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Original article

Genetic control of the time of transition from juvenile to mature wood in *Pinus radiata* D. Don

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Abstract – The success of selective breeding for growth rate and subsequent reduction in rotation age in *Pinus radiata* has resulted in almost 40% of the log constituting juvenile wood in some cases. Juvenile wood properties in radiata pine are known to be limiting in factors such as low density, spiral grain, fibre length, and compression wood. Juvenile wood quality may be improved by breeding for increased stiffness of juvenile wood or an early transition age from juvenile to mature wood. The objective of this study was to investigate the age of transition from juvenile to mature wood and quantify genetic control in time of transition from juvenile to mature wood using 1866 radiata pine samples. Wood samples from two 16-year-old Australia-Wide Diallel (AWD) radiata pine tests and two 28-year-old open-pollinated (OP) progeny tests were submitted to X-ray densitometry procedures. An important finding of this study is the site difference in latewood density transition-age between tests at Flynn and Silver Creek in Gippsland, Victoria (mean = 7.5 y) and at Tantanoola in Green Triangle, South Australia (mean = 12.6 y). This finding suggests that site has a major effect on juvenile-mature transition in radiata pine. We detected moderate levels of genetic control in latewood density transition age that would allow for selective breeding for a shorter juvenile wood formation phase. These results suggest that there may be an opportunity to select for a reduction in transition age and therefore, increase the overall wood uniformity.

***Pinus radiata* / juvenile wood / mature wood / transition age / heritability**

Résumé – Contrôle génétique de l'âge de transition 'bois juvénile-bois adulte' chez *Pinus radiata* D.Don. L'amélioration génétique pour la croissance a permis de réduire avec succès la révolution chez le pin radiata mais elle a aussi abouti dans certains cas à faire augmenter la proportion de bois juvénile à près de 40 %. Il est bien connu que plusieurs propriétés (densité, angle du fil, longueur de fibre, bois de compression) sont modifiées dans le bois juvénile du pin radiata. La qualité du bois juvénile peut être améliorée par sélection pour une plus grande rigidité du bois juvénile ou pour une transition plus précoce du bois juvénile-bois adulte. L'objectif de cette étude était d'évaluer l'âge de transition bois juvénile-bois adulte et de quantifier son niveau de contrôle génétique. À cette fin, 1866 échantillons de pin radiata ont été analysés. Des échantillons de bois prélevés en Australie dans deux tests diallèles (AWD) âgés de 16 ans et dans deux tests de descendances issues de pollinisation libre (OP), âgés de 28 ans, ont été analysés par densitométrie à rayons X. Un résultat majeur de cette étude met en évidence un effet environnemental significatif pour l'âge de transition pour la densité du bois d'été. Il est en moyenne de 7,5 années sur les sites de Flynn et Silver Creek à Gippland (Victoria) et de 12,6 années à Tantanoola (Green Triangle, Australie du Sud). Ce résultat suggère que le site a un effet majeur sur la période de transition bois juvénile-bois mature chez le pin radiata. Nous avons détecté des niveaux de contrôle génétique modéré pour l'âge de transition pour la densité du bois final ; cela devrait permettre de réduire par sélection la période de formation du bois juvénile. Ces résultats suggèrent donc qu'il est possible de réduire l'âge de transition bois juvénile-bois adulte et d'augmenter en conséquence l'homogénéité générale du bois.

pin radiata / bois juvénile / bois adulte / âge de transition / héritabilité

1. INTRODUCTION

Selective breeding in *Pinus radiata* D. Don for the first two generations has produced more than 30% improvement in growth rate with substantial benefits from the increased volume of harvested wood in pine plantations in Australia [24, 42, 45], with substantial benefits from the increased volume of harvested wood. Breeding for growth rate and tree form in the first two generations has reduced average machine strength grade of structural timber by almost 3% in radiata pine due to the negative genetic correlation between growth rate and wood density [9, 43]. However, this reduction in density may not be a great concern for mature wood harvested from Australian plantations, which in general have relatively high density compared to juvenile wood. Mature wood has characteristics, such as high wood density, low microfibril angle (MfA) and high stiffness (MoE- Modulus of Elasticity) more suited for structural timber [40]. A major concern for faster-grown radiata pines is the occurrence of higher proportion of juvenile wood in the logs partly due to reduced rotation age.

