations based on both family means and individual trees were investigated and compared in radiata pine populations with five different inbreeding levels ($F = 0, 0.125, 0.25, 0.5$ and 0.75). Trends in additive genetic variance, environmental variance, heritability and age-age

additive genetic correlations were estimated from an outcrossed population ($F = 0$).

For cross-sectional area at breast height, additive genetic variance increased from 3.7% at age 3 to 29.4% at age 5, remained at about 30% up to age 10, then declined to 15.6% at age 13.

¹) CSIRO Forestry and Forest Products, PO Box E4008, Kingston, ACT 2604, Australia

* Corresponding Author: Harry.wu@csiro.au.

²) CSIRO Forestry and Forest Products, GPO Box 252-12, Hobart Tasmania 7001, Australia

³) Present address: Shell Forestry, Shell Centre, London SE1 7NA, UK

The trend for heritability was similar to that for additive variance. Age-age additive correlations between early ages and at age 13 were very high in this study (> 0.76 for sectional area at age 3). Early selection for cross-sectional area at age 13 would have been most efficient if carried out between ages 5 and 9 in the outcrossed population. Higher values for age-age correlations based both on individuals and family means were obtained at the higher levels of inbreeding. This indicates that early selection would be more efficient among inbreds than among outcrosses in radiata pine.

Key words: Radiata pine, age-age correlation, inbreeding, genetic variance, heritability, early selection.

Introduction

Long-generation turnover and severe depression from selfing in conifers have been obstacles to a breeding strategy involving the production of superior hybrids through crossing inbred lines (which we call the inbreeding/crossbreeding method). Long-generation turnover makes the generations of inbreeding required to produce inbred lines time-consuming and expensive. Severe depression among selfed progeny in seed production, seedling survival and growth and adult fecundity in conifers has so far prevented the use of selfing as a practical tool in the production of useful inbred lines. Sib mating has been recommended in the early generations of an inbreeding program to reduce inbreeding depression by purging deleterious alleles from small breeding populations or elite lines more slowly, so that favourable alleles are not also lost in the process (WILLIAMS and SAVOLAINEN, 1996).

We have previously reported on a trial involving five levels of inbreeding in which inbreeding reduced survival and growth while at the same time as increasing variance in radiata pine (*Pinus radiata*). We observed that inbreeding depression for vigour and survival in this species was among the least in conifers so far reported (WU *et al.*, 1998a). In addition, seed viability and growth did not decline significantly from the first-generation of selfs (S_1) to the second-generation of selfs (S_2) (GRIFFIN and LINDGREN, 1985; WU *et al.*, 1998a). Further, the greatest DBH trees were observed to be among S_2 progeny (WU *et al.*, 1998b). In addition, selfing has been observed to have little impact on adult fecundity in radiata pine (PAWSEY, 1964). These findings suggest that selfing might be effective in purging deleterious alleles from populations of radiata pine and could be used to produce superior inbred lines relatively quickly. If inbreeding depression and segregation among individuals can be identified at a relatively early age, then early selection would also be effective. We have observed that inbreeding depression was highest in the initial stage of growth, declined at the onset of competition, increasing again later (WU *et al.*, 1998b). If there is substantial juvenile-mature correlation for growth in sib-mated or selfed progenies, early selection could be used to select superior lines carrying fewer deleterious alleles. In this way, selfing combined with early selection could be used as a rapid means to purge deleterious alleles and to create superior inbred lines.

Age-age correlations and the effectiveness of early selection have been extensively reported among different species for non-inbred populations. Several authors have addressed juvenile-mature correlation studies in conifers (NANSON, 1968; WAXLER and VAN BULJTENEN, 1981; LAMBETH, 1983; JIANG, 1985; GILL, 1987), the results of which vary widely. The results are often controversial due primarily to differences between species, sample size, the differences in age comparisons, test environments, design, and silvicultural treatments (WU, 1993). Two contrasting theories concerning age-age correlation and

early selection have been proposed. FRANKLIN (1979) proposed a hypothetical growth model to explain long-term trends in genetic variance and heritability based on data from four conifers (*Pinus elliottii*, *P. taeda*, *P. ponderosa*, *Pseudotsuga menziesii*). In his model, stand development was divided into juvenile-genotype, mature-genotype and codominant-suppression phases. The model suggests that heritability reaches a high level early in stand development followed by a marked decrease to its lowest point at about the time of stand closure. Additive genetic variance and heritability increase again after reaching a maximum about the middle of the second phase, after which it declines. FRANKLIN's model also suggests a trend of strongly positive age-age correlations within phases and generally weak or negative correlations between phases. This means that little or no genetic gain would result from very early selection in these populations, and FRANKLIN recommends that, under typical stand conditions, selection should be deferred until about half rotation age. However, not all patterns of stand development follow FRANKLIN's model (FOSTER, 1986; KING and BURDON, 1991; MATHESON *et al.*, 1994) and it seems possible that correlations between early and late stages may be more predictable than FRANKLIN's model would suggest. Age-age correlations are often positive and increase as the age of the early stage approaches the mature age. LAMBETH (1980) found that age-age correlations (r) for height in several species (*Pinus elliottii*, *P. taeda*, *P. ponderosa*, *P. monticola*, *P. resinosa*, *P. palustris*, *P. echinata*, *Pseudotsuga menziesii*) could be estimated with reasonable accuracy by the following regression:

$$r = a + b \cdot \log_e (t_j/t_m)$$

where a and b are estimated intercept and regression coefficient respectively and t_j , t_m are ages of early (juvenile) and later (mature) measurements. This relationship applied except when the juvenile ages were between one to three years. In applying his model to loblolly pine, LAMBETH concluded that selection at ages five and six years was optimal for a rotation age of 20 years and selection at ages seven and eight was optimal for a rotation age of 50 years.

