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Original article

Inbreeding in *Pinus radiata*. IV: the effect of inbreeding on wood density

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Abstract – The effects of inbreeding on basic wood density in a 17-year-old radiata pine trial were studied using five populations, each inbred to one of five inbreeding levels: outcross (OC, $F = 0$), half-sib (HS, $F = 0.125$), full-sib (FS, $F = 0.25$), selfing (S_1, $F = 0.5$) and two-generations of selfing (S_2, $F = 0.75$). These five populations were derived from a founder population of eight clones. Although inbreeding resulted in slightly depressed wood density (inbreeding depression was 1.47%, 2.50%, 1.65%, 0.02%, respectively at $F = 0.125$, 0.25, 0.50 and 0.75), the effects were not significant. However, the variation of wood density among trees was increased by inbreeding, by 3.70%, 3.40%, 15.74%, and 29.01% respectively for populations at $F = 0.125$, 0.25, 0.5, and 0.75. In all five populations, the basic wood density increased linearly from 400 kg m^{-3} at age 4 (the earliest age for most samples) to about 525 kg m^{-3} at age 12 and stabilized with some fluctuation thereafter. There were significant differences among pedigrees in response to inbreeding for wood density. The pedigrees can be divided into three classes according to their response patterns to inbreeding: no decline of wood density under any inbreeding level; a linear decline from $F = 0$ to $F = 0.75$; and an initial decline at mild inbreeding levels contrasted with an increase in selfed generations. The lack of significant inbreeding depression of wood density at the population level combined with increased variation in wood density in the inbred populations suggests that it will be possible to quickly develop inbred lines with high wood density. The combination of low inbreeding depression for growth with a lack of inbreeding depression for wood density makes radiata pine a species ideally suited for the use of inbreeding as a breeding tool.

radiata pine / inbreeding depression / wood density / purging

Résumé – Consanguinité chez *Pinus radiata*. IV : l'effet de la consanguinité sur la densité du bois. Les effets de la consanguinité sur la densité basale du bois sont étudiés dans une expérience de pins radiata âgés de 17 ans. Cinq types de croisements (et donc niveaux de consanguinité) sont considérés : intercroisement (OC, $F = 0$), croisement demi-frère (HS, $F = 0{,}125$), plein frère (FS, $F = 0{,}25$), auto-fécondation (S1, $F = 0{,}5$) et deux générations d'auto-fécondation (S2, $F = 0{,}75$). Ces 5 populations sont dérivées d'une population fondatrice de 8 clones. Bien que la consanguinité produise une densité du bois légèrement plus basse (la dépression de consanguinité atteignant 1,47 %, 2,50 %, 1,65 % et 0,02 % respectivement avec un $F = 0{,}125$, 0,25, 0,50 et 0,75), les effets ne sont pas significatifs. Cependant, la variation de la densité du bois entre arbres augmente avec le niveau de consanguinité de 3,70 %, 3,40 %, 15,74 % et 29,01 % respectivement pour les populations avec un $F = 0{,}125$, 0,25, 0,50 et 0,75. Dans les 5 populations, la densité du bois augmente linéairement de 400 kg m^{-3} à l'âge de 4 ans (le plus jeune âge pour la plupart des échantillons) à environ 500 kg m^{-3} à l'âge de 12 ans ; puis elle se stabilise ensuite avec quelques fluctuations. Pour la densité du bois, des différences significatives entre pedigrees ont été mises en évidence en réponse à la consanguinité. Les pedigrees peuvent être répartis en 3 classes : pas de diminution de la densité du bois quelque soit le niveau de consanguinité, une diminution linéaire de $F = 0$ à $F = 0{,}75$ et une diminution initiale pour des faibles niveaux de consanguinité contrastant avec une augmentation dans les générations autofécondées. L'absence de dépression de consanguinité significative pour la densité du bois au niveau population combinée avec l'augmentation de la variabilité de la densité du bois dans les populations consanguines suggère qu'il est possible de développer rapidement des lignées consanguines avec du bois de haute densité. La combinaison d'une faible dépression de consanguinité pour la croissance associée à l'absence de dépression pour la densité du bois fait du pin radiata une espèce idéale pour l'usage de la consanguinité comme outil d'amélioration.