The typical rotation age for radiata pine has been shortened from 40–45 y to 25–30 y throughout much of the radiata plantation in Australia. Because of this, juvenile wood now accounts for a much higher proportion of harvested wood than it has in the past. Juvenile wood in fast growing conifers has lower density and strength than mature wood [4, 6, 18, 25]. Sawn boards with high proportion of juvenile wood usually

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do not meet the structural grades which command higher prices [34].

Juvenile wood formed near the pith throughout the trunk of a tree can have different properties from wood produced in the outer rings, termed mature wood. However, definition of juvenile wood can be difficult and is to some degree subjective; it is often described in terms of the number of rings from the pith [6]. The demarcation boundary in the stem between juvenile and mature wood is diffuse and the region where one type of wood starts and the other stops, frequently referred to as transition wood [49]. Generally, transition from juvenile to mature wood occurs gradually over two to five growth rings depending on the wood property [48]. Harris and Cown [14] describe juvenile wood in radiata pine as the first 10 growth rings from the pith, mainly on the basis of the known variation in wood density and outer wood properties. As such, varying criteria have been used to delineate juvenile and mature wood.

Juvenile wood quality can be improved through breeding or through silvicultural management. Improvement by breeding has become a priority along with growth rate for the third-generation selections of radiata pine in Australia. Log quality may be improved through reduction of juvenile wood and increasing the stiffness of juvenile wood [27, 38]. It is well understood that the stiffness of juvenile wood in radiata pine can be improved through breeding, either through improvement of MoE or other component traits such as wood density and microfibril angle [22]. Numerous studies on inheritance of wood quality in radiata pine have shown high heritabilities for wood density, and other stiffness related traits such as microfibril angle [19, 43–45]. With the invention of new wood technologies for measuring wood properties such as SilviScan® [11], and acoustic tools, e.g., IML® hammer, TreeTap®, Director ST300® [2, 5, 37], estimation of inheritance on MoE and stiffness became possible. There is considerable genetic variation for MoE in radiata pine and selection would be effective [22, 43].

In addition to breeding trees with improved juvenile wood properties, it may be possible to breed for an early transition age from juvenile wood to mature wood. We define transition age as the age at which the transition from juvenile wood to mature wood is completed, leading to a stable wood density in growth rings. Reducing the volume of juvenile wood would increase the overall wood density and the quality of certain wood products [35, 47]. Thus, reducing the proportion of low density wood by selecting for a shorter juvenile wood formation phase is an attractive option for improving wood quality.

To use transition age as a selection criterion for improving wood quality in radiata pine, an understanding of the genetic variability of transition age is critical. Few studies have examined the genetic mechanisms influencing transition age in fast growing pines. For example, Loo [20] reported a family heritability estimate for wood specific gravity transition-age of 0.36 in *Pinus taeda* and suggested moderate gains (earlier transition ages) could be obtained by selecting on a family mean basis. For *Pinus elliottii*, Hodge and Purnell [15] reported an average transition age for ring density, latewood density, and latewood percentage of 9.4, 7.5 and 10.3 y, respectively; and the heritability of these traits ranged from 0.16 to 0.22. Genetic control of earlywood density, latewood density and latewood percentage in radiata pine is moderately heritable [17,48]. However, if we can ascertain the genetic control in time of transition from juvenile to mature wood in radiata pine, there may be an opportunity to select for a reduction in transition age and therefore decrease the proportion of the log containing juvenile wood.

A prelude to an accurate estimation of the proportion of juvenile wood in a tree is to be able to detect the boundary between juvenile and mature wood. Several traits (e.g., fiber length, microfibril angle, ring density, latewood density) have been used to determine the point of demarcation between juvenile and mature wood [1, 15, 20, 39]. However, the issue is complicated by the fact that the transition point from juvenile to mature wood varies with the trait under investigation [3]. Several methods have been proposed to estimate transition age, including mathematical approaches such as the Gompertz function, iterative and constrained solutions and segmented regression techniques [1, 20, 35, 49].

The objectives of this study on radiata pine were to: (1) estimate age of transition from juvenile to mature wood; (2) quantify genetic control in time of transition from juvenile to mature wood; and (3) explore the possibility of selection for a shorter juvenile wood formation phase.

