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Effect of genotype by spacing interaction on radiata pine genetic parameters for height and diameter growth

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ABSTRACT

Effect of genotype by spacing interaction on radiata pine (*Pinus radiata* D. Don) height and diameter at breast height (DBH) growth was studied using three spacings (1 × 1 m, 1 × 2 m and 2 × 3 m) and 55 half-sib families in a long-term progeny trial. Examined were the effect of spacing and family on early tree height and diameter growth up to 10 years, and on annual ring width (RW) and accumulated DBH of the surviving trees up to age 28 years. The effects of spacing on heritability, and age–age genetic correlations were also studied using multiple-year measurements. Spacing had little or limited impact on tree height growth, but a highly significant effect on diameter growth. Spacing also had no significant effect on heritability for tree height, but a very significant effect on the patterns and values of heritability for diameter and DBH growth. Closer spacing was found to depress heritability estimates for DBH. Spacing was also observed to have a significant impact on age–age genetic correlation, and the higher competition level at closer spacing treatment distorted the age–age genetic correlation patterns for DBH due to higher mortality. The spacing effect on heritability was more apparent from early growth measurements due to relatively small mortality compared with the late age measurements. Our current study for the first time revealed significant and useful genotype by spacing interactions in radiata pine for DBH growth. The significant genotype by spacing interactions were mainly caused by a few well-performing families reacting more to spacing changes. Therefore, matching genotype with spacing has the potential to increase productivity of radiata pine plantations.

1. Introduction

Radiata pine (*Pinus radiata* D. Don) is the most important commercial coniferous forest species planted in Australia, with about 750,000 ha of plantations (Wu et al., 2007b). Genetic improvement of radiata pine was initiated in the 1950s in Australia with initial plus tree selection, with mainly open-pollinated family testing in 1960s and 1970s, and then control-pollinated family testing in 1980s and 1990s (Wu et al., 2007a). Sizable additive and non-additive genetic variation for growth and form traits were estimated from these early trials (Cotterill and Zed, 1980; Dean et al., 1983; Matheson and Raymond, 1984; Matheson et al., 1994; Wu and Matheson, 2004, 2005). The first two generations of radiata pine selective breeding were focused on growth and form traits, and were effective for improving these traits. An estimate of realized genetic gain up to 33% was reported for individual tree volume at age 15 years from first generation selections based on a designed genetic gain trial (Matheson et al., 1986). An average volume gain of 20–25% was estimated at age 10–15 years in other genetic gain trials (Johnson et al., 1992a,b). There was also a trend for genetic gain to increase with age. An internal rate of return of 20% was estimated as the economic return from the first generation of breeding (Eldridge, 1982). A 10% of improvement for stem straightness and branch quality was observed for the first generation, based on data from 71 field trials (Boomsma and White, 1992). Predicted genetic gain from the second generation breeding population was about 14% (the average of 11–17%, White et al., 1999). With the successful improvement for volume and form traits, the average rotation length for radiata pine plantations declined from about 40–55 years to about 30–35 years (Li and Wu, 2005).

A concurrent effect of improved growth rate and reduced rotation age is increased juvenile wood and a decline in overall wood density (Wu et al., 2008). To improve both growth rate and wood quality traits simultaneously from the third generation of breeding radiata pine in Australia, genetic variation in wood quality traits and genetic correlation between growth rate and wood quality

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traits were extensively examined for juvenile and mature wood (Baltunis et al., 2007; Gapare et al., 2007, 2008, 2009; Matheson et al., 2008). Economic breeding objectives were developed by estimating optimal economic weights for targeted breeding traits (designated as breeding objective traits, Ivković et al., 2006a,b).

Growth traits and wood quality traits are not only affected by genetics, but also by stand management and silvicultural treatments. It has been shown that different genetic entries might show differences in growth and form in response to different management regimes and environmental conditions (Zobel and Talbert, 1984; Haapaen et al., 1997). To capture realized genetic gain in plantation environments, the best silviculture regimes should be established and matched with genetic stocks. Among all silvicultural treatments, spacing between trees has been one of the most important factors in regulating growth rate and wood quality traits. Indeed, two of the most important decisions made during the establishment of a radiata pine plantation are the selection of appropriate genetic material and a suitable spacing (Lasserre et al., 2005). Therefore, information on how genetics, spacing and their interaction jointly influence radiata pine growth and wood quality is particularly important for optimally managing radiata pine plantations for desired end products.