***Pinus radiata* / dépression de consanguinité / densité du bois / épuration**

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1. INTRODUCTION

Selfing and subsequent cross breeding is a principal breeding method for the improvement of many outcrossing agronomic species [14]. There are three major advantages of using a single-cross hybrid in crop breeding: (1) high yield; (2) uniformity and (3) stability. (1) Inbreeding and subsequent cross breeding with selected inbred lines has produced superior growth in maize [12]. (2) Cross of two essentially homozygous genotypes produces a uniform genotype, attractive for its uniform appearance, maturity and harvesting characteristics. (3) As the progenies produced from single crosses are heterozygous, the yields are more stable under variable environments.

Selfing as a breeding tool for forest trees was first advocated three decades ago, using the experience with maize as a justification [18]. Righter advocated the development of selfed lines in conifers to produce hybrid seed for plantation forestry. Wilcox [25] suggested selfing and pair-wise crosses among the best S1 as a possible breeding strategy in the loblolly pine (*Pinus taeda*) program at N.C. State University. Lindgren [11] recommended the inclusion of S1 selection in the outcrossing program to enhance genetic gain. However, inbreeding followed by cross breeding still has not yet been used as a practical breeding tool in tree improvement. There have been three major obstacles: (1) most conifer breeding programs in the last three decades were in their infancy and most of their resources were devoted to assemble and evaluate plus trees in the wild; (2) the long generation turnover makes the production of inbred lines time-consuming and expensive [9, 22, 23]; (3) early experiments revealed severe inbreeding depression in conifers, affecting seed production, growth and adult fecundity (see Williams and Savolainen [27] for a review). Prior to our work with radiata pine [13, 28, 29], there was no documented evidence that high quality inbred lines in tree could be obtained from selfing. In particular, there were no long-term inbreeding experiments to provide evidence of useful heterosis in tree growth [6, 7].

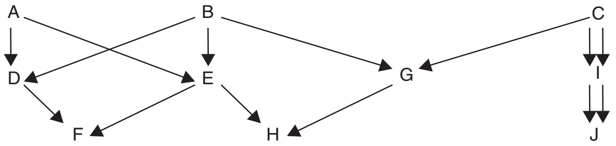
Thus, early conifer breeding programs worldwide were managed for inbreeding avoidance and relied upon open-pollinated production seed orchards [27]. Sib- or random-mating was recommended in early generations of conifer domestication to reduce inbreeding depression in the breeding population. Simple recurrent selection for a single, large breeding population was preferred at that time, today population subdivision strategies are more commonly used [3, 15, 24]. Recently, selfing as a breeding tool has been revived because of the growing interest in small elite breeding populations [27] and the possibility of purging deleterious alleles [10, 16]. Successful use of the inbreeding and cross breeding method in trees will depend on its effectiveness in purging deleterious alleles and in producing heterosis. Recently we observed that it is possible to derive highly productive inbred lines in radiata pine [28]. Data from radiata pine inbreeding trials involving five inbreeding levels revealed: (1) inbreeding depressed mean diameter growth and survival but increased the variance (segregation). However, continued selfing to a second generation (S2) did not further reduce growth [28]; (2) the best trees in the trial were from two-generations of selfing; (3) higher level of inbreeding had more segregation for tree growth; (4) the effect of inbreeding is pedigree dependent (some pedigrees have no inbreeding depression); (5) inbreeding affected the growth curve, and the age-trend of inbreeding depression was affected by competition [29]; (6) age-age correlation increased with inbreeding level, allowing effective early selection of selfed lines at age as young as five and six [13].