2. MATERIALS AND METHODS

2.1. Sample origin and sampling procedures

Table I provides general information about the field trials examined in this study. Two half-diallel trials comprised families from seven sets of 16-years old 6 × 6 half-diallels in the Gippsland region, Victoria. However, there were several missing crosses from the half diallels in each of the tests. The half-diallel tests were part of Australia-Wide-Diallel (AWD) tests originally designed to provide reliable estimates of GCA (General Combining Ability) and SCA (Specific Combining Ability) for radiata pine in Australia. Details of the Australia-Wide-Diallel program are given in Wu and Matheson [45]. Summary results on growth and form traits are summarised in Wu and Matheson [45]. VRC52 was planted in 1986 at Flynn with 100 full-sib families of which 13 were controls and 4 tree plot in 4 replications. VRC54 was planted at Silver Creek in 1986 with 52 full-sib families of which 4 were controls and single tree plot in 20 replications. In VRC52, there were 42 parents with an average of 4 crosses per parent, whereas in VRC54, there were 31 parents with an average of 3 crosses per parent. There were differences in previous land-use between the two sites: VRC54 is a second-rotation site and VRC52 is an ex-pasture first-rotation site. Ex-pasture sites are usually more fertile than second-rotation sites [23, 45].

The second two trials comprised 30 open-pollinated families excluding controls. The field designs of the open-pollinated trials were randomized complete blocks with 10-tree row-plots in 6 replications planted in 1971 at Tantanoola, South Australia (PT5042) and harvested at age 27 y and a 2 × 3 tree plots in 9 blocks planted in 1969 at Flynn, Gippsland, Victoria (PT47) and harvested at age 31 y. Soils at PT47 are characterised as sandy loam whereas at PT5042, they are characterized as sandy clay loam.

Variable sampling strategies were applied depending on trial design, number of blocks, families and trees per family. At VRC52,

Table I. Site characteristics, details of families, number of blocks sampled, sample size of wood disks and trial age for juvenile-mature wood transition study for four *Pinus radiata* progeny trials in Australia.

Trial	VRC52	VRC54	PT47	PT5042
Site	Flynn Creek	Silver Creek	Flynn Creek	Tantanoola
Year of planting	1986	1986	1969	1971
Age at harvest (years)	16	16	31	27
Latitude	38° 14' S	38° 15' S	38° 12' S	37° 29' S
Longitude	146° 41' E	146° 39' E	146° 40' E	140° 40' E
Elevation	93	184	100	62
Mean annual rainfall (mm)	760	785	760	900
Soil type	Sandy loam	Sandy loam	Sandy loam	Sandy clay loam
Site type[a]	Ex-pasture	2nd PR	Ex-pasture	2nd PR
Family structure	Full-sib	Full-sib	OP	OP
No. families	100	52	36	33
No. blocks sampled	3	6	9	6
Average No. trees/family sampled	6	6	18	27
No. trees sampled	600	312	648	780

[a] 2nd PR: second rotation of radiata pine crop.

wood disks at breast height (1.3 m) were collected from two trees per plot from the first three blocks, giving a sample size of 600, using a systematic approach, i.e., sampling trees 2 and 4 in every plot. In VRC54, the single tree per plot was sampled from the first 6 blocks and giving the overall sample size of 312 (Tab. I). At PT47 trial, two trees were selected from each of 6-tree plots and harvested at age 31 y from planting, giving a sample size of 648. At PT5042, three out of 10 trees per plot were sampled at age 27 y in blocks 1, 2, and 6. In blocks 3, 4 and 5, all remaining trees were sampled except for obviously suppressed ones. As a consequence, the number of sampled trees per plot in blocks 3, 4 and 5 ranged from 3 to 9. On average, 27 trees per family were sampled out of a possible 39. In total, 780 trees were sampled in PT5042. A total of 2340 cross-sectional disks were collected at the four sites, but only 1904 samples were used after exclusion of control lots and several dozen disks that had incomplete outside rings.