In *Pinus radiata*, COTTERILL and DEAN (1988) estimated additive genetic correlations for height growth and basal area between ages 2.5, 6.5, 10.5 and 16 years and observed that correlations with age 16 data were low to negative for age 2.5 but were over 0.7 by age 6.5 years for both traits. KING and BURDON (1991) observed highly positive genetic correlations among ages 5, 10 and 17 for diameter in a large population (410 families), and that it was as effective to select at age 10 as to wait until age 17. MATHESON *et al.* (1994) studied age-age correlations based on annual cross-sectional area of breast-height disks and observed that age-age correlations were close to zero between ages less than 4 with age 14, but that after age 4, correlations with age 14 improved and were higher for all age-age correlations the closer the two ages involved were. However, these correlations were not linearly related to the logarithm of the age ratio as suggested by LAMBETH (1980).

Within an inbred population, age-age correlations might be larger and early selection might be more effective since there is more differentiation between inbred individuals in radiata pine and other conifers (WU *et al.*, 1998a). In the absence of non-additive effects and assuming very large numbers of loci, each with small effect, inbreeding should increase genetic variance linearly so that $V_g = V_0(1+F)$, where V_g is the genetic variance for inbreeding level F (coefficient of inbreeding) and V_0 is the genetic variance in the base population ($F = 0$). If inbreeding results in a subdivision of the population, this genetic variance would be distributed both between lines ($2FV_0$) and within lines ($(1-F)V_0$). The greater differentiation (due to both additive

and non-additive genetic variance) observed in inbred populations may also be enhanced through stand development, thus increasing age-age correlations and hence leading to more efficient early selection in the inbred population.

In this paper, we report on age-age correlations of cross-sectional area at breast height up to age 13 in radiata pine at five inbreeding levels (inbreeding coefficient $F = 0, 0.125, 0.25, 0.5$ and 0.75 , respectively) and correlations between early height measurements and later cross-sectional areas. In particular, we investigated the following:

- (1) age trends of additive and non-additive genetic variance, and heritability for the outcrossed population ($F = 0$);
- (2) age trends of age-age correlations for additive and non-additive genetic variation in the outcrossed population ($F = 0$);
- (3) the effects of inbreeding levels on age-age correlation;
- (4) the effects of inbreeding levels on early selection efficiency.

Material and Methods

1. The experiment

The radiata pine inbreeding experiment reported here was set up in the 1970s at CSIRO's Gippsland Research Station, Victoria, Australia as a comprehensive study of inbreeding in radiata pine. The mating design and field experiment were described by WU *et al.* (1998a). In summary, five populations with different inbreeding levels were created from eight founder clones; crosses were carried out among founder clones (a Design II mating) to create a non-inbred population ($F = 0$), half-sib matings among the progeny of eight founder clones created an $F = 0.125$ population, full-sib mating among the progeny of founder clones created an $F = 0.25$ population, selfing of founder clones created a one-generation selfed population ($F = 0.5$, also called S_1) and selfing of progeny from first-generation selfing created a two-generation selfed population ($F = 0.75$, also called S_2). Both outcrossed and inbred progenies were produced by controlled pollination in several years. The five populations were planted at Symonds near Mount Gambier, South Australia in 1981 with four replicates. Two populations ($F = 0$ and $F = 0.50$) were replanted at nearby site called Kilsbys in 1982 with six replicates. Both were split plot designs with populations (inbreeding levels) as main plots and families within populations as sub-plots. Six trees were planted in a single row plot for each family at each replicate. Spacing at both sites was 2 m x 3 m.

In 1993, the second and third trees were felled in each plot and discs at breast height (1.3 m) were cut from these felled trees. If the second or third tree in the plot was not available (dead or a replacement tree), then the next available tree was selected. Cross-sectional areas for each age were measured in the discs by measuring annual ring widths in two directions (WU *et al.*, 1998b) and were used to study age-age correlations.

Two families in population 1 (outcrosses) and four families in population 4 (half of population 4, $F = 0.5$) were planted only at the Kilsbys site. It was desirable to incorporate these families into the analysis of main Symonds trial. Six families in population 1 and four families in population 4 were planted at both sites. For these common families, a linear model was fitted to investigate family by site and family by replicate interactions in the two populations separately. It was found that the interaction between families and sites was not significant for either population at any age and thus data across sites could be validly combined. Data from Kilsbys were adjusted and combined with data from Symonds for analysis of sectional area using the method described in WU *et al.* (1998a).

Tree height was measured 3 months, one year, and three years from planting at the Symonds site (15 months, two years, and four years from sowing at the nursery, respectively). At Kilsbys, tree height was also measured at 3 months, two years from planting (15 months, and three years from sowing at nursery). The three-year data at Kilsbys were adjusted to be commensurate with two and four-year data from Symonds for analysis. The all ages referred in this report are time from the date of sowing seeds.

2. Statistical analysis

For the outcrossed population ($F = 0$), additive, non-additive and environmental variance, heritability and additive genetic correlations were estimated. Preliminary analysis showed interaction between replication and male and between replication and female were not significant (i.e. male parent and female parent performance was consistent across replicates) and so analyses of variance and estimates of variance and covariance were conducted based on an individual tree model as follows:

$$Y_{ijkl} = \mu + R_i + M_j + F_k + MF_{jk} + E_{ijkl} \quad (1)$$

where μ is grand mean, R_i is the replicate effect, M_j is the male parent effect, F_k is the female parent effect, MF_{jk} is the interaction between male and female, and E_{ijkl} is the residual. All effects were assumed random except for grand mean. Due to unequal numbers of trees among plots, SAS type III estimable functions (SAS Institute Inc. 1989) were used to estimate mean squares, mean products and expected mean squares for different ages and between ages. The expected mean squares and mean products are listed in Table 1.

