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Correlated response of pulpwood profit traits following differential fertilisation of a *Eucalyptus nitens* clonal trial

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Abstract

Silvicultural treatments that are aimed at increasing plantation growth rate may also impact directly or indirectly on wood properties. We examined this impact in a fertiliser × clone trial in northwestern Tasmania, Australia. Nitrogen (N) and phosphorus (P) fertilisers were applied at planting to three *Eucalyptus nitens* (Deane et Maiden) Maiden clones and one F_1 hybrid clone of *E. nitens* and *E. globulus* Labill. in a factorial design with each clone exposed to two levels of nitrogen (0 and 23 kg N/ha) and two levels of phosphorus (0 and 21 kg P/ha) spot-applied close to each seedling. The trial comprised four replicates per treatment with 5 × 5 tree clonal plots. Height was measured at ages one and two years, and diameter at breast height over bark at age 11 years. Increment cores at breast height were obtained from one fast- and one slow-growing ramet within each clonal plot to determine corewood basic density, near infrared-predicted kraft pulp yield, cellulose content, and extractives content. No significant interactions among main treatments were detected for any of the growth- or wood-property traits. Nitrogen application increased cellulose content ($p < 0.05$). Phosphorus application significantly increased diameter ($p < 0.01$), but resulted in lower wood density ($p < 0.001$). Within clonal plots, large trees had lower wood density ($p < 0.001$) and a higher extractives content ($p = 0.004$) than the corresponding small trees. Pulpwood production per hectare (calculated from plot volume, mean whole-tree adjusted density and mean plot kraft pulp yield) indicated that: (i) the choice of germplasm had a much larger effect on plantation profitability than did the starter fertiliser application; and (ii) that failure to account for adverse changes in wood properties in calculating pulp fibre production would result in over-estimation of the gain in pulp production due to starter phosphorus application by up to 0.6 t/ha or 20% per 12 year rotation.

Keywords: clone; *Eucalyptus nitens*; pulp yield; pulp productivity; wood density; growth; co-variation; nutrition.

Introduction

Eucalyptus nitens (Deane et Maiden) Maiden is an important hardwood plantation species in temperate countries such as Australia, New Zealand, Chile and South Africa (Eldridge et al., 1993). In Australia, Spain and Chile it is used instead of *Eucalyptus globulus* Labill. on colder sites (Tibbits et al., 1997), and while there is increasing interest in using *E. nitens* plantations for solid-wood production (Muñoz et al., 2005; Pinkard & Neilsen, 2003), the majority of stands are grown in 12 – 15 year rotations for kraft pulp production (Parsons

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& Gavran, 2005). Economic models developed for breeding purposes have shown that the major plant-based traits affecting kraft pulp production costs are: (i) growth rate (measured in terms of standing wood volume at harvest age); (ii) wood density; and (iii) the pulp yield as a percentage of dry weight (Greaves et al., 1997). Management decisions, such as choice of silvicultural regime or choice of planting stock, may change the value of one or more of these profit traits and have a marked effect on the cost of producing kraft pulp.

A key issue in the prediction of pulpwood production from plantations is whether the profit traits are independent or related in some way. Independence means that improvement in more than one trait may be attempted simultaneously. If they co-vary, traits will exhibit a correlated response following genetic selection or a silvicultural treatment, which may result in favourable or unfavourable changes in the non-target trait. Such co-variation may be due to genetic or environmental factors, the magnitude and direction of which are not necessarily similar. Their effects may, therefore, be confounded in observed phenotypic correlations (Falconer & Mackay, 1996). For breeding, deployment or silvicultural purposes, there is a need to understand, predict and account for such correlated responses among the traits affecting production costs (Gonçalves et al., 2004).