2.2. Sample preparation

From the wood discs, bark-to-bark-through-pith flitches of 2 mm thick were prepared using a specially designed electric twin-blade saw. In order to obtain density values that are not an overestimate in the juvenile wood section (initial growth rings from the pith), it was necessary to extract resins from the samples in which heartwood was well developed and highly resinous, particularly in the first three growth rings. Absolute value of optimally determined density may be an overestimate if resin is not extracted [28]. Resin was extracted by boiling the samples in acetone for 24 h and the samples were air-dried to 10% moisture content.

2.3. Wood density measurement

Wood density of 2 mm flitch was measured using X-Ray densitometry and WinDENDRO software package [31]. Wood density was measured from pith to bark of the two radii. The average density of the two radii was taken to represent a sample tree. Densitometry readings were calibrated with samples of known wood density. Comparisons of gravimetric density of X-ray samples with density determined by direct scanning densitometry by SilviScan® gave $R^2 = 0.94$. In this study, wood density is expressed in g cm^{-3}. Using the indirect reading X-Ray densitometer [29], the samples were scanned to determine the basic wood density (oven-dry weight/green volume) for each ring from pith to bark. The first and last annual rings of each sample were rejected because they were too narrow for densitometry analysis.

For each annual ring, earlywood and latewood boundary was delineated. The boundary between earlywood and latewood was defined as the point within a growth ring at which positive slope of the densitometric trace exceeds 50%. In most cases this boundary coincided almost exactly with the midpoint between average earlywood density and average latewood density of the ring. Ring and latewood boundaries assigned automatically by WinDENDRO were edited to remove false rings and other obvious aberrations. The data obtained and processed, consist of average values for each growth ring; ring width-RW, ring density-RD, minimum density-MINDEN, maximum density-MAXDEN earlywood density-EWD, latewood density-LWD and latewood percentage-LWP.

2.4. Determination of transition age

Segmented regression approach has been used to determine the age of transition from juvenile to mature wood [1, 20, 36]. It is assumed that the radial development of a specified wood density trait from pith-to-bark can be described by two functions/models, one for the steep slope over the first years beginning at the pith (juvenile wood) and the second for the later part of the curve (mature wood). These models characterize change of slope in the radial density trend. With segmented regression, a statistical model (Eq. (1)), can simultaneously estimate parameters of the two curves and a breakpoint between juvenile and mature wood [1, 26]. A solution can be directly obtained by using nonlinear least squares procedures (PROC NLIN) in SAS [30, 33] with the transition age being the ring number which minimizes the mean squared error. Since the transition age is unknown, the least squares procedure in SAS [33] was used to obtain estimates of the regression parameters and the transition age (join point). The fitted regression model takes the form:

$$Y_i = \beta_0 + \beta_1 X_i + \beta_2 (X_i - \alpha) I + \varepsilon_i \quad (1)$$

where
Y_i is the independent variable for wood property,
X_i is ring number,
α is the ring number at which wood changes from juvenile to mature wood,
I is an indicator variable where $I = 1$ if $X_i - \alpha \geq 0$, or $I = 0$ otherwise,
β_0 is the intercept of the line of the juvenile wood,
β_1, β_2 are regression coefficients, and
ε_i is error.

In order to use segmented regression approach to determine transition age, the pith-to-bark profiles of the six density related variables (ring width-RW, ring density-RD, minimum density-MINDEN, maximum density-MAXDEN, earlywood density-EWD, latewood density-LWD, and latewood percentage-LWP were plotted using the GPLOT procedure [33]. Preliminary analyses indicated that ring width-RW, ring density-RD, minimum density-MINDEN, maximum density-MAXDEN earlywood density-EWD, and latewood percentage-LWP were not suitable for a clear differentiation between juvenile and mature wood. For latewood density, it can be readily divided into juvenile and mature wood and two separate regressions can be reasonably fitted for the whole profile from pith-to-bark of latewood. Therefore, transition age was estimated for latewood density only.