These findings demonstrated the great potential to develop high-quality inbred lines and produce highly productive hybrids in radiata pine. In accordance with these observations, we have established an experimental inbred population in radiata pine to further explore the inbreeding and cross breeding method and to develop superior inbred and hybrid lines for radiata pine. Tree improvement of radiata pine was mainly focused on growth and form in the past. Currently, wood quality improvement is a major focus because of the observed decline in wood density in some elite breeding material. Thus, characterizing the effect of inbreeding on wood quality is timely, relevant and important for further inbreeding and cross breeding work. In this paper, we report results from an investigation of the effect of inbreeding on wood density in a mature inbreeding trial (17 years old) and discuss the potential effectiveness of the inbreeding and cross breeding strategy for improvement of both wood quantity and quality in radiata pine.

2. MATERIALS AND METHODS

2.1. Mating design and field trial

Five populations with different inbreeding levels were created in 1970 from eight founder clones (pedigrees, *figure 1*). They included



Inbreeding level (F)	Population constitution	Abbreviation
0.0	Full-sib families of unrelated parents (eg D)	OC
0.125	Families from crosses of half sibs (eg H)	HS
0.25	Families from crosses of full-sibs from unrelated parents (eg F)	FS
0.5	Families from selfing non-inbred individuals (eg I)	S1
0.75	Families from selfing S_1 individuals (eg J)	S2

Figure 1. Generalised diagram of crossing structure to obtain different inbreeding levels of five populations (not all pedigrees are shown).

outcrossed progenies (OC, F = 0, population 1) of eight unrelated grandparents, progenies from mating of half-sib relatives (HS, F = 0.125, population 2), progenies from mating of full-sib relatives (FS, F = 0.25, population 3), selfed progenies from grandparents (e.g. first-generation selfs S1, F = 0.5, population 4) and second-generation selfs (S2, F = 0.75, population 5). The pedigree 1 was only inbred to S1. The detailed mating design for each population was described before [28, 29].

A split-plot field design was used in the field trials, with inbreeding level as the main plot and families within each of five inbreeding levels as sub-plot. A single row of six-tree sub-plot for each family was randomized within the main plot. The trial has two sites, the main site is in Symonds, South Australia with all five populations planted in four replications in 1981 and the supplement site is in nearby Kilsby (two kilometers from Symonds), with two populations in six replications planted in 1982. In 1993, two trees were thinned in each plot. The thinning was systematic: the second and third trees were taken out from each six-tree row plot. After thinning, most plots still had four trees left. However, some plots had less than four trees and a few plots had no remaining trees, particularly for the selfed populations. The trial had a total of 1912 surviving trees in the five populations after thinning.

2.2. Sampling of increment wood cores and assessment of wood density

The first two remaining trees in each plot were sampled in 1997. Since the second and third trees were felled before, this meant the first and fourth trees were sampled where possible. If the first or forth trees were not available (dead or replaced by a fill tree), the next tree was sampled within each plot. Increment core samples were collected using a 12-mm diameter tree corer at 1.30 m from the ground. The cores were then soaked in three fresh batches of 100% ethanol, each batch lasting at least 3 days. This process prevented blue stain and removed surface resins from the samples. The samples were then air-dried.

A twin-bladed saw was used to cut 2-mm thick representations of each core, one to show the cross section view and the other to show the longitudinal view of incremental growth. The cross section cuts of the samples were used for this study. Gravimetric densities of the samples were estimated for calibration to WinDENDRO X-ray densitometry scanning [19]. Any remaining resins from the samples were then extracted in a liquid extractor filled with acetone. The samples were then air-dried before exposure to X-ray. The X-rayed films were scanned for density profile analyses using WinDENDRO software [19]. Densities of each annual increment and for whole core were computed for each tree for genetic analyses.

