Genetic control of growth and wood density of *Eucalyptus pellita x urophylla* hybrid families under two nutrient conditions

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Abstract

A controlled crossing experiment by using factorial mating design was conducted at Wanagama Forest Research Station Yogyakarta to develop *E. pellita* x *urophylla* hybrid. Genetic materials derived from this experiment were used to establish progeny trials to evaluate genotype responses to contrasting nutrient conditions and to predict genetic control on growth and wood density of *E. pellita* x *urophylla* hybrid. Restricted maximum likelihood (REML) method was employed to predict variance components. Predicted variance components were then used to calculate genetic parameters i.e. the narrow sense heritability (h^2), proportion of the dominance (d^2), and the proportion of female additive variance from total additive variance (A_F/A). Growth and wood density appear to be under low to moderate genetic control both under low and high nutrient condition. Relative contribution of the additive and the dominance genetic effect on growth is affected by growth stages and nutrient conditions. Under low nutrient condition, all traits are under additive genetic controls except for height at 66 months. Whilst under high nutrient condition, contribution of the dominance genetic effect at juvenile stage becomes stronger than those under low nutrient condition. Dominance genetic effect is relatively more important than the additive genetic effect at 12 months. Both under high and low nutrient condition female additive effect are relatively more important than male effects. At older stage, contribution of the additive genetic effect on growth is more important than dominance genetic effect. Proportion of the genetic variance of wood density is solely attributable to the additive genetic both under low and high nutrient conditions. The additive variance on wood density is solely attributable to the female parents. There is a strong nutrient by genotype interaction on growth and wood density. Genotypes can be categorized into four groups based on their response to nutrient conditions i.e.: (i) Adaptive genotypes that are superior both under high and low nutrient conditions; (ii) High nutrient demanding genotypes that are superior under high nutrient conditions; (iii) Low nutrient demanding genotypes that are superior under low nutrient conditions; and (iv) Genotypes that are always inferior both under high and low nutrient condition.

Key Words
Additive variance, controlled crossing, dominance variance, factorial mating design, restricted maximum likelihood.

Introduction

The global trend toward plantation forest has been driven by two major forces – economic and environment. It is widely recognized that plantation forest is more productive than natural forest and provides higher economic benefits as experienced in many places (Sedjo, 2001). Government of Indonesia has stated that planted forest should supply all wood for forest industries by 2010 and targeted five millions of planted forest by 2009. Acacia and Eucalypts have become the most important tree species grown in commercial plantation to meet the demand of pulp and paper industries in Indonesia. A varied number of Eucalypts species and provenance and the unique ability to hybridize have led to development of many commercial hybrid breeds (Martin, 1989). Maximizing yield per hectare is increasingly important to sustain wood supply and to reduce the unit cost of wood. To maximize plantation production, improved genetic planting stock should be managed under intensive silviculture regime. Breeding strategies of Eucalypts to increase yield and wood properties have been implemented successfully in many places including Portugal (Boralho et al., 1992), Chile (Arnold et al., 1991), Brazil (Campinos and Ikemori, 1988), Spain and China (Eldrige et al., 1993), Congo (Vigneron et al., 2000), South Africa (Verryn, 2000) and Indonesia (Mulawarman et al., 2001). Although hybrid has been used extensively, many questions regarding both genetic basis of hybrid superiority and the most appropriate breeding methods to produce better hybrid remain unanswered because of insufficient information (Dieter et al., 1995). An effective hybrid breeding program depends on reliable genetic parameter estimates including additive and dominance variances, heritability, and genetic correlation (Gwaze et al., 2000).