2.5. Genetic analyses

Single-site analyses of variance components for diallel data were carried out using an individual tree model. The fitted model was:

$$y = Xb + Z_1 a + Z_2 s + W_1 m + e \quad (2)$$

where y is the vector of individual tree observations; b is the vector of block fixed effects; a is the vector of random general combining ability (GCA) effects of individual trees; s is the vector of random specific combining ability (SCA) effects due to specific combinations of males and females; m is the vector of random plot effects; e is the vector of random residual deviations of individual trees; X, Z_1, Z_2 and W_1 are incidence matrices relating to the model effects. It is assumed that the random terms are jointly normal with moments:

$$\mathrm{E(a) = E(s) = E(m) = E(e) = 0}$$

$$\mathrm{VAR} = A\sigma^2 a \quad \mathrm{I}\sigma^2 s \oplus \mathrm{I}\sigma^2 m \quad \mathrm{I}\sigma^2 e$$

where $\oplus$ is the direct sum of matrices related to the random terms in the model; A is the additive genetic relationship matrix between trees and I is an identity matrix; $\sigma^2 a$ is the additive genetic variance; $\sigma^2 s$ is the variance due to specific combinations of males and females; $\sigma^2 m$ is the plot variance; $\sigma^2 e$ is the residual variance. In the case of open-pollinated data, the s term was dropped from model (2).

Restricted maximum likelihood (REML) estimates of variance components and their standard errors were obtained by using the average information REML algorithm [13]. Narrow-sense heritabilities and residual were estimated according to standard formulae [12]. The standard errors of the estimated parameters were calculated from variance of ratios, using an approximation based on a Taylor series expansion. The significance of the variance component was determined by the ratio of the component relative to its standard error. If the variance component was more than two standard errors from zero, then the variance component was considered significant. If the variance component was less than one standard error from zero, then the variance component was considered insignificant. For variance components between 1 or 2 standard error from zero, Likelihood ratio test (LRT) was used to test for any significant differences among the effects (e.g., Gilmour et al. 1999). The Log-likelihoods were compared as LRT = 2(Log $_{\mathrm{Lp+g}}$ – Log $\mathrm{L_p}$) where Log $\mathrm{L_{p+g}}$ is the Log-likelihood with the variance component and $p+g$ degrees of freedom and Log $\mathrm{L_p}$ is the Log-likelihood without the variance component with p degrees of freedom. The LRT was distributed as a χ^2_q with q degrees of freedom.

BLUPs of the additive genetic values (i.e., predicted breeding values, PBV) for individual trees for transition age were predicted from model (2). Individual trees were ranked on PBVs based on early transition age for each trial. Ten % of the individuals in each trial were selected to give an indication of the genetic gain expected from selecting individuals having the shortest juvenile wood formation phase.

3. RESULTS AND DISCUSSION

3.1. Search for a suitable ringwood variable as indicator of juvenile-mature wood transition zone

Previous studies examining transition age from juvenile to mature wood have considered several traits as indicators of juvenile-mature wood transition zone. These include density, microfibril angle, fiber length, lignin/cellulose ratio and latewood density [1, 15, 38, 39]. These characteristics are closely related to tracheid differentiation, which changes with cambial age. While the transition zone for each of these characteristics is of scientific interest, for practical purposes, we are more concerned with those properties that are closely related to end-product quality and that can be repeatedly and economically measured.

The radial development of wood density components (ring width-RW, ring density-RD, minimum density-MINDEN, maximum density-MAXDEN earlywood density-EWD, and latewood percentage-LWP showed considerable fluctuations with age, making it unclear as to where the demarcation between juvenile and mature wood could be drawn. For example, earlywood density (EWD) showed low variation from pith to bark with no obvious change (e.g., sample # T-445, Fig. 1). This type of curve characterised all sample trees, with very few exceptions. These findings are similar to those for Douglas-fir [1]. The same pattern of changes in EWD was also mentioned for radiata pine grown in Chile [47]. EWD trends from pith to bark showed that early wood density was not suitable for a clear differentiation between juvenile and mature wood.