Traditionally, forest breeding and silviculture have focused on enhancement of growth rate. If the improvement of growth is accompanied by adverse genetic or environmental effects on wood density or pulp yield, the benefits of improved growth rate may be compromised. This possibility has been reviewed from both silvicultural (Zobel & van Buijtenen, 1989) and forest genetics standpoints (Zobel & Jett, 1995), and overall conclusions from hundreds of studies of conifers and hardwoods have been equivocal. Unfortunately, narrowing of the focus to the pulpwood production traits of eucalypts has not provided clarity where either wood density (Barrichelo et al., 2001; Gonçalves et al., 2004; Raymond & Muneri, 2000; Thomas et al., 2005; Wilkes, 1984; Wiseman et al., 2006) or pulp yield (Beadle et al., 1996; Little et al., 2003; Miranda et al., 2001; Vigneron et al., 1995) has been considered. In a review of silvicultural effects on the productivity and wood quality of eucalypt plantations, Gonçalves et al. (2004) concluded that there is no general correlation between growth rate and wood basic density in eucalypts and that fertiliser application has little or no effect on wood quality. They also noted that inconsistency in reported responses may be due to the confounding of environmental and genetic effects. They emphasised the importance of using clonal material in order to separate these effects in silvicultural trials.

We examined the growth and wood properties of three *E. nitens* clones and one *E. nitens* × *E. globulus* F_1 hybrid clone used in a fertiliser trial. We aimed to determine whether differences in individual-tree or whole-plot growth rates, as induced by: (i) fertiliser treatment; or (ii) non-genetic differences between ramets within treatment plots, were associated with adverse changes in the key kraft pulp wood properties of basic density and kraft pulp yield. We then examined the magnitude and the manner in which overall pulp production (the product of growth, basic density and kraft pulp yield) is distorted if basic density and pulp yield are assumed to be constant.

Methods

This study was based on a genotype × fertiliser trial at Hampshire (41° 16' S, 145° 45' E, 500 m elevation) in northwestern Tasmania, Australia. The trial was established by APPM (now Gunns Ltd) in 1994 on an ex-*Pinus radiata* (D.Don) plantation site. Mean annual rainfall is 1506 mm (Bureau of Meteorology, 2009) with a seasonal winter peak. Soil parent material is Tertiary basalt, and soil is classified as Oxisol (Soil Survey Staff, 1999) or Ferrosol (Isbell, 2002). Surface soils to 10 cm depth on a similar adjacent site are acidic with relatively high concentrations of total carbon (C), nitrogen (N) and phosphorus (P) but low concentrations of available (mineralisable) N (Wang et al., 1996) and low P availability due to high P-fixing potential (Mendham et al., 2002). Nowadays, when N and P availability is restricted for reasons such as these, common practice is to increase the concentration of N and P in the soil solution available to seedlings by applying fertiliser close to the seedling roots (Gonçalves et al., 2004).

The genetic material consisted of three *E. nitens* genotypes, one selected from each of three unrelated full-sib families, and one genotype from an unrelated *E. nitens* × *E. globulus* F_1 hybrid full-sib family. These genotypes were selected on the basis of their ability to be clonally multiplied, rather than for wood quality or growth traits They are not planted operationally. Two starter fertiliser treatments were used: (i) presence or absence of N applied as urea ($(NH_2)_2CO$; 50 kg/ha, 46 % N); and (ii) presence or absence of P applied as triple superphosphate (100 kg/ha, 21.1 % P, $Ca(H_2PO_4)_2$). Fertilisers were applied by depositing a measured dose into a slit in the soil on either side of each seedling, one month after planting. The experimental design was a four-genotype by two-N by two-P factorial with complete randomisation of the 16 treatments in each of four adjacent replicates (a total of 64 treatment plots). Each plot contained 25 ramets of the clone of one genotype arranged as 5 rows × 5 trees spaced at 3.3 m between and 2.65 m within rows. The stocking of 1140 stems/ha was typical of that used operationally by Gunns Ltd.

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Height of all trees was measured at ages one and two years. At age 11 years, stem diameter over bark at breast height (shortened to "diameter") (1.3 m above ground level), and tree status (alive, dead or missing) were recorded at all 25 sites in each plot. The inner nine trees per plot were ranked by diameter. Of these, both the tree with diameter nearest the 25th and the tree nearest the 75th percentile were selected for wood sampling. This sampling approach was intended to provide a systematic selection of trees that included a small and large ramet from within each plot. The diameter differences were substantial, had a non-genetic origin, and arose from microsite variability between planting positions, inter-tree competition, and/or nursery propagation effects. The height of each sampled tree was recorded.