Planted forests are frequently established on marginal soils where nutrients such as nitrogen, phosphorus, and potassium are among the growth limiting factors. Supplementary fertilizers are required in such sites to ensure desired growth. Considering the economic aspects of fertilization, screening genotypes that are able to synthesize maximum biomass for each unit nutrient absorbed is of importance (Clarkson and Hanson, 1980). Consequently, information regarding genetic difference in response to nutrition condition is valuable in increasing productivity of planted forest. In the advance cycle of selection, breeders tend to move away from the approach of breeding genotypes which grow well across a broad range of different sites (general performer). To improve the gain further, breeders will probably concern with identifying genotype which grow well in certain silvicultural regime – nutrient, weed control etc. (Matheson and Cotterill, 1990). When genotypes are grown in several environments, some show stable performance or genotypes are unresponsive to the change of environments. Other genotypes show improvement in better environment (Owino, 1997). This paper discusses the genetic control on growth and wood density of *E. pellita* hybrid families and evaluates performance of genotypes in two nutrient conditions.

Material and Methods

Genetic material

Genetic materials were derived from a controlled crossing experiment at Wanagama Forest Research Station using a factorial mating design conducted in February 1999. Parents were randomly selected from progeny test for controlled pollination. Nine female parents of *E. pellita* were pollinated by 5 male parents of *E. urophylla* and 4 male parent of *E. deglupta*. Not all crossings successfully produced seeds. Forty eight families – 37 families of *E. pellita* x *urophylla*, 4 families of *E. pellita x deglupta* and 7 open pollinated families derived from the same female parents – were tested in this experiment. Identity of families that are included in the trials is listed in Table 1. Since only a few *E. pellita* and *E. pellita x deglupta* included in the trial, they were excluded in genetic control analysis. Seeds were germinated in green house in September 1999 and transplanted into polybag that were filled with top soil. Seedlings were planted in the field 12 weeks after transplanting.

Table 1. Crossings and corresponding family identity that are included in the trials

Female	Male								
	Open pollination	EU01	EU02	EU03	EU04	EU05	ED02	ED03	ED05
EP01	1	2		3	4				
EP10	5		6	7	8		9		
EP11		10	11	12	13				
EP12	14	15	16	17	18	19			
EP14			20	21		22			
EP15	23	24	25	26	27	28			
EP16	29		30	31	32	33			
EP17	34	35	36	37	38	39			
EP18	40	41	42	43	44	45	46	47	48

Note: EP, EU, ED is *Eucalyptus pellita*, *Eucalyptus urophylla*, and *Eucalyptus deglupta* respectively

Field trial

Progeny trials were established in two adjacent sites in Wanagama Forest Research Station, Yogyakarta, Indonesia (7°48' S and 110°34' E) in December 1999. Both sites have similar biophysical conditions and have been used for cassava by local people for many years without fertilizer applications. The sites are situated 150 – 200 m above sea level and 3-8° slope with north aspect. The climate is tropical with 6 rain months and an annual rainfall of about 1500 mm of which most falls between November and April. The soil is lithosol that is derived from limestone parent material with depleted nutrient condition (FONC, 1986). Progeny trials were established in two nutrient

conditions – without fertilizer and with application of 100 kg N, 50 kg P_2O_5, and 50 kg K_20 per hectare. The low nutrient condition was assigned to the first site and the high nutrient condition to the second site. A row-column design with 6 replicates was used for each site. Forty eight families were randomized in 6 replicates. Two trees for each family were planted in a line plot at a spacing of 3 m by 3 m. Tree height and basal stem diameter were measured at 6 and 12 months. Height was measured to the nearest 0.1 cm by using scaling stick and basal diameter was measured to the nearest 0.01 cm by using caliper. Height and diameter at breast height were assessed at the age of 66 months. Height was measured by hypsometer and diameter by using diameter tape. Wood core samples for wood density determination were taken at the age of 66 months by using 1 cm bits bore. Wood volume was calculated by the following equation:

$$V = \pi\ f\,(d/200)^2\,h$$

in which π, V, f, d, h is constant number (3.142857), wood volume (m^3), form factor (0.40), stem diameter (cm), and tree height (m) respectively.