Ring density increased linearly from pith-to-bark showing little variation (e.g., sample # T-445, Fig. 2) and we considered

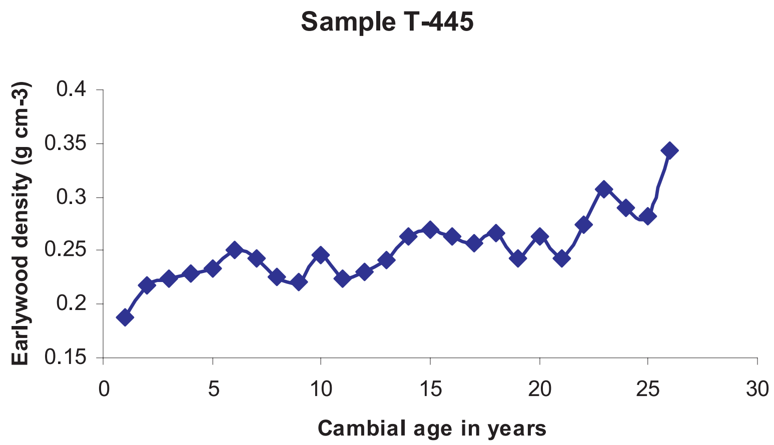

Figure 1. Development of earlywood density from pith-to-bark for sample T-445.

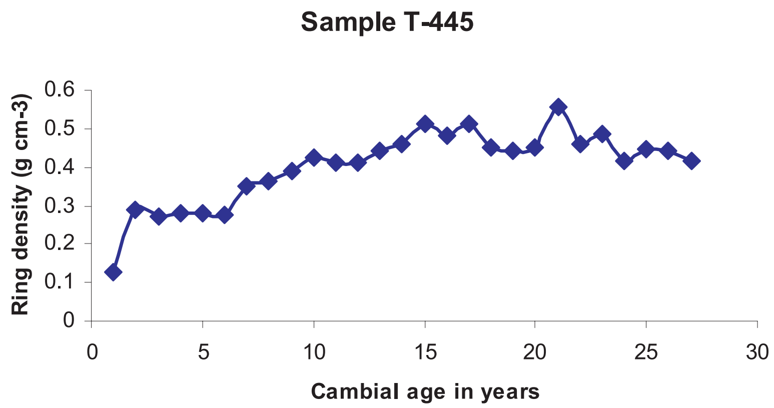

Figure 2. Development of ring density from pith-to-bark for sample T-445.

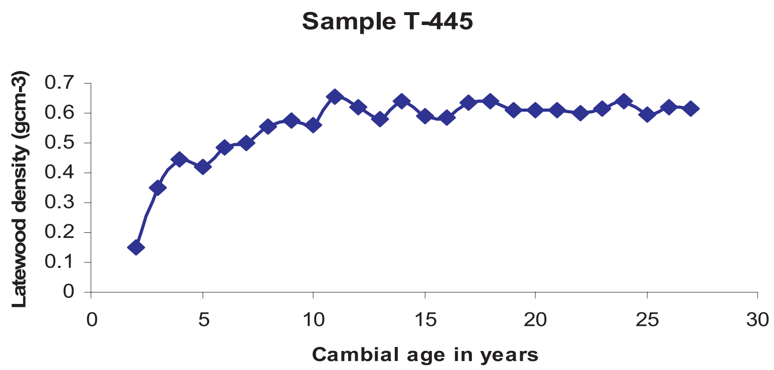

Figure 3. Development of latewood density from pith-to-bark for sample T-445.

it unsuitable for differentiating between juvenile and mature wood. When the segmented regression models were applied, it was deduced that the use of ring density was not appropriate, because of low coefficients of determination and large range of ages for transition from juvenile to mature wood. Such a trend was unexpected as other studies on fast growing conifers were able to use ring density to estimate transition age [15, 20]. Cown and Parker [8] reported that radiata pine, like most coniferous species show a tendency to increase value in ring density, outwards from the pith.

Latewood density increased rapidly for about the first 4 y, and thereafter remained relatively steady (e.g., sample # T-445, Fig. 3). For the purpose of determining juvenile-mature wood transition, only the latewood density data gave reasonable results, and produced visibly identifiable breakpoints in segmented regression models applied to pith-to-bark density profiles. Latewood density is a characteristic that is closely related to stiffness (MoE) which in turn is one of the most important mechanical properties for most end uses of wood-based biomaterials [21, 32].