Initial stand spacing has important biological and economic implications for both forest managers and industrial end-users. Long et al. (2004) observed that the initial spacing determined the time of crown closure and that the subsequent competitive interaction between trees further influenced stand development and production of forest tree. There have been a considerable number of tree spacing experiments indicating that wide initial spacing could enhance tree diameter growth and individual tree size but decrease stand level volume production regardless of tree species (Salminen and Varmola, 1993; Clark et al., 1994; McClain et al., 1994; Harms et al., 2000; Harrington et al., 2009; Zhao et al., 2011; Liziniewicz et al., 2012). Moreover, wood quality traits have also been shown to vary with different initial spacing (Watson et al., 2003; Roth et al., 2007; Gort-Oromi et al., 2011). In economic terms, initial spacing influenced the costs of plantation (Granhus and Fjeld, 2008) and the timing and intensity of thinning required (Long et al., 2004). Results from trials of initial spacing and spacing regulation have also been applied to earlier plantation practices. In New Zealand, with very successful breeding and silvicultural practice from the 1970s, the average planting spacing has declined from 1800 to 960 stems ha^{-1} (Lasserre et al., 2005). Recently, as interest in energy wood production and carbon storage has increased, there could also be increasing interest in wider spacing at planting to maximize biomass production during early stand development (Fang et al., 2007; Harper et al., 2007).

For radiata pine, genotype by environment interactions (G × E) have been reported for several series of progeny trials in Australia and New Zealand (Matheson and Raymond, 1984; Johnson and Burdon, 1990; Carson, 1991; Wu and Matheson, 2005; Raymond, 2011; Baltunis et al., 2010; Gapare et al., 2012). Most of work was focused on G × E for growth and wood quality traits between different sites. There are a few studies on genotypic and spacing effects on wood properties in radiata pine using small numbers of clones or varieties (Lasserre et al., 2005, 2008, 2009; Waghorn et al., 2007). Experiments on genotype by spacing interaction for growth traits in other forest trees are also few and short-term (Campbell and Wilson, 1973; Fries, 1984; Patino-Valera and Kageyama, 1990; Bouvet et al., 2003; Land et al., 2003; Benomar et al., 2012) and most studies have observed no significant and useful genotype by spacing interaction for growth traits (Campbell and Wilson, 1973; Land et al., 2003). Therefore, long-term genotype by spacing interactions on growth traits and their effect on heritability and age–age correlations are poorly understood.

In this study, tree height and diameter at breast height (DBH) of 55 families were monitored up to 21 years on radiata pine planted at three spacings in a trial in Tasmania, Australia. The study objectives were: (1) to evaluate tree growth responses to initial spacing, (2) to examine whether there were genotype by initial spacing (G × S) interactions and the effects of tree age on G × S interactions, and (3) to examine the cause of G × S (i.e. whether G × S effects were a result of a few families reacting more than others to changes in spacing).

2. Materials and methods

2.1. Experimental design

Open-pollinated seeds from 55 parent trees in the Upper Natone clonal seed orchard were collected for sowing in 1980. All of the selections were from local Tasmanian plantation, and the spacing trial was established in August 1981 at West Takone (about 41.15°S 145.15°E, in northwest Tasmania. The site had an annual rainfall of ca. 1500 mm and relatively high site quality.

The experiment was designed with four initial spacings as four independent blocks. Each spacing was sub-divided into five replications. 55 families were randomly arranged into each replication with four trees in each plot row. Four spacings were constructed as: 0.5 × 1 m (S0), 1 × 1 m (S1), 1 × 2 m (S2), and 2 × 3 m (S3), which were equivalent to about 20,000, 10,000, 5000, and 1667 trees per ha, respectively. However, most trees died in the S0 spacing at a relative early age, and so we measured and analysed only three spacing (S1, S2 and S3) in this study.

2.2. Data collection

Immediately following planting, and after the first five growing seasons, total tree height for all trees in three spacings was measured. Diameter at 0.3 m above ground was also measured for the first five growing years and diameter at 1.3 m (DBH_{all}, mm) in the tenth year after planting was also measured. A total of 1456 wood cores at breast height were collected at age 28 for further study of spacing effect on surviving trees. A total of 298, 419 and 739 surviving trees were sampled from S1, S2, and S3, respectively. The wood cores were polished before scanning to high quality images of 600 points per mm^2 for measuring annual growth ring width. Annual ring width (RW) was measured from pith to bark by the WinDENDRO® software (Regent Instruments Inc., 2001). Based on individual annual rings, a cumulative width from pith was calculated as diameter at breast height for sampled surviving trees (DBH_s). Because of the severe competition at late ages, particularly for S1 and S2, many sampled increment cores could only have effective measurements of ring width up to age 21 after planting even though the trials were 28 years old. For this reason the ring data only from ring 2 to 21 was used for current analyses. Except three families having one, two and three trees left at age 28, respectively, most families have 6–12 trees.

2.3. Statistical analysis

Summary statistics were computed using R software (R Version 2.15.1, 2012) and genetic analyses were conducted using ASReml 3.0 software (Gilmour et al., 2004). Response variables of diameter at 0.3 m and at breast height and height were analyzed separately using the following general linear mixed model with spacing and replication as fixed effects, and family and family by spacing interaction as random effects:

$$Y_{ijkl} = \mu + S_i + R_{(i)j} + F_k + SF_{ik} + e_{(ijk)l}$$