Two 12 mm diameter bark-to-bark cores were taken with a motorised corer from each sample tree at heights of 0.9 and 1.0 m above ground level. Each core was immediately labelled, sealed in plastic film and refrigerated. Basic core density was determined from the 0.9 m sample using principles described for wood discs (Technical Association of the Pulp and Paper Industry, 1989), whereby the oven-dry weight (105 °C, 24 h) of each specimen is divided by the core green volume.

Wood core preparation for analysis of kraft pulp yield, cellulose and extractives content followed the method of Poke et al. (2004). Cores were dried, powdered and their near infra-red (NIR) spectra (wave numbers between 3 500 and 12 000/cm) obtained using a Bruker Optics Co. MPA spectrophotometer with resolution set at 8 waves/cm. Sixty-four scans were obtained from each sample and averaged. A generic kraft pulp calibration model based on 500 eucalypt standards (R^2 = 0.90) was used to predict kraft pulp yield from the sample spectra. This model has predicted pulp yield from other NIR data sets with an average R^2 of 0.75 (Downes et al., 2009). Models based on Tasmanian and mainland Australian *E. nitens* and *E. globulus* that had been developed by the Co-operative Research Centre for Forestry were used to predict the content of cellulose and the content of extractives. Calibrations had high R^2 values (cellulose 0.91; extractives 0.85). A sub-sample of the predicted values was selected (Workman, 1992) and analysed for cellulose (Wallis et al., 1997) and organic solvent extractives (Australian Pulp and Paper Industry Technical Association, 1994). The fit of predictive models to the laboratory values was high for extractives (R^2 = 0.91) and moderate for cellulose (R^2 = 0.75).

Tree basal area per plot (BA, m^2/ha) was calculated from the estimated ground area and tree diameters in the inner nine-tree plots. Mean plot height was estimated from the two 11-year tree height measurements per plot. A generalised volume function developed for *E. nitens* plantations in Tasmania (Candy, 1997) was used to calculate wood volume (m^3/ha) per plot. Although this function required stand basal area and mean dominant height (MDH) as inputs, the mean height of one dominant and one subdominant tree was considered to approach the desired sampling intensity for a nine-tree plot. Mean height was likely to have underestimated MDH, but there was no suggestion of bias in clone or treatment comparisons.

Pulp productivity ($PP_{Variable}$) was calculated for each plot as the product of: (i) wood volume/plot; (ii) core density adjusted to whole tree values (Raymond & Muneri, 2001); and (iii) the mean of the two plot pulp yield values. A control value for pulp productivity (PP_{Fixed}) was generated in the same way but with density and pulp yield fixed within each replicate and genotype to that of the N0P0 fertiliser treatment.

Statistical analysis

Univariate analyses of all traits were performed using a mixed model with Replicate, Genotype, N, P, size and their various interactions all treated as fixed effects. Random terms in the model were "Plot" (the Replicate × N × P × Genotype interaction) and "Residual". The "Plot" term was used as denominator to test fixed effects of variables in which size did not feature purely as a category (height at age one year, diameter, volume, $PP_{Variable}$, PP_{Fixed}). The "Residual" term was used to test the effects of variables (density, pulp yield, cellulose content, extractives content) in which size did feature purely as a category (Table 1). Restricted Maximum Likelihood (REML) mixed models were fitted using SAS PROC MIXED (Version 9.1, SAS Institute Inc.). Least squares means were calculated and the Tukey test was used to identify differences. Phenotypic Pearson correlations were calculated at the individual-tree level and at the "pooled within plot" level where the effects of N, P and genotype were removed in order to illustrate the effect of tree size on the phenotypic correlation. These correlations were calculated, and their significance tested, using the SAS PROC CORR calculation.

The volume of one plot (*E. nitens* Clone 3, N0P0) had a high residual (+3.5 × residual standard deviation). Removal of this value from the dataset reduced the mean volume of *E. nitens* Clone 3 by 6 m^3/ha; the mean volume for the N0 treatment by 2.8 m^3/ha; and the mean volume for the P0 treatment by 2.9 m^3/ha. The derived values $PP_{variable}$ and PP_{fixed} were affected by a similar proportion and the significance of the effect of P on volume, PP_{fixed} ($p < 0.01$), and $PP_{variable}$ ($p < 0.05$) was also increased ($p < 0.001$). Least square means (Table 2) are presented with the outlying data value removed.