Table 1. – Expectations of mean squares and products for analyses of variance and covariance for Design II mating experiment ^a.

Sources of variation	EMS or EMCP
Replication	$\sigma_e^2 + k_1 \sigma_r^2$
Male	$\sigma_e^2 + k_2 \sigma_{mf}^2 + k_3 \sigma_m^2$
Female	$\sigma_e^2 + k_4 \sigma_{mf}^2 + k_5 \sigma_f^2$
Male*female	$\sigma_e^2 + k_6 \sigma_{mf}^2$
Residual	σ_e^2

^a For cross-sectional area, $k_1 = 31.741$, $k_2 = 10.722$, $k_3 = 42.888$, $k_4 = 11.348$, $k_5 = 45.39$, $k_6 = 11.784$.

For height, $k_1 = 83.579$, $k_2 = 27.811$, $k_3 = 111.25$, $k_4 = 29.799$, $k_5 = 1119.2$, $k_6 = 30.943$.

Assuming no epistatic or maternal effects, the variance due to male (σ_m^2) or female (σ_f^2) parents each represents one quarter of the additive genetic variance, and variance due to interaction between male and female (σ_{mf}^2) represents a quarter of non-additive variance (COMSTOCK and ROBINSON, 1952). Thus, total additive genetic variance was estimated by $\sigma_{additive}^2 = 2(\sigma_f^2 + \sigma_m^2)$ and individual-tree heritability was estimated by

$$h_i^2 = \frac{\sigma_{additive}^2}{\sigma_f^2 + \sigma_m^2 + \sigma_{mf}^2 + \sigma_e^2}$$

where σ_e^2 is the residual variance. Additive genetic correlations between ages were estimated by

$$r = \frac{\text{cov}(f_x, f_y)}{\sqrt{\sigma_{fx}^2 \sigma_{fy}^2}}$$

where $cov(f_x, f_y)$ is the family covariance between two ages X and Y, estimated from linear model (1) and $\sigma_{f_x}^2$ and $\sigma_{f_y}^2$ are their corresponding family variances. Standard errors of both heritability and genetic correlation were estimated by Taylor expansion (NAMKOONG, 1979; KENDALL *et al.*, 1987).

Product-moment phenotypic correlations for individual trees and family means were also computed for each of the five inbred populations. The relationship between age-age correlations and logarithm of the age ratio was also calculated according to the method of LAMBETH (1980) and genetic gain in sectional area at age 13 from early indirect selection was computed according to FALCONER and MACKAY (1996, p. 317).

Results

1. Analysis of variance for outcrosses ($F = 0$)

For the three early height measurements (15 months, 2 and 4 years from sowing), female parents were observed to have a significant effect only at age 4 and male parents were not significant at any of the three ages (Table 2). In contrast, male by female interaction was significant at both age 15 months and 4 years for height. For cross-sectional area, male parents were observed having a significant effect from age 4 to age 13, although female parents were significant from age 4 only to age 10. The interactions between male and female parents were never significant for cross-sectional area at any age (Table 2).

2. Age trends for additive, non-additive, and environmental variance, heritability and age-age additive genetic correlation among outcrosses ($F = 0$)

Trends for environmental, additive and non-additive variance are shown in Figure 1. For early height measurements, environmental, additive and non-additive variances fluctuated greatly. At age 15 months, additive genetic variance was nearly zero and non-additive variance was larger (78%) than the environmental variance (22%). Additive variance became significant at age 4 (9.9%) while non-additive variance decreased to 24% at age 4. Since estimates of non-additive variance for cross-sectional area were estimated to be zero for all ages, only environmental and additive genetic variances are shown in Figure 1. For cross-sectional area, additive genetic variance increased from 3.7% at age 3 to 29.4% at age 5 and remained

at about 30% up to age 10 after which it declined to 15.6% by age 13.

Figure 2 shows the trends of heritability at different ages and additive genetic correlations between younger ages and age 13. For early height measurements, heritability increased from zero at 15 months to 0.10 ± 0.12 at age 4. For cross-sectional area, the trend of heritability was similar to the trend of additive genetic variance: i.e. heritability increased from 0.04 ± 0.05 at age 3 to 0.29 ± 0.19 at age 5 and then remained at about 0.3 to age 9, then declined from 0.22 ± 0.16 at age 10 to 0.14 ± 0.13 at age 13. Additive genetic correlations among early height measurements and for cross-sectional area between early data and data at age 13 were much higher except for very early ages (for height at 15 months and at two years, the correlations with cross-sectional area at age 13 were 0 and 0.43 ± 1.24 , respectively). However, additive genetic correlation between height at age 4 and sectional area at age 13 was high (0.81 ± 0.32). Additive genetic correlation between age 3 and age 13 for cross-sectional area was also high (0.76 ± 0.83) and increased from age 4 (0.88 ± 0.26) to age 6 (0.93 ± 0.11). There was a small reduction in additive genetic correlation with age 13 for ages 7 and 8 (0.89) and then there was a steady increase from age 9 to 13.

