

# Genotype-environment interaction in wood basic density of *Eucalyptus* clones

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**Summary** Wood basic density was determined in samples taken from eight-year-old trees of 26 *Eucalyptus* clones growing in tests at four sites in Brazil. Within-clone variation in basic density was low. The broad sense heritability of basic density was 0.96 when estimated from five clones growing on two sites and 0.64 when estimated from 26 clones on four sites. Analysis of variance showed that there were significant differences in basic density between clones and sites, and that the clone  $\times$  site interaction was also significant. Regression analysis was used to examine the stability of clones over environments. There were marked differences in stability between clones (linear regression coefficients 0.03 to 1.93). Interactions were variable (coefficients of determination zero to 93%), and in most cases it was not possible to predict the basic density of wood produced at one site from its value at another site. However, interactions accounted for less than 4% of the total variance in basic density; rank correlations between sites were all significant, and it was possible to identify clones which produced wood of consistently high or low basic density on the four test sites.

## Introduction

The mass of oven-dried wood substance present in a given green volume of wood (basic density) is often used as an indicator of wood quality, since both values are reproducible and basic density correlates well with wood properties such as strength and stiffness (Alexiou, 1994), dimensional stability (Chafe, 1990) and permeability (Kollmann and Cote, 1968). Thus, basic density is normally the first

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wood property to be assessed in a tree improvement programme. Raymond (1995), reviewing the genetic control of wood and fibre properties in *Eucalyptus*, reported that amongst the physical properties of wood, basic density is notable for the relatively large number of estimates of heritability.

Wood properties are affected not only by genetic factors and the sites where trees are grown, but also by interactions between genotype and environment (Zobel and Jett, 1995). For example, Malan and Verryin (1996) showed the existence of a clone  $\times$  site interaction for several wood properties, density amongst them, in *Eucalyptus* clones grown over a wide range of sites in South Africa. Following a study of interactions it may be possible to identify genotypes with high general adaptability (for example, genotypes which produce wood with high basic density on a range of sites) and others which perform better on particular sites.

The implications of genotype  $\times$  environment interactions for plant breeding and the methods used for detecting them have been discussed by a number of authors including Matheson and Cotterill (1990) and Romagosa and Fox (1993). Pswarayi et al. (1997) have recently discussed five methods of evaluating the importance of genotype  $\times$  environment interactions in tree species, using *Pinus elliottii* as an example.

The work described in this paper forms part of a larger study of the influence of genetic and environmental factors on the mechanical properties of the wood of *Eucalyptus* clones. The objective of this part of the study was to examine genotype  $\times$  environment interactions in wood basic density of 26 clones grown on four sites in Brazil. Interactions were examined using analysis of variance, rank correlations and regression analysis (Finlay and Wilkinson, 1963).

## Material and methods

### Field sampling

The wood samples used in this study were collected from eight-year-old clones of natural hybrids *Eucalyptus* collected in plots of *E. grandis* and *E. urophylla* produced and selected by Aracruz Celulose S.A. in Brazil. Clones were growing in clonal tests planted in October 1988 at four sites (Table 1). Each test was laid out in a randomised block design with three blocks, 26 treatments (clones) and 21 (7  $\times$  3) plants per plot. Spacing was 3.0  $\times$  3.0 m.

Felling of sample trees was carried out in August 1996. Some of the trees in the tests had already been felled for studies of the relationship between yield and soil characteristics, and the block structure of the experimental design was no longer intact. The blocking was therefore ignored during sampling. Sample trees were considered representative of dominant and co-dominant trees. One tree of each clone was felled at two of the sites, São Mateus 1 and São Mateus 2 (Table 1). At the other two sites, Aracruz and Southern Bahia (Table 1), three trees of five clones (numbers 3, 5, 7, 8 and 20) and one tree of the remaining 21 clones were felled. Each tree was cut as close to ground level as possible, and the 3.0 m long basal log immediately above the cut was collected.

### Determination of basic density

A 2.5 cm disc was removed from the top and base of each log and cut into quarters for basic density determination using the immersion method (oven dry mass/green volume) (Vital, 1984). The basic density of each disc was considered to be the average value of the density of two opposite quarters of each disc

**Table 1** Characteristics of four experimental sites in Brazil planted with *Eucalyptus* clones in October 1988

Characteristic	Site	São Mateus 1 - SM1 (State of Espírito Santo)	São Mateus 2 - SM2 (State of Espírito Santo)	Aracruz - ARA (State of Espírito Santo)
Latitude	17°50'S	18°40'S	18°40'S	19°48'S
Longitude	39°50'W	39°45'W	39°45'W	40°17'W
Altitude	5-100 m	5-60 m	5-60 m	4-50 m
Topography	Flat	Flat	Flat	Flat
Climate	Af	Aw	Aw	Aw
Average temperature	25 °C	24 °C	24 °C	24 °C
Annual relative humidity	82%	82%	82%	83%
Annual rainfall	1374 mm	1282 mm	1282 mm	1290 mm
Soils	Ufisol, kaolinitic, acidic, very low natural fertility			

The difference between the two sites at São Mateus (São Mateus 1 and São Mateus 2) are defined by details of soil type, and especially by textural differences which imply a greater or lesser availability of water to the plants

(Lima et al., 1992), and the mean basic density of each log was taken as the average of the values obtained for the two discs cut from it. The remaining portion of the log was used for the determination of mechanical properties and for anatomical studies.