Statistical analysis

Though the trials were using row-column design, their effects were not significant. Thus row and column effect were excluded from analysis. The effect of female, male and female by male interaction on the measurements (y) was tested using the following generalised linear mixed model:

$$y = \mu + rep + plot + female + male + female.male + e$$

in which y is the measurement of individual tree, μ is the overall mean; *rep* is the fixed effect of the replicates; *female* is the random effect of female parent with null expectation and variance σ_F; *male* is the random effect of the male parent with null expectation and variance σ_M; *female.male* is the random effect of female by male interaction with null expectation and variance σ_{FM}; and e is the random effect of error term with null expectation and variance σ_e. The date set is unbalance because of failure in producing seed in several crosses. Thus restricted maximum likelihood (REML) method was used to estimate the variance components because it provides best, linear, and unbiased predictor (Corbeil and Searle, 1976). Under the assumption that the populations are sampled at random, and there is no inbreeding and epistasis effects, the general combining ability variance (σ^2_F and σ^2_M) is one-fourth of the total additive variance (¼ σ^2_A) and the specific combining ability variance (σ^2_{FM}) is one-forth of the total non additive (dominance) variance (¼ σ^2_D) as described by Backer (1992). The following formulae were used to calculate the genetic parameters – narrow sense of heritability (h^2), proportion of dominance (d^2) and proportion of female additive from total additive variance (A_F/A). ASReml Release 2.0 was used to predict the variance component and the genetic parameters (Gilmour et. al., 2006).

$$\sigma^2_F = ¼\ \sigma^2_{AF};\ \ \sigma^2_M = ¼\ \sigma^2_{AM};\ \ \sigma^2_A = 2\ (\sigma^2_F + \sigma^2_M);\ \sigma^2_{FM} = ¼\ \sigma^2_D;\ A_F/A = \sigma^2_{AF}/\sigma^2_A$$

$$h^2 = (\sigma^2_A)/(\sigma^2_F + \sigma^2_M + \sigma^2_E + \sigma^2_E);\ \ d^2 = (\sigma^2_D)/(\sigma^2_F + \sigma^2_M + \sigma^2_E + \sigma^2_E)$$

Results and Discussion

Trend in genetic control under different nutrient condition

Growth and wood density appear to be under low to moderate genetic control both under low and high nutrient condition. However, relative contribution of the additive and the dominance genetic effect on growth is affected by growth stages and nutrient conditions (Table 2 and 3). There is a slight change in variance structure as affected by age and nutrient condition. Under low nutrient condition (Table 2), proportion of the genetic variance at juvenile stage (6 -12 months) is solely attributable to the additive genetic effect. Female additive effect contributed 82 % - 100 % of the additive variance. Relative contribution of the dominance genetic effect becomes more important at older stages (66 months) where dominance variance contributes mainly to the genetic variance of height. Male additive effect is also more important at older stage which contributes 61 % and 62 % of additive genetic variation of diameter and volume respectively. Genetic variance in wood density is also solely attributable to the additive variance.

Under high nutrient condition (Table 3), contribution of the dominance genetic effect appear to be stronger than those at low nutrient condition, particularly at 12 months in which the dominance genetic effect is relatively more important than the additive genetic effect. At juvenile stage (6 – 12 months), the dominance variance contributes 45 % to 69 % of the genetic variance. Relative contribution of the additive variance becomes more important at older stages (66 months) where additive variance contribute solely to the genetic variance of growth. As observed in low nutrient condition, male additive effect solely contributes to additive genetic variance. Genetic variance of wood density is solely attributable to additive variance in which the female additive variance contributes 94 % of the variance.