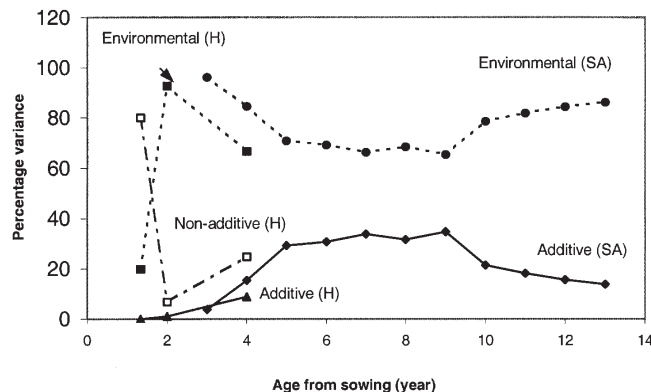


Fig. 1. – Additive, non-additive and environmental variances at different ages for height (H) and sectional area (SA).

Table 2. – Male, female, male*female interaction and residual mean squares for analyses of variance of height and cross-sectional area in radiata pine.

Sources of variation	D.F	Height at age		
		15m ^a	2	4
Replication	5	254**	1598**	14320**
Male	3	6.8	72.5	7371
Female	3	217	338	12229*
Male*female	9	300**	252	4918**
Residual	507	34.7	166	1576

Sources of variation	D.F	Cross-sectional area for years										
		3	4	5	6	7	8	9	10	11	12	13
Replication	5	37.6	258	373	757	963	986	1244	1990	3069	4259	5795
Male	3	24.4	479**	2193**	3434**	3699*	4396*	6282*	8752*	12508*	18148*	23515*
Female	3	10.5	406*	2454**	4484**	7657**	9136**	9949**	9927*	11143	11166	11122
Male*female	9	9.2	72	296	616	886	1267	1572	2298	3472	4796	6266
Residual	179	19.0	196	529	815	1039	1310	1743	2630	3826	5322	6905

^a m=month

*P<0.05, ** P<0.01

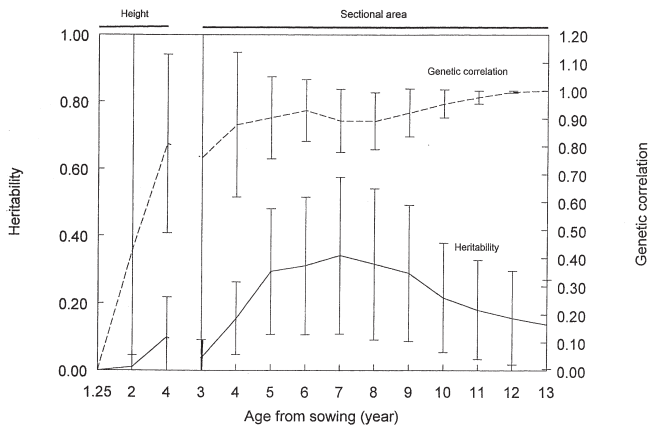


Fig. 2. – Heritabilities (\pm se) at different ages and genetic correlations (\pm se) between age 13 years of cross-sectional area and younger ages of height and cross-sectional area of breast height in radiata pine.

3. Individual and family-mean age-age correlation for five inbreeding levels

a. Height.

The individual phenotypic correlations between early height growth and cross-sectional area at age 13 are presented in *Figure 3*. Correlations were low for age 15 months and rose rapidly with age for all populations, particularly for the outcrosses and S_1 populations. The correlations for outcrosses began low ($r = 0.01$ at age 15 months) but reached 0.49 by age 4 compared with 0.58 for the full-sib mated population and 0.56 for the selfed population. After age 2, correlations for the S_2 population ($F = 0.75$) and half-sib mated ($F = 0.125$) populations increased less rapidly than the others.

Family mean correlations are presented in *Figure 4* in which the results are less clear. Correlations for outcrosses increased rapidly from 0 at age 15 months to 0.88 at age 4. That for selfs ($F = 0.5$) also increased rapidly at first from 0 at age 15 months but reached only 0.5 by age 4. Correlations for S_2 s ($F = 0.75$) increased much less rapidly with age increasing, from 0.42 at 15 months to 0.69 by age 4. Those for full- ($F = 0.25$) and half-

sib ($F = 0.125$) mated populations fell initially after age 15 months before increasing again.

Thus, age-age correlations between heights and age 13 cross-sectional area varied with age. In particular, for outcrosses ($F = 0$), the correlation between height and cross-sectional area at age 13 was zero and increased rapidly whether based on individuals or family means so that by age 4, both individual and family-mean correlations with sectional area at age 13 were higher than those for sectional area at a similar early age.

b. Cross-sectional area

Age-age correlations between cross-sectional area at young ages and age 13 shows a similar trend for all five populations whether based on individual measurements or on family means (*Figs. 3 and 4*). Individual correlations between ages 3 and 13 were generally low (from 0.09 for outcrosses to 0.31 for the S_2), but increased rapidly between ages 3 and 6 (*Fig. 3*). At age 6, individual correlations with age 13 ranged from 0.76 for outcrosses to 0.88 for the S_2 . Family-mean correlations between ages 3 and 13 were higher than individual correlations (from 0.26 for outcrosses to 0.56 for the S_2). Family-mean correlations also rapidly increased between ages 3 and 5. By age 5, the family mean correlation with age 13 varied from 0.72 for the full-sib mated population ($F = 0.25$) to 0.88 for the S_2 population ($F = 0.75$).

An interesting observation is that age-age correlation for cross-sectional area in the S_2 population (highest inbreeding level) was the highest among all five populations for both individual and family-mean correlations. In addition the correlation for the S_1 population based on family means was the second highest. The effect of inbreeding level on age-age correlation in cross-sectional area is more discernable after age 6. There is a trend towards higher age-age correlations (*Figs. 3 and 4*) at higher inbreeding levels. For example, at age 6, individual correlations were between 0.75 and 0.88, by age 7 were between 0.83 and 0.92, and by age 10 were between 0.96 and 0.99 (*Fig. 3*). A similar pattern exists for the family mean correlations which rose from between 0.84 and 0.91 at age 6, and by age 10, they had reached to between 0.94 and 1.00 (*Fig. 4*).