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TABLE 1: F values and significance levels[1] of genotype, nitrogen (N), phosphorus (P), and size effects and their interactions on growth traits at age 1 and 11 years, and wood properties at age 11 years. Pulp production is calculated with variable ($PP_{Variable}$) and fixed (PP_{Fixed}) pulp yield and wood density values. The error term for the plot stratum is Replicate × N × P × genotype, and the error term for effects that include individual-tree size is the Residual.

Stratum	Source	df	Growth			Corewood properties			Derived properties		
			Height, age one (m)	Diameter (cm)	Density (kg/m³)	Pulp yield (%)	Cellulose (%)	Extractives (%)	Volume (m³/ha)	$PP_{Variable}$ (t/ha)	PP_{Fixed} (t/ha)
Rep	Replicate [2]	3									
Rep.Plot	N	1	0.4	2.0	3.6	2.6	5.6*	0.1	3.2	2.2	2.5
	P	1	28.1***	9.6**	14.9***	1.9	0.1	4.6*	16.8***	11.8***	13.3***
	Genotype	3	5.0*	24.6***	52.7***	11.1***	39.6***	28.6***	41.6***	40.3***	36.7***
	N×P	1	0.3	0.1	0.0	0.3	0.5	0.2	1.0	1.0	0.8
	N×Genotype	3	1.4	0.2	0.3	2.1	1.2	0.7	1.3	1.6	1.1
	P×Genotype	3	2.0	2.6	0.9	1.8	1.7	0.1	1.3	0.8	1.0
	N×P×Genotype	3	0.4	0.2	0.8	0.4	0.1	1.2	0.3	0.2	0.3
	Rep×N×P×Genotype	45[3]									
Rep.Plot.Tree	Size	1			14.2***	2.2	0.4	14.8***			
	N×Size	1			0.0	0.7	0.0	0.0			
	P×Size	1			0.6	3.1	1.0	0.0			
	Genotype×Size	3			1.1	1.6	0.4	0.4			
	N×P×Size	1			1.1	0.8	1.2	1.5			
	N×Genotype×Size	3			0.3	0.4	1.3	0.7			
	P×Genotype×Size	3			1.5	1.3	1.3	0.5			
	N×P×Genotype×Size	3			0.9	0.3	0.3	2.5			
	Residual	48[4]									
	Total	127									

*Note: Pulp production is calculated with density and pulp yield both variable ($PP_{variable}$) and fixed (PP_{fixed}). Error term for the plot stratum is rep*nitrogen*phosphorus*genotype, and error term for effects including size is the residual.*

*[1] Significance levels * p < 0.05; ** p < 0.01; *** p < 0.000*

[2] Rep fitted as a random term accounted for 3 denominator df

[3] 44 (down from 45) residual df for Volume, $PP_{variable}$, PP_{fixed} due to excluding one outlier of each

[4] 44 (down from 48) residual df for Pulp Yield, Cellulose and Extractives is due to 4 missing tree values

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Results

Site means

At 11 years of age, survival rate across the entire trial was 95%, mean over-bark stem diameter was 15.9 cm, and the mean volume across all genotypes was 93.8 m^3/ha. This was equivalent to a mean annual increment (MAI) of 8.5 m^3/ha/yr. Mean diameter, volume, and MAI of the *E. nitens* genotypes (excluding the hybrid ramets) were all approximately 10% higher than that of all trees including hybrid ramets (data not shown). For *E. nitens* genotypes alone, mean core density was 423 kg/m^3; predicted whole-tree density 450 kg/m^3; whole-tree pulp yield 52.2%; core cellulose content 39.7%; and core extractives content 3.9%. Average estimated pulp production ($PP_{Variable)}$ for these *E. nitens* genotypes was 22.6 t/ha, which equates to an annual pulp production of 2.1 t/ha.

Phenotypic and within-treatment associations

The relationships among growth traits and those among pulp yield and cellulose content were positive at both the phenotypic and within-treatment levels (Table 3). However, for most other variables the overall correlations were driven by treatment effects, with random environmental effects only apparent in the relationship between extractives and pulp yield or cellulose content.