Table 2. Mean and genetic control on growth and wood density under low nutrient condition

Traits	Mean	h^2	d^2	A_F/A	Genetic effect
		6 months			
Height (cm)	75.2 (23.4)	0.19 (0.15)	0.00 (0.00)	1.00 (0.00)	Female additive
Diameter (cm)	0.53 (0.18)	0.24(0.16)	0.00 (0.00)	0.82 (0.28)	Female additive
		12 months			
Height (cm)	134.1 (104.5)	0.13 (0.11)	0.00 (0.00)	1.00 (0.00)	Female additive
Diameter (cm)	1.54 (0.77)	0.33 (0.22)	0.00 (0.00)	1.00 (0.00)	Female additive
		66 months			

Height (m)	16.9 (4.9)	0.01 (0.10)	0.06 (0.17)	1.00 (0.00)	dominance
Diameter (cm)	11.8 (4.0)	0.05 (0.10)	0.00 (0.00)	0.39 (1.20)	Male additive
Volume (m^3)	0.093 (0.076)	0.06 (0.11)	0.00 (0.00)	0.38 (0.94)	Male additive
Wood density (kg m^{-3})	529 (51)	0.33 (0.26)	0.00 (0.00)	1.00 (0.00)	Female additive

Note: figures in bracket are the standard error, h^2 = narrow sense heritability, d^2 = proportion of dominance, A_F/A = proportion of female from additive variance,

Table 3. Predicted mean and genetic control on growth and wood density under high nutrient condition

Traits	Mean	h^2	d^2	A_F/A	Genetic effect
		6 months			
Height (cm)	118.9 (41.6)	0.16 (0.15)	0.15 (0.15)	1.00 (0.00)	Female additive
Diameter (cm)	1.02 (0.39)	0.11 (0.12)	0.09(0.13)	1.00 (0.00)	Female additive
		12 months			
Height (cm)	206 (85.5)	0.08(0.11)	0.13 (0.15)	1.00 (0.00)	Dominance
Diameter (cm)	2.73 (1.32)	0.08 (0.12)	0.18 (0.16)	1.00 (0.00)	Dominance
		66 months			
Height (m)	18.4 (3.9)	0.05 (0.10)	0.00 (0.00)	0.97 (1.00)	Female additive
Diameter (cm)	13.4 (4.2)	0.10 (0.11)	0.00 (0.00)	0.00 (0.00)	Male additive
Volume (m^3)	0.124 (0.086)	0.13 (0.13)	0.00 (0.00)	0.00 (0.00)	Male additive
Wood density (kg m^{-3})	535 (52)	0.18 (0.20)	0.00 (0.00)	0.94(0.47)	Female additive

Note: figures in bracket are the standard error, h^2 = narrow sense heritability, d^2 = proportion of dominance, A_F/A = proportion of female from additive variance,

The relative importance of additive effect over the dominance effect is also reported for *E. urophylla x pellita* and *E. urophylla x grandis* (Bouvet and Vigneron, 1996 and Vigneron et al., 2000). They reported that additive variance represents 80 % of the genetic variance in *E. urophylla xgrandis* and only 40 % in *E. urophylla x pellita*.male. They also reported that additive effect was less importance than female additive effect. Volker (1995) also reported similar result in *E. nitens x globulus* and other pure species (*E. globulus* and *E. nitens*). These trials also showed that more additive variation could be exploited for wood density than for growth. In *Eucalyptus globulus*, more additive variation can be exploited for growth (11%) than for wood (<9%) as reported by Apioloza et al. (2005). It is difficult to predict hybrid performance from their parental performance even though the level of dominance is relatively low as reported by Volker (1995) in *E. nitens x globules.* This is in contrast with hybridization in tropical pines where hybrid performance can be predicted from their parental performance since there is a good correlation between parental performance (general combining ability) and hybrid performance (general hybridizing ability) as reported by Dieters et al. (1995).