2.3. Statistical analyses

Data from Kilsby were incorporated into the main data set from the Symonds site according to the method described in [28]. Annual increment and whole core wood density were arranged in a two-way factorial format according to founder clones (pedigrees) and populations (inbreeding levels). Since not all founder clones had balanced contribution from other seven clones for the three populations (outcrossed, half-sib, and full-sib mated), inbreeding level is not exactly orthogonal to pedigree. Such factorial analysis can be regarded as the best approximation for studying population by pedigree interactions. The following linear model was fitted using the SAS GLM procedure [20] to study the effect of pedigrees, populations and their interaction,

$$Y_{ijkl} = \mu + R_i + C_j + P_k + CP_{jk} + E_{ijkl} \quad (1)$$

where μ is grand mean, R_i is replicate effect, C_j is the pedigree effect, P_k is the population (inbreeding) effect, CP_{jk} is the interaction effect between pedigree and population and E_{ijkl} is the residual. All effects were assumed random except for the grand mean and population effects. Satterthwaite's synthesis [21] was used for deriving the appropriate denominator mean square for testing the significance of founder clones and inbreeding levels.

Inbreeding depression was estimated by: ID = 1 – S/O, where S represents the performance of inbred progenies and O is the performance of outcrossed progenies.

3. RESULTS

3.1. Effect of inbreeding on populations

Mild inbreeding (mating among half-sibs and full-sibs) reduced wood density slightly at population levels (*figure 2*), but their trend reversed at higher inbreeding (S1 and S2), with the wood density from the progenies of the S2 being virtually same with that of the OC, and higher than that of the S1. The mean inbreeding depression was 1.47%, 2.50%, 1.65%, 0.02%, respectively for the HS, FS, S1 and S2 populations. However, those differences were not statistically significant (*table I*).

Inbreeding increased the variation of wood density among individual trees and the progenies of second-generation selfing had the largest variation (*figure 3*). The increase of

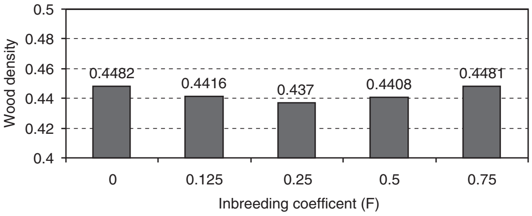


Figure 2. Relationship between inbreeding coefficient and wood density of increment cores at breast height in a 17-year-old radiata pine trial.

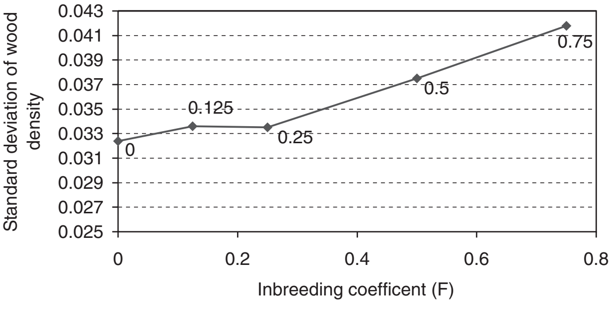


Figure 3. Relationship between inbreeding coefficient and among-tree variation of wood density in a 17-year-old radiata pine trial (inbreeding levels are marked on the trend line).

Table I. Results of analysis of variance for wood density of whole cores at breast height in a 17-year-old radiata pine inbreeding trial.