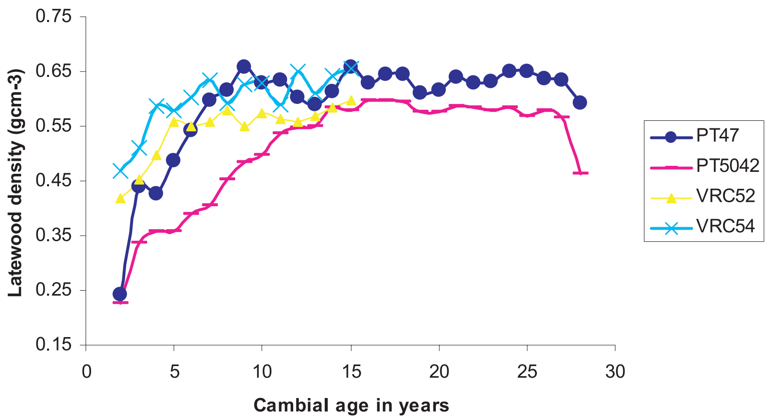

Figure 4. Trends in latewood density from pith to bark at PT5042, PT47, VRC52, and VRC54.

Table II. Individual trial estimates of mean transition age (years), additive genetic ($\sigma^2 a$), specific combining ability ($\sigma^2 s$) and residual ($\sigma^2 e$) variances, heritabilities (h^2_i) and genetic gain (Δ_G) for transition age in four trials of *Pinus radiata*. The approximate standard errors for the estimated parameters are given in parenthesis.

Trial	Min–Max	Mean	$\sigma^2 a^1$	$\sigma^2 s$	$\sigma^2 e$	h^2_i	Δ_G (%)
VRC52	5.6–14.8	7.7 (1.4)	0.546 (0.08)	0.23E-5[a]	3.689 (0.71)	0.13 (0.04)	5.2
VRC54	5.9–11.2	7.2 (1.2)	0.268 (0.13)	0.85E-6[b]	0.910 (0.17)	0.23 (0.08)	6.6
PT47	5.1–11.5	7.5 (1.6)	0.185 (0.07)	–	0.912 (0.13)	0.17 (0.05)	4.6
PT5042	6.3–21.6	12.6 (2.7)	1.738 (0.73)	–	3.576 (0.63)	0.33 (0.04)	10.1

[a] Additive genetic variance estimates were all significantly ($P \leq 0.05$) different from zero.
[b] SCA effects not significantly different from zero.

3.2. Trends in latewood density

Average latewood density values at VRC52 and VRC54 stabilised at ring 7 with a value of 0.597 g cm^{-3} with no further significant increase or decrease in latewood density (Fig. 4). Latewood density at PT47 increased from 0.241 g cm^{-3} at cambial age two and stabilized at cambial age nine with a latewood density of 0.658 g cm^{-3}. In contrast, latewood density at PT5042 increased from 0.226 g cm^{-3} at cambial age two to 0.584 g cm^{-3} at cambial age 14 (Fig. 4). Average latewood density values at PT5042 stabilized at ring 12 with a value of 0.576 g cm^{-3}. Trees reaching an early plateau in latewood density would have a shorter period of juvenile wood formation (Fig. 4). The profile patterns in our data can be described as typical of a transition from juvenile to mature wood (e.g., Hodge and Purnell [15]; Zamudio [46]).

Several studies have reported that some coniferous species show a tendency to increase values of ring density components outward from the pith (e.g., [8,41,47–49]). Zamudio [47] observed that latewood density in radiata pine increased with cambial age in 31 open-pollinated families. A similar pattern was observed by Wang [41], in families of lodgepole pine that showed that latewood density increased during the first years, reached its maximum at age six. Latewood density for loblolly pine grown in the south-east USA was found to increase rapidly with ring number from the pith, stabilizing at ring five [20]. Similar trends in latewood density changes from pith to bark have been reported by Zobel and Sprague [49] for other conifers.

Transition age at VRC52 varied from 4.3 to 9.3 y, with a mean around 7.7 y, and at VRC54 it varied from 5.9 to 11.2 y, with a mean around 7.2 y. Similarly, transition-age for the OP material at PT47 varied from of 5.1 to 11.5 y with a mean around 7.5 y. However, transition age for OP material at PT5042 varied from 6.3 to 21.6 y with a mean around 12.6 y (Tab. II). The first three trials were located in Gippsland, Victoria whereas PT5042 was planted in Green Triangle in South Australia (Tab. I). Differences in transition age between PT47 and PT5042 would seem to suggest that transition age may be site-specific.