Genotypes response to nutrient conditions

Eucalypts is highly responsive to nutrient condition. Growth at high nutrient condition is better than those at low nutrient condition ($p < 0.001$ for all traits), however, no difference in wood density as the effect of nutrient condition ($p = 0.459$) as shown in Table 1 and 2. Similar result was also reported by Vigneron et al. (1995) who found that for a given genotype, more intensive fertilization lead to an increase of growth and wood density of Eucalypt hybrids. Since growth does not affect pulp quality adversely, it is recommended that pulpwood plantation should be worked on shorter rotation with accelerated tree growths (Varghese et al., 1995). Even though growth and wood density are under moderate genetic control, there is no correlation between wood density and volume (Figure 3) as also reported in other Eucalypts (Raymond, 1995 and Apioloza et al., 2005). Wood quality parameters were found to depend weakly on environment, genetic origin, or silviculture thus allowing a growth enhancement management without negatively influencing wood properties (Pereira et al. 1995).

Genotypes perform differently at different nutrient conditions, implying significant effect of genotype by nutrient interaction (Table 4, Figure 1 and 2). This phenomenon is obvious for growth wood density traits. There was no correlation between the ranks under low nutrient condition and those under high nutrient conditions for wood density. Whilst for wood volume, although performance of the genotypes changed as nutrient conditions was altered, there was still a positive correlation between the ranks of wood volume under low nutrient condition and those under high nutrient conditions (Spearman rank correlation (Rs) = 0.43, $p = 0.003$). This result indicates consistent performance of some genotypes and significant change of rank for other genotypes. Some genotypes are not responsive to the change in nutrient condition whilst others are responsive. Genotypes can be categorized into four groups based on their response to nutrient conditions i.e.: (i) Adaptive genotypes that are superior both under high and low nutrient conditions (families 25, 26, 30, 39 and 45); (ii) High nutrient demanding genotypes that are superior under high nutrient conditions (family 42); (iii) Low nutrient demanding genotypes that are superior under low nutrient conditions (families 28, 6, and 19); and (iv) Genotypes that are always inferior both under high and low nutrient condition (familes 8, 1, 7 47 and 13). There are hybrid families which show better performance than *E. pellita* derived from the same female parent, but not consistent for all female parents.

Table 4. Significance of interaction effects

Random effects	Component variance – standard error ratio							
	6 months		12 months		66 months			
	Height	Basal Diameter	Height	Basal Diameter	Height	DBH	Volume	Wood density
Nutrient*Male	0.00	0.00	0.25	0.00	0.00	0.83	0.92	0.00
Nutrient*Female	1.17	1.10	1.32	1.13	0.57	0.66	0.65	1.29
Nutrient*Female*Male	1.81	1.61	0.31	1.57	0.00	0.03	0.25	0.00

Note: Component variance – standard error ratio > 1.00 shows significant effect of random effect

For traits that are significantly affected by genotype x environment interaction, there is a possible inversion of the ranking of genotype from one nutrient regime to the other. It is important to pay attention to those variables. There are two alternatives to solve the problem: to find genotypes which perform well in a wide range of sites or to select genotypes specifically adapted to each type of site (Van Buijtenen, 1992). Growth differences among genotypes in response to nutrient condition indicate the benefit of genetic selection in optimizing site productivity. Genotype selection should consider nutrient condition or site quality (Chang, 2003). Identification of genotypes that grow well under specific nutrient regime is very important to improve stand production (Matheson and Cotterill, 1990). Screening genotypes for specific nutrient regime results proper balance between soil input and tree adaptability. Thus lower nutrient input and higher utilization of nutrient input can be implemented to maintain desired productivity (Clark, 1982). Adaptive genotypes can be established in wide range of nutrient conditions; however, their best performance will be under an intensive fertilization regime. High nutrient demanding genotypes are responsive to fertilization, thus suitable for intensive fertilization regime or good sites, while low nutrient demanding genotypes are superior under low fertilization regime and adaptive to marginal soil where nutrient availability is low. Genotypes that are poor performer both under low and high nutrient condition should not be deployed. Good performing genotypes generally have high nutrient use efficiency resulting from efficient root absorption, which enables them to absorb more nutrients (Mulawarman, 2004).