Sources of variation	D.F.	M.S.	F	EMS
Replication	3	0.0010	1.00	$\sigma^2_E + k_1\sigma^2_R$
Founder clone (pedigree)	7	0.0136	5.00**	$\sigma^2_E + k_2\sigma^2_{CP} + k_3\sigma^2_C$
Inbreeding level (population)	4	0.0046	1.45	$\sigma^2_E + k_4\sigma^2_{CP} + Q(P)$
Pedigree × population	22	0.0034	3.38**	$\sigma^2_E + k_5\sigma^2_{CP}$
Residual	641	0.0010		σ^2_E
Total	677	0.833/677		

D.F.: degree of freedom, M.S.: mean square, F: F statistic, EMS: expected mean square. $k_1 = 100.02$; $k_2 = 12.99$; $k_3 = 52.97$; $k_4 = 16.63$; and $k_5 = 18.39$.
** $Pr < 0.01$ and * $Pr < 0.05$.

variation in wood density with inbreeding level followed a linear trend. Inbreeding increased the variation of wood density among trees by 3.70%, 3.40%, 15.74%, and 29.01%, respectively, for the HS, FS, S1 and S2 populations.

3.2. Effect of inbreeding on individual pedigrees

There was a significant difference among pedigrees in their response to inbreeding, as indicated by the significant "pedigree × population" interaction effect (*table I*). The eight pedigrees can be divided into three categories according to the pattern of their responses (*figure 4*). Wood density declined from F = 0 to F = 0.75 more or less linearly for pedigrees 5 and 6 while wood density changed very little for pedigrees 3 and 4. For pedigrees 1, 2, 7, and 8 wood density declined initially at mild inbreeding levels (F = 0.125 and F = 0.25) and then increased at more severe levels of inbreeding (F = 0.50 and F = 0.75). For pedigree 2, 7 and 8, the average wood densities in the S2 were higher than in the OC.

3.3. Effect of inbreeding on wood density of annual increments

Wood density increased almost linearly from about 400 kg m^{-3} at age 4 (the earliest age for complete annual increment in most samples) to about 525 kg m^{-3} at age 12 with little change thereafter in all five populations (*figure 5*). Statistically, there were no significant differences among the five populations for wood density of annual increment at any age (*table II*). However, wood density varied significantly among pedigrees at all ages except the earliest age 4.

Variation of wood density increased with age for all five populations (*figure 6*). But the variation among-trees in the inbred populations increased faster than in the outcrossed population. Furthermore, variation among-trees was smallest in the outcrossed population at all ages. After age 13, the variation among-trees in the S1 and S2 populations was always larger than that in the two sib-mated populations.

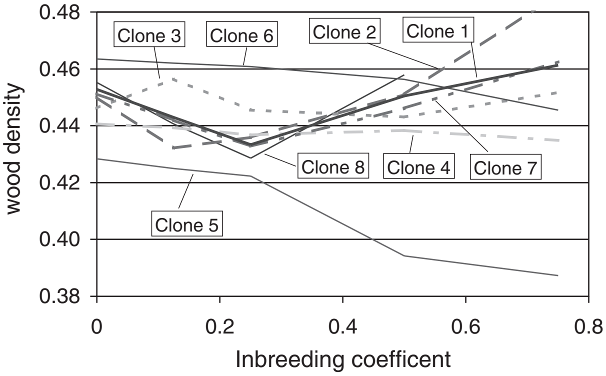


Figure 4. Differential responses of wood density to inbreeding among eight founder clones (pedigrees) in a 17-year-old radiata pine trial.

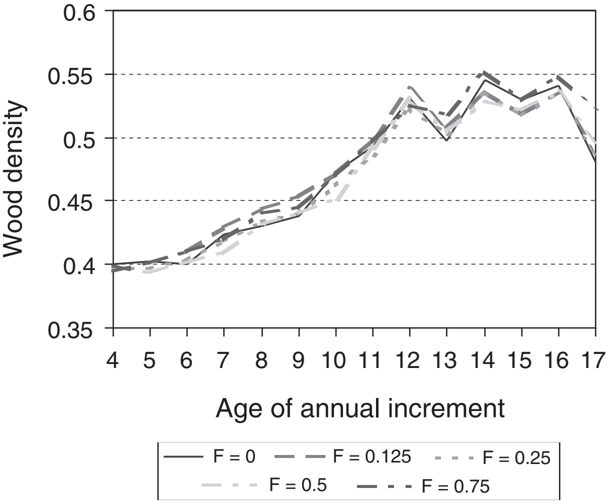


Figure 5. Wood density of annual increments in five populations inbred to different level from a 17-year-old radiata pine trial.