Treatment effects on stem diameter and volume

Tree diameter varied between genotypes, responded to P input (Table 1), and provided a substantial range of growth rate differences with which wood-property responses could be compared. No significant interactions were detected among main effects in the fitted model for any growth or wood trait. Phosphorus fertiliser application ($p < 0.001$) and genotype ($p < 0.05$) affected height growth at age one year; and at age 11 years both genotype ($p < 0.001$) and P treatment ($p < 0.01$) affected diameter (Table 1). Application of P increased diameter at 11 years by an average of 1.0 cm (6.5%) and stem volume by 15.5 m^3/ha (18.0%). Increases in diameter (0.85 cm, 5.8%) and volume (6.8 m^3/ha, 7.5%) following N application were not statistically significant. At age 11 years, the mean diameter of each genotype ranged from 13.9 to 18.1 cm (Table 2), with values for the F_1 hybrid lower than any of those for *E. nitens* genotypes. Among the *E. nitens* genotypes, "*nitens 3*" had the largest diameter, and had produced 51% more volume than the other two clones. The mean diameters of trees selected at the 25 and 75 percentiles within plots were 14.1 and 18.1 cm respectively.

Treatment effects on core density

Genotype strongly affected core density ($p < 0.001$, Table 1). The density of the F_1 hybrid (460 kg/m^3) was higher than the mean (423 kg/m^3) for the three *E. nitens* genotypes (Table 2). There was a 16 kg/m^3 range between *E. nitens* genotypes. The positive response of diameter to fertiliser treatment (P and/or N) was associated with a decrease in wood density, but this was only statistically significant for P application ($p < 0.001$, Table 1) which reduced density by 10.5 kg/m^3 (Table 2). Within plots, the mean wood density in large trees was 8.5 kg/m^3 less (Table 2) than that in corresponding smaller trees ($p < 0.001$, Table 1).

The negative relationship between growth rate and core density detected at the environmental (P fertiliser and size) level was not apparent at the genetic level among the *E. nitens* genotypes, where trees of the largest clone had the highest density. However, the F_1 hybrid, which was the slowest-growing genotype, had the highest wood density.

Treatment effects on predicted pulp yield, cellulose and extractives content

The factor exerting the greatest effect on pulp yield and cellulose content (as predicted by NIR-spectroscopy) was genotype ($p < 0.001$, Table 1). Among the *E. nitens* genotypes, pulp yield ranged from 51.8 to 52.8 % (a difference of 10 kg pulp/t of oven dry wood) and cellulose content from 39.3% to 40.8% (Table 2). As with density, the *E. nitens* clone with the largest diameter had the highest pulp yield and cellulose content. Application of P fertiliser did not affect pulp yield or cellulose content. Treatment with N fertiliser significantly increased cellulose content from 39.7 to 40.0% ($p < 0.05$) but had no significant effect on pulp yield. Large and small trees in the same plot did not differ in terms of pulp yield or cellulose content (Table 2). Extractives content ranged from 3.3 to 4.3% among genotypes, increased with increasing diameter, and was lowest in the hybrid. Wood of larger trees had a higher extractives content (3.9%) than smaller trees (3.6%) from the same plot ($p = 0.004$). The P treatment resulted in a higher extractives content (3.8 versus 3.6%, $p = 0.02$).

Treatment effects on pulp production

Genotype had the greatest effect on pulp productivity ($PP_{Variable}$, $p < 0.001$). Genotype means ranged between 16.4 and 29.0 t/ha (Table 2), the F_1 hybrid having the lowest value. Within *E. nitens*, genotype differences accounted for a 60% range (18.1 – 29.0 t/ha). This was much larger than the differences due to P application, which increased pulp productivity by 15% (19.6 to 22.5 t/ha, $p = 0.001$). Treatment with N had no significant effect (Table 2).

In combination, N and P application increased PP_{Fixed} by 27% (18.5 to 22.8 t/ha) and $PP_{Variable}$ by 23%. The

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TABLE 2: Least square means for age 1 height and age 11 diameter, density, pulp yield, cellulose, extractives, volume, pulp production variable ($PP_{Variable}$) and fixed (PP_{Fixed}). Within a treatment class, means with common letters for the same trait are not significantly different at $p < 0.05$ using the Tukey-Kramer adjustment for multiple comparisons. Absence of suffix letter denotes no significant differences ($p > 0.05$).