Our results are in general agreement with those of other fast growing conifers. For example, Hodge and Purnell [15] reported a transition age for latewood density to be 7.5 rings from the pith. Loo [20] used similar approach to investigate transition age for specific gravity and tracheid length in loblolly pine. They reported mean ages of transition of 11.5 and 10.4 y for specific gravity and tracheid length, respectively. Szymanski and Tauer [35] reported a higher transition age of 12.7 y for east Texas sources than the average transition age (11.5 y) for east Texas families of loblolly pine reported by Loo [20]. This suggests that the transition from juvenile to mature wood varies not only among species, but among families, traits and sites. Cown and Ball [7] also reported the average age of onset of mature wood formation (in this study referred to as transition age) as varying among sites, ranging from five years at one site to 20 y at other sites.

The rate of change in wood density from pith to bark determines the size of the juvenile wood zone and has a major effect on the uniformity of the wood within the bole. Jayawickrama [16] reported that *Pinus taeda* L. families that grow in height later into the growing season start forming latewood later, often leading to lower wood specific gravity at the genotype level. Dodd and Power [10] attributed the variation pattern in specific gravity from pith to bark to earlywood width, which was more important than latewood width. They hypothesized that time of shoot growth initiation controlled the transition from earlywood to latewood production and thus the slope of the juvenile wood curve. Together, these studies provide evidence for an association between height growth cessation and latewood transition at family and individual tree level. In addition, time of latewood transition at family and individual tree level does help to explain differences in percent latewood and density in fast growing radiata pine trees [28].

3.3. Genetic control of transition age

Additive genetic variance (GCA) estimates at VRC52 and VRC54 were significantly different from zero whereas the SCA effects were not significantly different from zero (Tab. II). Additive genetic variance estimates for the open-pollinated material (PT47 and PT5042) were also significantly different from zero. Narrow-sense heritability for transition age at the two full-sib sites were 0.13 ± 0.04 (VRC52) and 0.23 ± 0.08 (VRC54) and at the two OP sites were 0.17 ± 0.05 (PT47) and 0.33 ± 0.04 (PT5042) (Tab. II). In comparison, individual tree narrow-sense heritability estimates in slash pine were 0.22 and 0.17 for latewood density and ring density transition age, respectively, [15]. Similarly, Loo et al. [20], reported individual tree narrow-sense heritability of 0.12 for ring density transition age in loblolly pine.

3.4. Prediction of breeding values

Predicted genetic gains, estimated using individual tree breeding values, for a shorter juvenile wood formation phase are reasonable (Tab. II). Assuming a selection intensity of one in ten, genetic gains of up to 10% per breeding cycle are possible. These gains can be interpreted as the change in population mean that could be achieved by selection in the field trials. Although in practice the selection method may be different, these gains provide some indication of the change possible in the population, from a selection intensity of only 10%. Predicted genetic gains of 10.1% at PT5042 would be equivalent to shortening the juvenile wood formation phase by 22 months compared to population mean in one generation.

4. IMPLICATIONS OF THE RESULTS

Results from this study provide some useful information that may be incorporated into breeding strategies for radiata pine. Breeding for growth or wood quality is a controversial matter, and many approaches have been suggested [50]. One plausible approach would be to select for high wood density within families with high growth rate. If valid, this approach should maximize wood production with acceptable, or even superior, wood density. However, this approach may result in the production of non-uniform wood, or wood with a high proportion of juvenile wood. Thus, integrating other criteria into this approach would be beneficial for wood quality. Using radial profiles of latewood density, it would be possible to identify radiata pine individuals and families with high growth rate, high latewood density, low juvenile wood proportion, and uniform wood. A selection index integrating all these traits would certainly help develop radiata pine varieties possessing all desired traits. This approach would be useful to improve wood properties of fast-grown plantation trees known to have a high proportion of juvenile wood and low density.

5. CONCLUSION

Segmented regression analysis proved to be a practical and objective method to estimate cambial age of transition from juvenile to mature wood in a study of radiata pine. The age of transition from juvenile to mature wood in radiata pine can be estimated only with reference to a particular wood property such as latewood density. Transition age for radiata pine is under moderate genetic control and may be site specific. A comprehensive study to examine transition age across the Australian radiata pine plantation environment would identify the best genotypes for early transition age in the different environments.

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