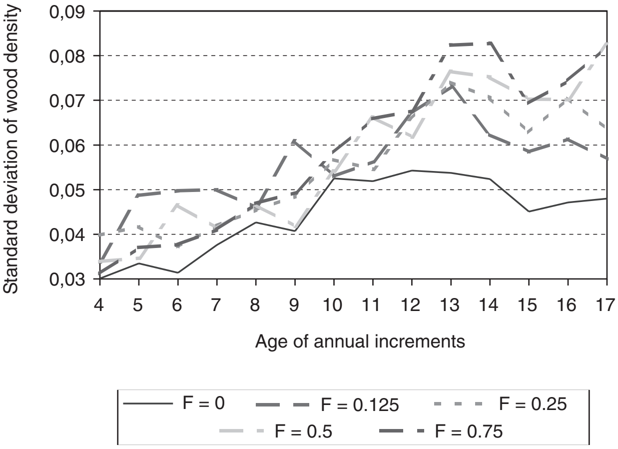


Figure 6. Variation of annual wood density for five populations of different inbreeding levels in a 17-year-old radiata pine trial.

Table II. Results from analysis of variance (variance ratio and significance level) for wood density of individual annual increment from age 4 to age 17 from increment cores at breast height in radiata pine.

		Age													
Sources of variation	D.F.	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Replication	3	4.94**	4.16**	3.88**	6.41**	10.6**	10.9**	2.71*	0.26	0.68	0.92	0.60	0.85	1.36	2.47*
Pedigree	7	2.56	4.01**	4.45**	5.74**	7.00**	4.79**	6.28**	7.90**	7.70**	6.12**	4.95**	5.97**	5.02**	5.03**
Population	4	0.55	1.12	0.82	1.02	0.66	0.78	1.07	0.59	0.72	0.76	0.91	1.04	0.52	2.61
Pedigree × population	22	0.99	1.46	2.65**	2.00**	1.89**	2.06**	1.83*	1.62*	1.72*	2.15**	2.66**	2.43**	2.69**	2.14**

* $P < 0.05$; **$P < 0.01$.

4. DISCUSSION

The observation of negligible inbreeding depression of wood density in this long-term and comprehensive experiment is similar to earlier preliminary observations in radiata pine [26]. Wilcox [26] observed that, at age 7, the average wood density for 25 selfed families was a little larger (302 kg m^{-3}) than for 25 outcrossed families (298 kg m^{-3}). The insignificant inbreeding depression of wood density in radiata pine contrasts with the significant inbreeding depression observed for growth traits (height and diameter at breast height – DBH), both in our earlier investigation of same trial [28] and the Wilcox's study [26]. Selfing depression for DBH was 15% at age 13 in this trial [28] and was 14% at age 7 in the Wilcox trial [26].

To understand the genetic causes of the different patterns of inbreeding depression for growth versus wood density is a challenging task, both from empirical and theoretical perspectives. This is because wood density is not only affected by genetics; it is also heavily influenced by growth rate and other factors. It appears that wood density is a lesser life-history trait and may not affect the fitness of the tree as much as growth traits do. It is also possible that wood density has fewer lethal or deleterious recessive loci. Further, there might be less variation in genes that affect wood density. Genetic correlations between wood density and growth are usually negative [4]. In radiata pine, the correlation between growth rate and wood density has been found to be either zero [1, 17] or negative [2, 5]. Hence slower growing trees in inbred populations may have maintained or increased their wood density through negative genetic or environmental correlations.