Treatment	Level	Growth			Corewood properties			Derived properties		
		Height, age one (m)	Diameter (cm)	Density (kg/m^3)	Pulp yield (%)	Cellulose (%)	Extractives (%)	Volume (m^3/ha)	$PP_{Variable}$ (t/ha)	PP_{Fixed} (t/ha)
Genotype	F_1 hybrid	0.45 c	3.9 c	460 a	51.7 c	40.1 b	3.3 c	68.9 d	16.4 c	16.2 c
	nitens 1	0.55 a	15.8 b	415 c	52.1 b	39.3 c	3.9 b	84.1 c	18.1 c	18.6 bc
	nitens 2	0.48 ab	15.6 b	423 c	51.8 c	39.1 c	3.5 c	94.9 b	20.8 b	21.1 b
	nitens 3	0.51 ab	18.1 a	431 b	52.8 a	40.8 a	4.3 a	127.3 a	29.0 a	29.8 a
Nitrogen	nil	0.50	15.4	435	52.0	39.7 b	3.7	90.4	20.4	20.7
(N, kg/ha)	23.0	0.51	16.3	430	52.2	40.0 a	3.7	97.2	21.7	22.2
Phosphorus	nil	0.45 b	15.3 b	438 a	52.0	39.8	3.6 a	86.1 b	19.6 b	19.7 b
(P, kg/ha)	21.1	0.56 a	16.3 a	427 b	52.2	39.9	3.8 b	101.6 a	22.5 a	23.2 a
Size	Small		14.1	437 a	52.0	39.9	3.6 a			
	Large		18.1	428 b	52.2	39.8	3.9 b			
Means	All trees	0.50	15.9	432	52.1	39.8	3.8	93.8	21.1	21.4
	E. nitens	0.51	16.5	423	52.2	39.7	3.9	102.1	22.6	23.2

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TABLE 3: Pearson Correlation Coefficients (below diagonal) and mean of correlation coefficients for each Clone×N×P×size treatment (above diagonal); and the significance of differences of correlations from zero using the Students *t* test (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$) to compare growth, wood density and chemistry traits.

Trait	n	Height (age one year)	Height (age two years)	Diameter	Density	Pulp Yield	Cellulose	Extractives
Height, age one year	561		0.77***	0.39***	-0.09	-0.01	0.09	0.12
Height, age two years	548	0.80***		0.41***	-0.15	0.03	0.16	0.10
Diameter	546	0.51***	0.64***		-0.15	0.03	0.13	0.11
Density	128	-0.40***	-0.31***	-0.40***		-0.02	-0.10	0.07
Pulp Yield	124 [1]	0.15	0.19	0.32***	-0.17		0.64***	-0.32**
Cellulose	124 [1]	0.00	0.20*	0.21*	0.21*	0.60***		-0.47***
Extractives	124 [1]	0.36***	0.42***	0.55***	-0.32***	0.21*	0.05	

[1] Four missing values for wood chemical data

smaller $PP_{Variable}$ response was expected as it was associated with the negative response of wood density to fertiliser application described above. Values for PP_{Fixed} over-estimated those for $PP_{Variable}$ by 0.2 t/ha in response to N, and by 0.6 t/ha in response to P. While these are small absolute differences, they represent up to 20% of the total response.

Discussion

Growth

The response of plantation growth to a starter application of N and P must be regarded as site-specific because it is dependent on factors including fertility, previous management, and climate (Mendham et al., 2002). A response to starter fertiliser can be expected for *E. nitens* grown on ex-forest sites in northwestern Tasmania (Smethurst et al., 2003), and was observed in the present study. If a site is likely to provide a response to starter fertiliser, the effect on growth is usually detectable within one or two years (Cromer et al., 2002; du Toit et al., 2001; Mendham et al., 2002). In the present study, height responses to starter P were evident at age one year and ranking in diameter growth was maintained to age 11 years without addition of extra fertiliser. The 15.5 m^3/ha gain in wood volume at age 11 years due to application of 21 kg/ha of starter P is a relatively large response to this dose rate (Smethurst et al., 2001). Early genotype differences (age two years, data not shown) in diameter and volume were still evident at age 11 years, the largest *E. nitens* genotype producing an additional 43.2 m^3/ha of stemwood. These substantial responses to fertiliser treatment provided unambiguous growth contrasts and an ideal basis for investigation of associated wood properties.