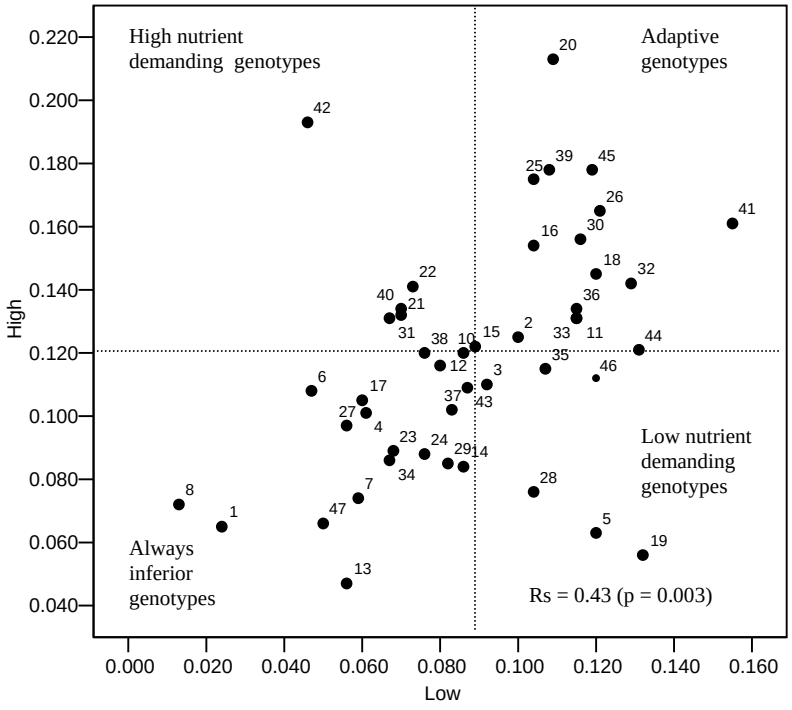

Figure 1. Predicted wood volume (m^3) of the families under low and high nutrient conditions

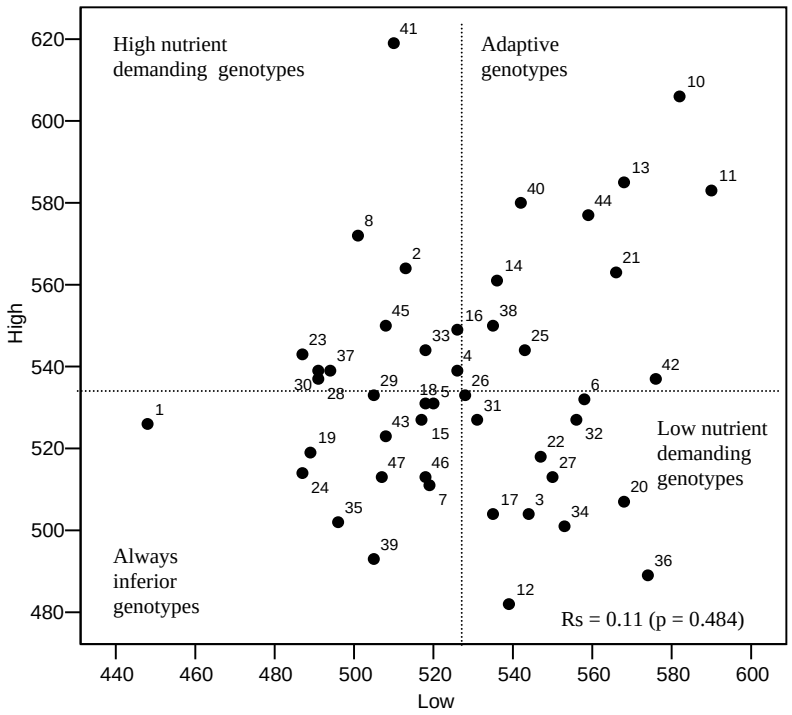

Figure 2. Predicted wood density (kg m^{-3}) of the families under low and high nutrient conditions