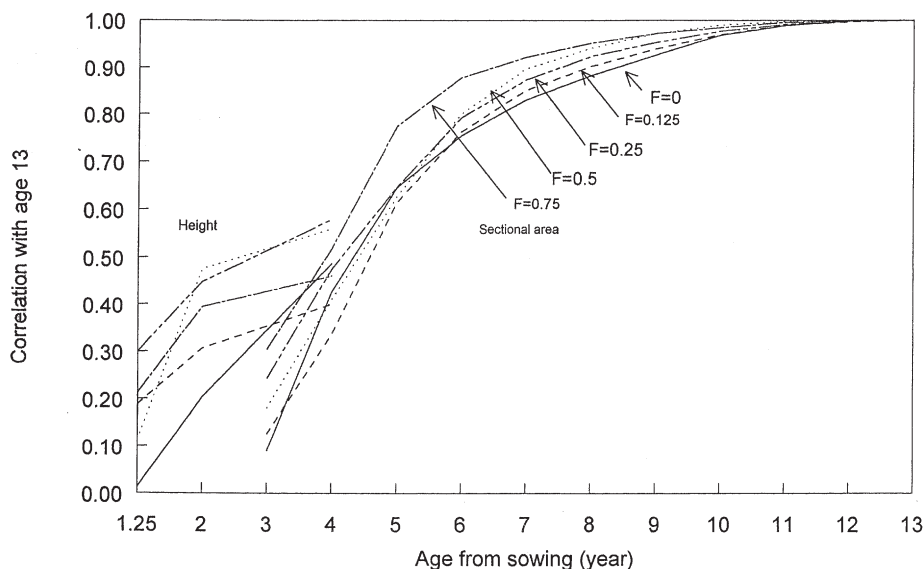


Fig. 3. – Correlation between sectional area of breast height at age 13 years and sectional area and height at younger ages for five inbreeding levels in radiata pine based on individual tree.

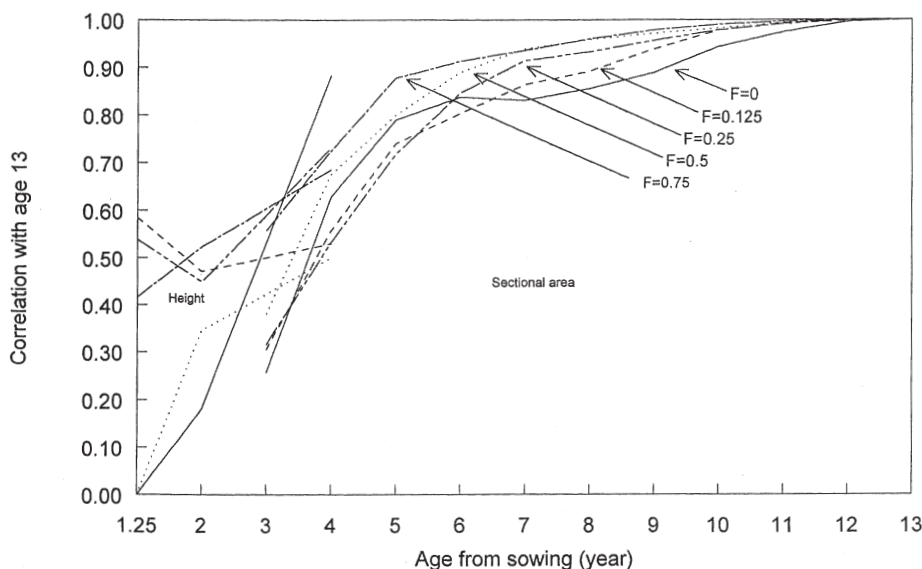


Fig. 4. – Family mean correlation between sectional area of breast height at age 13 years and sectional area and height at younger ages for five inbreeding levels in radiata pine.

4. The relationships between logarithm ratio of ages ($LAR = \log_e(t_j/t_m)$) and age-age correlations, and efficiency of early selection.

The relationship between LAR and age-age correlation was not linear for outcrosses whether they were additive genetic correlations or whether they were based on family means or individuals (Fig. 5). In general, age-age correlations were highest for additive genetic correlations, family correlations were in the middle and individual correlations were the lowest.

Genetic gain from selection at different ages can be compared for outcrosses since additive genetic variances are known. When genetic gain achievable from direct selection at age 13 was set as a benchmark, indirect selection at very early ages (age 3 and 4) for outcrosses was less effective than direct selection at age 13 (Fig. 6). However, selection efficiency increased greatly between ages 3 and 5. By age 5, early selection was more efficient than direct selection at age 13. Selection carried out between ages 5 to 9 was the most efficient in this sample (Fig. 6) and less efficient after age 9.

The efficiency of early selection using inbred populations compared with outcrossed populations is demonstrated from the percentage of correct selections made at an early age. For example, if the largest ten trees at age 6 in the outcrossed population were selected, only three trees (30%) selected at age 6 were still among the ten largest trees at age 13 (Fig. 7). However, eight such selections (80%) in the S_2 s were still among the ten largest trees at age 13 (Fig. 8). It is clear from Figures 7 and 8 that the outcrosses are much more loosely scattered than the S_2 s.