### Data analysis

Data from two groups of sample trees were analysed. Group I consisted of three trees representing each of five clones planted on two sites (i.e. 30 trees in total). Group II consisted of one tree representing each of 26 clones planted on all four sites (i.e. 104 trees in total).

Analysis of variance was carried out to determine the effects of clone, site and clone  $\times$  site interactions (Group I data only) on basic density. All effects were assumed to be random, since clones were not selected for wood properties, sites were random samples of the environments available for growing *Eucalyptus* clones in Brazil, and a random effects model is appropriate when deriving estimates of variance components for the calculation of heritability (Stonecypher, 1992). The expected mean squares for the analysis of Group I and Group II data are shown in Table 2.

Variance components derived from the analysis of variance were used to estimate the broad sense heritability of basic density ( $h_{BS}^2$ ).

$$h_{BS}^2 = \frac{\delta_C^2}{\delta_P^2},$$

where  $\delta_P^2$  is the phenotypic variance, calculated as

$$\delta_P^2 = \delta_C^2 + \delta_{SC}^2 + \delta_{T(C)}^2 \text{ (Group I data), or}$$

$$\delta_P^2 = \delta_C^2 + \delta_{SC}^2 \text{ (Group II data).}$$

Using Group II data, clones were ranked in the order of decreasing basic density at each of the four sites. Similarity of ranking between sites was determined by calculating Spearman's rank correlation coefficient (Snedecor and Cochran, 1980) for all pairs of sites.

The method of Finlay and Wilkinson (1963) was used to examine the response of the 26 clones to the different environments at the four test sites. For each clone, the linear regression was computed between the basic density of the clone at each

**Table 2** Expected mean squares for analysis of variance, showing variance components due to sites ( $\delta_S^2$ ), clones ( $\delta_C^2$ ), site  $\times$  clone interactions ( $\delta_{SC}^2$ ) and trees within clones ( $\delta_{T(C)}^2$ )

(a) Expected mean squares for the analysis of variance of Group I data		
Source of variation	df	Expected mean squares
Site	1	$\delta_{T(C)}^2 + 3\delta_{SC}^2 + 15\delta_S^2$
Clone	4	$\delta_{T(C)}^2 + 3\delta_{SC}^2 + 6\delta_C^2$
Site $\times$ clone	4	$\delta_{T(C)}^2 + 3\delta_{SC}^2$
Trees (within clone)	20	$\delta_{T(C)}^2$
(b) Expected mean squares for the analysis of variance of Group II data		
Source of variation	df	Expected mean squares
Site	3	$\delta_{SC}^2 + 26\delta_S^2$
Clone	25	$\delta_{SC}^2 + 4\delta_C^2$
Site $\times$ clone	75	$\delta_{SC}^2$

site (dependent variable) and the mean density of all clones at each site (independent variable). The mean performance of all genotypes growing in a particular environment is used as an environmental index (Finlay and Wilkinson, 1963), and gives a numerical indication of the average effect of the environment on the property being measured. The interpretation of the results of regression analysis is as follows:

- i) if a clone has a regression coefficient of the order of 1 (average stability over all environments), its response to the environment is similar to that of the average clone;
- ii) if a clone has a regression coefficient of more than 1 (below average stability), it is more sensitive to changes in the environment than the average clone;
- iii) if a clone has a regression coefficient of less than 1 (above average stability), it is less affected by changes in the environment than the average clone.

The procedure recommended by Freese (1984) for group regression analysis was used to determine whether any of the 26 linear regression coefficients were significantly different from 1. Coefficients of determination ( $R^2$ ) were calculated for all regressions.