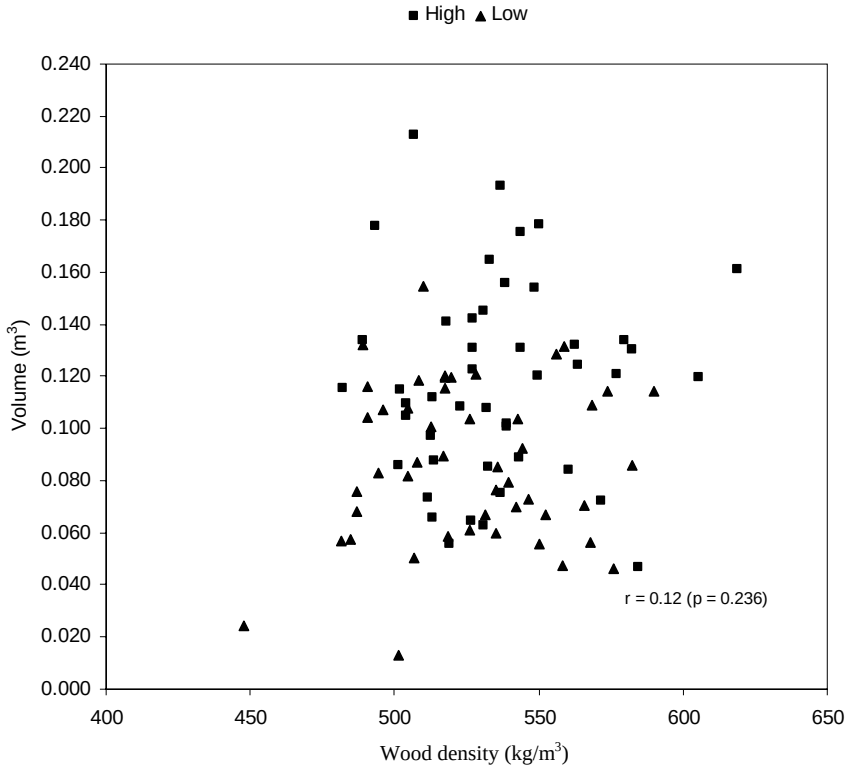

Figure 3. Family correlation between predicted volume and wood density at 66 month

Conclusion and Practical Implication

There are hybrid families which show good performance; however, hybrid performance is not predictable from parental performance in pure species even though the level of dominance is relatively low. Thus it is worth spending more effort on producing the hybrid rather than selecting the parents to be hybridized. All hybrid combinations need to be tested to find those crosses that are likely to produce outstanding individuals.

The difference in response to nutrient condition as shown in this study indicates the benefit of selecting genotype for specific nutrient regime. Nutrient problems in planted forest should not be solved exclusively by soil amendment as has been done previously. Selection should not focus only on general performing genotypes. Screening genotype for fertilization regime is important to optimize site productivity and maximize economic return of fertilization. The underlying processes that contribute to the differences in response to nutrient condition should be well understood. It is worth studying whether the genetic difference in response to nutrient condition is also expressed in genetic variation in nutrient use efficiency.

The dominance effect can be captured to improve growth by applying intensive fertilization. Fertilizer should be applied at 12 months to carry over the increasing growth up to mid rotation. This approach can lead to shorter rotation.

Acknowledgement

Authors wish to express gratitude to the field staffs of Wanagama Forest Research Station for their assistance in establishing, maintaining the trials and carrying out measurements and taking core sample, to Agus Kurnia and his staffs in Riaufiber Wood Technology Laboratory for determination of wood density. Authors would also like to extend the gratitude to G.D. Golani, Director of Riaufiber R&D and the management of Riaufiber for supporting the main author to attend the “Australasian Forest Genetic Conference (AFGC)” held on 11-14 April 2007 in Hobart, Tasmania. Last but not least, authors would also like to thank the organizing AFGC committee for allowing the authors to present this paper.

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