Discussion

For tree breeders to adopt the inbreeding/crossbreeding approach as an appropriate breeding strategy for conifers, four potential questions must be satisfied. First, it must be feasible to produce superior inbred lines (trees) from selfing; second, heterosis must exist in crosses between these inbred lines; third, inbreeding should not substantially delay reproductive age, and finally, early selection among inbreds must be effective in order to select superior inbred lines as quickly as possible.

We have demonstrated that inbreeding depression is relatively low in radiata pine and that it is possible to obtain superior inbred lines from selfing. WU *et al.* (1998a) showed that there is more segregation in the S_1 and S_2 than in less inbred populations and outcrosses, and that the largest trees in the trial

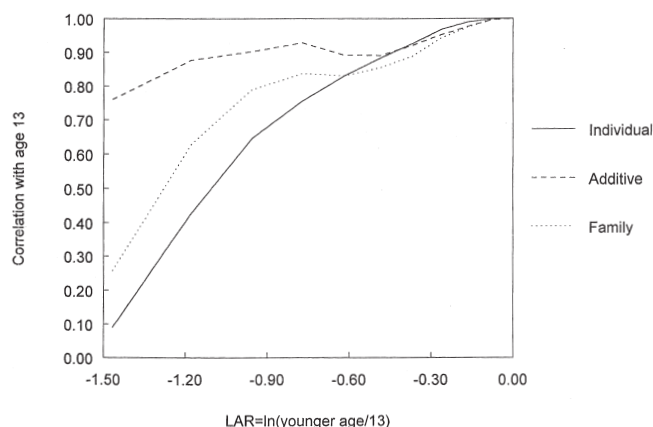


Fig. 5. – Relationship between Logarithm of age ratio (LAR) and age-age correlation of additive, individual and family mean of sectional area in the outcrossed population.

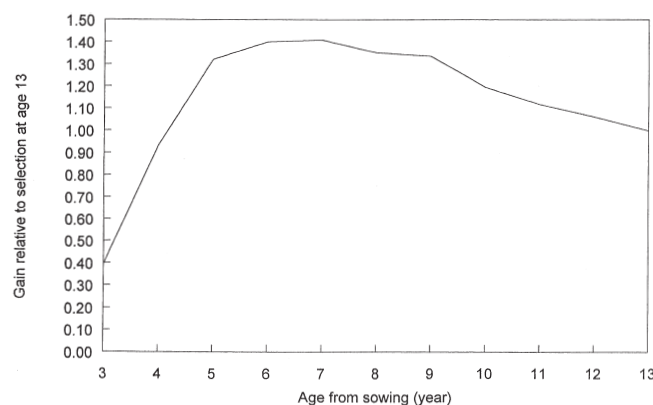


Fig. 6. – Genetic gain from early selection in the outcrossed population relative to selection at age 13 years.

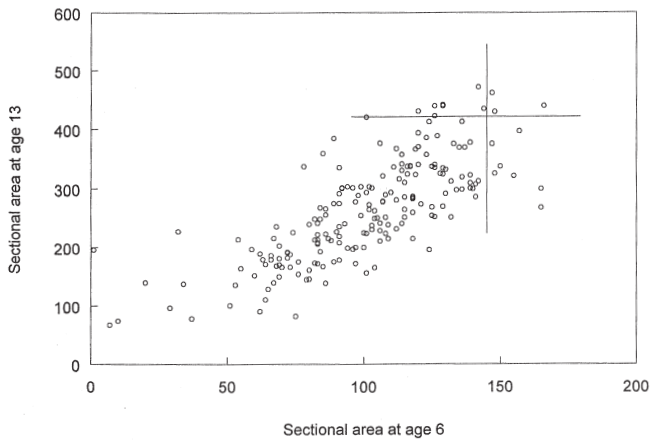


Fig. 7. – Relationship for sectional area of breast height between ages 6 and 13 years in the outcrossed population ($F = 0$).

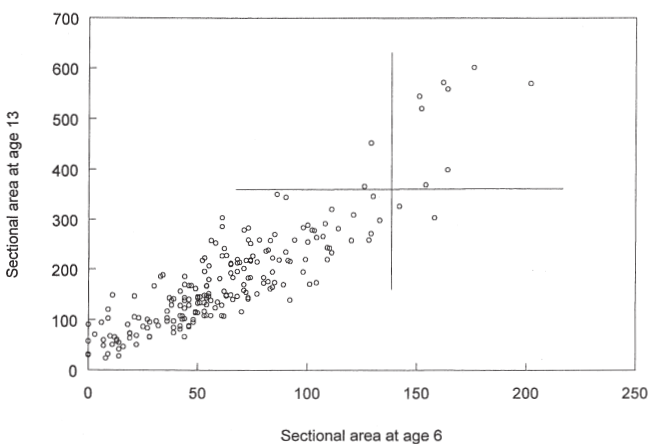


Fig. 8. – Relationship for sectional area of S2 population (second-generation of selfing, $F = 0.75$) between ages 6 and 13 years.

(including the outcrosses) were observed among the S_2 . Thus, if early selection among inbred lines is effective and there is potential heterosis, the inbreeding/crossbreeding approach would be an attractive alternative breeding strategy compared with current radiata pine breeding strategies (eg sublines and/or nucleus breeding).

In this study, we have observed that both genetic and phenotypic age-age correlations were very high among all five populations with different inbred levels, but highest among inbred populations. This indicates that although selection would be effective as early as 5 or 6 years in non-inbred radiata pine, it would be more effective in more highly inbred populations. This is because age-age correlations were the highest for the most inbred population (S_2) based on both individuals and family-means, and correlations for the S_1 (the second highest inbred level) were the second highest based on family means. Also, after age 6, age-age correlations increased with level of inbreeding.