Density

In contrast to general experience with eucalypts (Gonçalves et al., 2004), we found a significant negative relationship between growth rate and wood density where growth rate was influenced by fertiliser application or by variable growth among ramets of the same genotype within the same plot. Few other studies of the effects of fertiliser on *E. nitens* wood properties at the 'within-site' level have been reported. Wiseman et al. (2006) measured basic wood density in nine-year-old *E. nitens* that had received heavy dressings of fertiliser at ages one, two, three and four years (total N = 900 kg/ha; total P = 150 kg/ha), and had been pruned at age five years. They reported that fertiliser treatment had no effect on diameter or on wood density. Smethurst et al. (2003) reported that heavy N application (total N = 1600 kg/ha applied over several years) increased basic wood density in five paired diameter classes of *E. nitens*, but no statistical tests were presented. Studies of the related, and

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more widely-planted, *E. globulus* are more common. Raymond and Muneri (2000) reported a negative effect of starter N and P fertilisers on basic wood density and also on predicted pulp yield in the absence of a growth response. Mid-rotation fertiliser treatment decreased wood density of *E. globulus*, with little or no change in growth rate (Muneri et al., 2007). The significant effect of irrigation on wood properties of similar-sized trees reported by Downes et al. (2006) suggests that wood-property responses may be independent of growth response to silvicultural treatment.

Reported responses of subtropical and tropical eucalypts to fertiliser treatment also differ from our results. Application of fertiliser increased both growth and wood density in clones derived from hybrids among *E. albens*, *E. grandis* and *E. urophylla* in the Congo (Vigneron et al., 1995), *Eucalyptus grandis* in South Africa (du Toit et al., 2001), and in seedling-derived trees of *E. grandis* grown in tropical Australia (Cromer et al., 1998). Gonçalves et al. (2004) speculated that fertiliser treatment increases wood density if water is available to promote growth during the development of dense latewood, but may decrease it or have no effect if water availability limits latewood development. It is possible that the difference between these and our results is due to temperature and rainfall effects on growth dynamics or to the timing of fertiliser application. In our study, fertiliser was applied only at time of planting. Better understanding of the response to fertiliser treatment might have been gained from examination of wood density at an earlier age.

The negative environmental association between diameter and wood density observed in our trial is consistent with negative correlations reported for *E. nitens* in a review by Hamilton and Potts (2008). Genetic correlation (r_g) between diameter and directly measured wood density in ten studies averaged -0.27. The estimated genetic correlation between diameter and an indirect measure of wood density[1] was also negative, averaging 0.49 across six trials. The large difference in wood density among our *E. nitens* genotypes is consistent with the significant within-population variation in wood density reported for this species (Tibbits & Hodge, 1998). On the other hand the specific relationship between growth and wood density observed between three *E. nitens* genotypes in the present study was positive. This may well reflect the small number of genotypes used in our trial. *Eucalyptus nitens* has a lower basic wood density than *E. globulus*, and values for their F_1 hybrid are typically intermediate between the parents (Potts & Dungey, 2004; Tibbits et al., 1995). Our trial did not include *E. globulus* controls, but wood density of the single hybrid genotype was 39 kg/m^3 greater than the average for the *E. nitens* genotypes. This is consistent with the 24kg/m^3 difference between *E. nitens* and F1 hybrids reported by Tibbits et al. (1995).