Structurally, wood density is not a simple characteristic but is determined by several characteristics such as cell size, cell wall thickness, and the ratio of earlywood to latewood. Recessive alleles that reduce growth by slowing cell division may have no effect on wood density. Similarly, wood density may not be affected by alleles that result in smaller size of cells.

Although inbreeding did not significantly decrease the mean wood density of any of the inbred populations, it did increase the variation of wood density among trees. According to genetic theory, if there are only additive gene effects, inbreeding will increase genetic variance in a linear manner and, if the inbreeding results in population subdivision, this genetic variance will be distributed between lines and within lines. With dominance, the partitioning of genetic variance between and within lines is dependent upon the underlying gene frequencies [8]. The greater variation among trees in the inbred populations suggests that selection for wood density will be more effective after inbreeding according to genetic theory, but we don't know whether environmental variance was also increased with inbreeding.

There were significant differences among the pedigrees in their response to inbreeding. Different responses were also observed for growth rate in our earlier study [28]. However, the growth rate and wood density of individual pedigrees differed in their response to inbreeding. Four pedigrees (1, 2, 7, and 8) had initial decline and later increase for wood density as inbreeding level increases. Among these four pedigrees, only pedigree 7 had similar patterns of response for growth rate (e.g. initial decline and later increase). Pedigrees 3 and 4 had little change in wood density at all five levels, but their growth rate declined linearly with increasing inbreeding. Pedigree 6 showed a linearly declining trend for wood density. However its growth rate initially decreased from $F = 0$ to $F = 0.5$, then slightly increased from $F = 0.5$ to $F = 0.75$.

The most interesting finding is for pedigree 5, which had no significant inbreeding depression for DBH, variance of DBH or survival [28]. Indeed, the founder clone 5 had the highest breeding value for DBH and its corresponding pedigree had the best DBH among the outcrossed progenies. It was suggested that founder clone 5 might have many good alleles for growth that are fixed and should be highly prized for advanced-generation breeding for growth rate. However if it has few or no recessive and deleterious alleles for growth traits, then there may be little room for improvement in growth through the purging of deleterious alleles from this clone via inbreeding. However, as pedigree 5 had the highest inbreeding depression for wood density among the 8 pedigrees, there is great potential for improvement of this trait through purging. Although founder clone 5 is still one of the best growing clones in the current Australia breeding population, its low wood density is a major concern. Hence, improvement through crossing with other high-density clones is essential. Furthermore, due to its relatively large genetic load for wood density, progenies from matings among relatives of founder clone 5 should not been part of deployment population. This is particularly true for the current Australian and New Zealand breeding populations since many selected clones in these breeding populations are descendants of founder clone 5. Selfing of founder clone 5 and subsequent selection among progeny could further purge recessive and deleterious alleles for wood density and may be the best and quickest way to improve the wood quality of its descendants. Therefore, we may have found a genetic solution to derive later generations of both fast growing and high wood density clones.

Inbreeding had no significant effects on annual wood density. This is in contrast with our previous observation that inbreeding significantly depressed sectional area increment at breast height from age three onwards [29]. An important finding from our previous growth study was the bimodal age trend for inbreeding depression of sectional area increment. We observed that inbreeding depression of annual increment was the highest early in stand development, disappeared at about the time of crown closure in the plots of outcrossed trees and reappeared as the stand developed further under inter-tree competition. This bimodal trend of inbreeding depression in sectional increment (similarly observed in DBH) was attributed to differences in the timing of onset of stand competition in the different inbreeding levels. Different competition levels might have obscured the differences in increment between the various inbreeding levels and consequently obscured inbreeding depression. We did not observe a similar pattern for wood density. Inbreeding had no impact on wood density at the population level for any age. Wood density did increase from age 4 to age 12 and then fluctuated over the next 4 and 5 years. The age trend of wood density, the very small influence of inbreeding on mean wood density, the impact of growth rate on wood density, and the smaller sample size may all contributed the less defined age trend for inbreeding depression of wood density.

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