Selection was found to be more effective at age 5 and later for outcrosses than direct selection at age 13 for cross-sectional area in this experiment. In particular, the most effective years for selection for age 13 cross-sectional area were ages 6 and 7. This is mainly due to the higher heritability at these ages (6, 7

and very high genetic correlation with age 13. The observation that differentiation among individuals (i.e., variance) (WU *et al.*, 1998a) and age-age phenotypic correlations (individual and family mean) are higher in more inbred populations suggests that selection among inbred lines would be more efficient than conventional early selection in outcrosses.

While the main objective of the current investigation was to compare age-age correlations among populations with five different inbreeding levels, the Design II cross structure among outcrosses provided an opportunity to investigate age trends in additive and non-additive genetic variances, heritabilities and genetic correlations even though the sample is far too small to be definitive. The small size of the outcrossed population may be the reason that the male by female interaction (i.e., non-additive variance) was not significant. A much larger sample of parents is required for more reliable estimates of additive and non-additive genetic variance. Nevertheless, in spite of the small sample size, estimated genetic correlations and heritabilities were usually larger than their corresponding standard errors. Non-additive genetic variance has been reported in other studies of the quantitative genetics of radiata pine. MATHESON *et al.* (1994) observed that non-additive variance started at a low level, increased to a maximum of more than twice the additive variance at age 4 then declined to negligible levels by age 9. However, in a Design II experiment with similar structure to that of the outcrosses presented here, COTTERILL *et al.* (1990) estimated that dominance variance for diameter at age 8 was marginally less than the estimate of maternal additive variance and much less than the paternal estimates, but the interaction and female effect in their ANOVA table were not statistically significant. MATHESON *et al.* (1994) observed that environmental variance for cross-sectional area decreased in the first few years (2 to 4 year) and then increased (4-9 year) before it stabilised, while additive variance began at a low level but increased until about age 6 and then declined slightly before increasing again. We observed a different trend for both environmental and additive variance in this experiment: i.e. additive genetic variance increased from age 3 to 9 and then declined from age 9 to 13. The trend for heritability is similar to the additive genetic variance: i.e. increased from age 3 to 7 then declined from age 7 to 13, but it is unlikely that there were significant differences among additive variances for ages 5 to 9. The decline of individual heritability from age 7 to 13 is similar to the observation from age 5 to 17 in KING and BURDON's study (1991) of a much larger radiata pine sample. The estimate of individual-tree heritability (around 0.3) estimated in this study was larger than estimates from MATHESON *et al.* (1994) (around 0.15), but similar to estimates by COTTERILL and DEAN (1988) and KING and BURDON (1991) at similar ages.

Age-age genetic correlations in this study were higher than in other radiata pine studies reported. MATHESON *et al.* (1994) found that genetic correlation of cross-sectional area was low at early ages (<0.5 before age 5) for age 14. COTTERILL and DEAN (1988) report that for basal area age 2.5 had a negative correlation with age 16, but correlations at age 6.5 were very high (0.79). Early severe weed competition was suggested to cause low correlation between age 2.5 and 16. Genetic correlations were estimated to be high at all ages (>0.6) in the present study, although the standard error for age 3 was higher than the genetic correlation at that age. Early weed control by herbicide in this trial may have contributed partly to this high young-old genetic correlation. Thinning has also been suggested to have effect on both heritability and genetic correlation (MATHESON and RAYMOND, 1984; KING and BURDON, 1991). Differences between dominant and suppressed trees

which became established early would have been enhanced under strong competition without thinning, leading to higher age-age correlations, particularly at the individual-tree level.

The low age-age correlation between very early ages (soon after planting) and age 13 could be due to a number of factors including seed weight (maternal effects), nursery effects or out-planting shock. Thus, although very early selection within the first three years might be unreliable for radiata pine, the results suggest that selection after 5 or 6 years should be very reliable. However, comparisons of genetic parameters among various studies indicate that genetic parameters apply to the specific population and test environments in which they were estimated (e.g. different thinning regimes or the effects of *Cyclaneusma* infection in KING and BURDON's study (1991) may have affected age-age correlation).

Trends in additive genetic variance, heritability and age-age correlation in our experiment do not fit FRANKLIN's model (1979) that additive variance and heritability increase to a high level during early stand development, and then decrease to their lowest point at the time of stand closure. Competition seems to have a significant impact on both genetic variance and heritability. The current test sites were located in a highly fertile site for radiata pine in the region (ex-pasture land with podsolised sandy soil). On such a high quality site, with the planting space of 2 m x 3 m, competition among trees typically starts about 4 or 5 years after planting, and crowns are usually completely closed after 8 or 9 years. Trends in additive variance and heritability observed in the study seem to be closely related to this stand development: i.e. additive genetic variance increased before crowns closed completely at about age 9, after which it declined. We observed that genetic correlation was still high between the ages spanning crown closure, but we also noticed that correlations at ages 7 and 8 with later age were lower. The age-age correlations observed here did not conform to LAMBETH's linear model either. All three relationships show a curvilinear pattern and in the case of family and additive genetic correlation, the ratio was lower for ages 7 and 8, probably due to competition effects. The non-linear relationship is similar to that observed in radiata pine by MATHESON *et al.* (1994). Although KING and BURDON (1989) observed a close similarity to the LAMBETH model there were only three age points used to fit the model. Thus, we suspect that due to other complicating factors such as competition and disease, the true time trends probably will not conform exactly to either of these two models (FRANKLIN and LAMBETH) as suggested by KING and BURDON (1991).