Pulp yield

Genotype was the only factor that affected pulp yield in the present trial. Genotypic differences in pulp yield observed between our *E. nitens* clones add to the evidence of relatively strong genetic control previously reported for this trait (Tibbits & Hodge, 1998). Our finding that pulp yield is not affected by environmentally induced changes in growth rate agrees with observations from two other studies. The first concerned *E. nitens* in South Africa, where a 70% increase in volume growth across an environmental gradient did not affect pulp yield although wood density was increased by 14% (Clarke, 2000). In the second study, Little et al. (2003) demonstrated that pulp yield of eucalypt hybrid clones at age six years was not influenced by various weeding treatments even though volume growth was increased by 67% compared with an unweeded control. Our study and the previous ones indicate that pulp yield appears to be less sensitive than wood density to environmental conditions, silviculture, and competition from other plants, all of which affect growth. In other species, site and silvicultural factors influencing growth rate have been reported to affect pulp yield also, but the nature of the relationship varies. A pulp yield response to environmental variations (such as nutrients or water) may even occur in the absence of a growth response. For example, in the rain-fed *E. globulus* fertiliser trial described by Raymond and Muneri (2000), pulp yield declined in response to combined N and P application at three of the four sites studied. Yet, at two of these sites no diameter response was detected in sampled trees. Downes et al. (2006) specifically sampled same-sized trees from irrigated and non-irrigated plots and found pulp yield to be increased by irrigation. This was due to an increase in the proportion of latewood, which had a higher cellulose content than the earlywood. The positive relationship observed between pulp yield and soil clay content (and thus water retention and availability) in a clone of *E. grandis* (Gava & Gonçalves, 2008) may have been due to a similar process. Beadle et al. (1996) reported that pulp yield of *E. nitens* declined with increasing altitude in the absence of a growth response.

Extractives

The observed range in the extractives content of breast-height corewood (3.3 – 4.3 %) is consistent with values reported for 14-year-old *E. nitens* and nine-year-old *E. globulus* (Miranda & Pereira, 2002). In the present trial, the extractives content increased in response to P fertiliser application, larger trees having higher values than small trees. Large genotypes also had a higher extractives content than small genotypes. These observations point to a relationship with tree growth rate. They agree with the results of Gominho and Pereira (2005) which clearly showed that the extractives content of *E. globulus* is proportional

[1] Assessed using pilodyn penetration, where penetration increases with decreasing wood density.

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to heartwood content, and that both are positively correlated with tree size. Whether tree size has an effect on the extractives content of the heartwood per se (e.g. Wilkes, 1984) would require separate analysis of sapwood and heartwood.

Pulp production

Genotype was the factor that had the greatest influence on pulp production. The F_1 hybrid produced least pulp per hectare due to its poor growth. The *E. nitens* genotypes differed markedly, the most productive of the three (*nitens* 3) yielding 60% more pulp per hectare than the least productive one (*nitens* 1). This is a much greater response than the 6 and 13% increase associated with N and P fertiliser applied separately, and the 23% increase due to their combined effect. Previous studies of fertiliser treatment in *E. nitens* plantations (Pallett & Sale, 2004; Smethurst et al., 2003) have focused on growth, total biomass or fibre production, and have not investigated co-varying effects on wood properties. In the present trial, the negative effect of fertiliser on wood density was more than offset by the increase in growth, so the starter P treatment still showed an increase in pulp production.

Failure to take account of the negative response of wood density to fertiliser application would have over-estimated pulp production in 11-year-old trees by up to 0.6 t/ha (20%). Using a similar analysis, Miranda and Pereira (2002) found that failure to acknowledge a known positive correlation between pulp yield and growth in three *E. globulus* provenances resulted in underestimation of the variability in pulp production. This genetic effect would have existed among the *E. nitens* genotypes in the present study.

Conclusion

In this trial with *E. nitens*, growth rate, followed by wood density, were the profit traits most strongly influenced by genotype and starter fertiliser treatment. Pulp yield was not responsive to the environmental drivers of growth. Genotype had a greater effect than fertiliser treatment on harvest-age (11 y) wood properties, the fastest-growing *E. nitens* genotype (*nitens 3*) having the most desirable wood density. Non-genetic factors that increased growth rate tended to reduce wood density but had little impact on pulp yield. The consistency of this negative co-variation between growth rate and wood density at several levels suggests a common underlying mechanism. The response may be typical of *E. nitens*, but is at odds with that observed in other eucalypts, especially those of subtropical origin. When calculating an increase in pulp production due to fertiliser treatment of *E. nitens*, overestimation of the gain by up to 20% is likely if the associated change in wood density is ignored.

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