Conclusion

High additive genetic correlations between early sectional areas (age 5 and 6) and age 13 suggest that early selection for growth between and within inbred families would be more effective in inbred families than in outcrossed families. The higher is the inbreeding level, the higher is the age-age correlations. It would appear that generations of inbred lines can be turned over as soon as selections flower (at age 6 to 7), making rapid progress in purging deleterious alleles from the lines. It remains to be seen whether these results also apply to other traits such as wood properties.

Acknowledgements

Crosses for this inbreeding experiment were carried out by R. F. HAND. Field plantings were organised by K.W. JOHNSON. We are grateful to Green Triangle Forest Products Ltd for the use of the two sites (Symonds and Kilsbys) at Caroline Forest near Mt Gambier and for their help (with D. BELLINGHAM, CSIRO) during the harvesting operation. Disc digitisation was carried out by D. RADA and I. MCLEOD.

Literature

- COMSTOCK, R. E. and ROBINSON, H. F.: Estimation of average dominance of genes, in *Heterosis* (ed. J. W. GOWEN), Iowa State College Press, Ames, Iowa. Pp. 494–516, (1952). — COTTERILL, P. P. and DEAN, C. A.: Changes in the genetic control of growth of radiata pine to 16 years and efficiencies of early selection. *Silvae Genet.* **37**: 138–146, (1988). — COTTERILL, P. P., DEAN, C. A. and VAN WYK, G.: Additive and dominance genetic effects in *Pinus pinaster*, *P. radiata* and *P. elliottii* and some implications for breeding strategy. *Silvae Genet.* **36**: 221–232, (1987). — FALCONER, D. S. and MACKAY, T.: Introduction to quantitative genetics. Fourth edition, Longman, Harlow. 464 pp. (1996). — FOSTER, G. S.: Trends in genetic parameters with stand development and their influence on early selection for volume growth in loblolly pine. *For. Sci.* **32**: 944–959, (1986). — FRANKLIN, E. C.: Model relating levels of genetic variance to stand development of four north American conifers. *Silvae Genet.* **28**: 207–212, (1979). — GILL, J. G. S.: Juvenile-mature correlations and trends in genetic variances in Sitka spruce in Britain. *Silvae Genet.* **36**: 189–194, (1987). — GRIFFIN, A. R. and LINDGREN, D.: Effect of inbreeding on production of filled seed in *Pinus radiata* experimental results and a model of gene action. *Theor. Appl. Genet.* **71**: 334–343, (1985). — JIANG, I. B. J.: Early testing in forest tree breeding: a review. In *Forest tree improvement* No. 20, 1987, Proc. from a meeting on early testing, juvenile-mature correlations, and accelerated generation turnover. Horsholm, Denmark. Pp. 45–78, (1985). — KENDALL, S. M., STUART, A. and ORD, J. K.: KENDALL's advanced theory of statistics. 5th edition of Volume 1, Distribution theory. Charles GRIFFIN and Company, London. 604 pp. (1987). — KING, J. N. and BURDON, R. D.: Time trends in inheritance and projected efficiencies of early selection in a large 17-year-old progeny test of *Pinus radiata*. *Can. J. For. Res.* **21**: 1200–1207, (1991). — LAMBETH, C. C.: Juvenile-mature correlations in *Pinaceae* and implication for early selection. *For. Sci.* **26**: 571–580, (1980). — LAMBETH, C. C.: Early testing – overview with emphasis on loblolly pine. In *Proc. 17th South. For. Tree Improv. Conf.*, Athens. Pp. 297–311, (1983). — MATHESON, A. C. and RAYMOND, C. A.: Effects of thinning in progeny tests on estimates of genetic parameters in *Pinus radiata*. *Silvae Genet.* **33**: 125–128, (1984). — MATHESON, A. C., SPENCER, D. J. and MAGNUSSEN, D.: Optimum age for selection in *Pinus radiata* basal area under bark for age:age correlations. *Silvae Genet.* **43**: 352–357, (1994). — NAMKOONG, G.: Introduction to quantitative genetics in forestry. Technical bulletin no. 1588. Forest Service, USDA, (1979). — NANSON, A.: The value of early tests in forest tree selection especially for growth. (In French with English summary). *Dissert. Doc. Fac. Science Agro., Gembloux.* 242 pp. (1968). — PAWSEY, C. K.: Inbreeding radiata pine. *Dept Nat. Dev. For. and Timb. Bur. Leaflet No. 87*, 31 pp. (1964). — SAS Institute Inc.: SAS/STAT User's Guide, Version 6, 4th Edition, Volume 2, Cary, NC, 846 pp. (1989). — WAXLER, M. S. and VAN BUIJTENEN, J. P.: Early genetic evaluation of loblolly pine. *Can. J. For. Res.* **11**: 351–355, (1981). — WILCOX, M. D.: Inbreeding depression and genetic variances estimated from self- and cross pollinated families of *Pinus radiata*. *Silvae Genet.* **32**: 89–96, (1983). — WILLIAMS, C. G. and SALVOLAINEN, O.: Inbreeding depression in conifers: implications for breeding strategy. *For. Sci.* **42**: 102–117, (1996). — WU, H. X.: Theoretical and experimental evaluation of early selection in lodgepole pine. Ph. D. dissertation, University of Alberta, Edmonton, Canada. 264 pp. (1993). — WU, H. X., MATHESON, A. C. and SPENCER, D.: Inbreeding in radiata pine: I. The effect of inbreeding on growth, survival and variance. *Theor. Appl. Genet.* **97**: 1256–1268, (1998a). — WU, H. X., MATHESON, A. C. and SPENCER, D.: Inbreeding in radiata pine: II. Time course of inbreeding depression and effect on growth curve. *N. Z. J. For. Sci.* **28**: 123–139, (1998b).