## Results and discussion

### Basic density: five clones planted on two sites

Table 3 shows that mean basic density was higher on the site at Aracruz than at Southern Bahia in all five sampled clones. The same Table shows that within clone variation in basic density had associated with it very low coefficients of variation. Lima (1995) reported that within clone variation of basic density in *Eucalyptus saligna* decreased with increasing age, falling to less than 2.0% by the age of 42 months. Given this low variation, the ideal sample size, according to the formula given by Freese (1984), is equal to one tree per clone for the most variable case (clone 3, Southern Bahia). The small number of sample trees required for the estimation of basic density of clonal material represents great advantages in terms of the time and costs of experimentation. However, it is likely that this small sample size will only be acceptable when clones are grown on very uniform sites. It is also important to recognise that patterns of within tree variation may be such that a number of samples will be needed from each tree. Analysis of variance (Table 4) showed that there were significant differences between sites and between clones. Of more interest was the significance of the site  $\times$  clone interaction. Similar results were obtained by Malan and Verry (1996) for basic density in

**Table 3** Mean values and within-clone coefficients of variation (CV) for wood basic density of five *Eucalyptus* clones at two sites (Southern Bahia and Aracruz) in Brazil

Clone	Southern Bahia		Aracruz	
	Mean ( $\text{g} \cdot \text{cm}^{-3}$ )	CV %	Mean ( $\text{g} \cdot \text{cm}^{-3}$ )	CV %
3	0.420	1.94	0.460	1.52
5	0.503	1.06	0.545	0.28
7	0.466	1.52	0.482	1.69
8	0.536	1.03	0.560	1.24
20	0.457	1.10	0.488	0.41

**Table 4** Results of analysis of variance of wood basic density of *Eucalyptus* clones (three trees of each of five clones on two sites). \*\*P ≤ 0.01

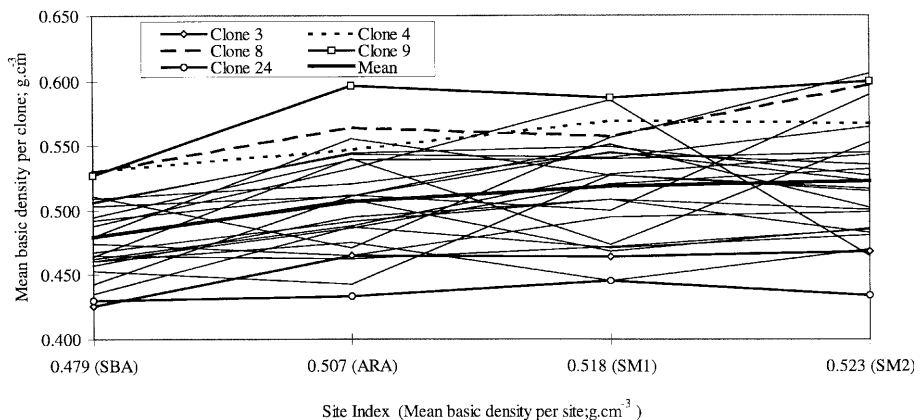
Source	DF	SS	MS	F	P
Clone	4	0.0452781	0.0113195	66.20	**
Site	1	0.0069312	0.0069312	40.53	**
Clone × Site	4	0.0006841	0.0001710	4.66	**
Trees (within clone)	20	0.0007334	0.0000367		
Total	29	0.0536268			

five-year-old clones of *Eucalyptus* raised in South Africa and by Demuner and Bertolucci (1993), who found significant clone × site interactions in eleven out of 22 wood properties, including basic density, of five-year-old *Eucalyptus* clones growing in Brazil.

In their review, Zobel and Jett (1995) stated that, although few well-designed studies of genotype × environment interactions for wood properties have been made, essentially all have found relatively small interactions unless the differences between the environments are very large. Work done since the publication of Zobel and Jett’s book generally supports this assertion, at least at the family level. Thus McDonald et al. (1997) found “relatively low genotype × environment interactions” for pilodyn pin penetration (an indirect measure of wood density) in open pollinated families of *Eucalyptus globulus* ssp. *globulus* growing on five sites in Tasmania. Similarly, Wei and Borralho (1997) felt that genotype × environment interactions for basic density of open pollinated families of *Eucalyptus urophylla* growing on four sites in China were “unimportant”.

**Basic density: twenty-six clones planted on four sites**

Figure 1 shows the basic density of the 26 clones at the four sites. The lowest mean basic density (i.e. the lowest site index) was 0.479 g/cm<sup>3</sup> at Southern Bahia and the highest was 0.523 g/cm<sup>3</sup> at São Mateus 2. Coefficients of variation of basic density were low at all sites, ranging from 6.4 to 8.8%.



**Fig. 1** Wood basic density of 26 *Eucalyptus* clones at four sites. Lines for clones 4, 8 and 9 (high density at all sites), clones 3 and 24 (low density at all sites) and the mean for all clones are marked. ARA – Aracruz; SBA – Southern Bahia; SM1 – São Mateus 1; SM2 – São Mateus 2

Analysis of variance showed that there were significant differences in basic density between sites and between clones (Table 5).

Table 6 shows the values of Spearman's rank correlation coefficients for all pairs of sites. All correlations were significant ( $P \leq 0.01$ ), suggesting that the ranking of clones is fairly consistent across sites and that it may be possible to identify clones which produce wood of high or low basic density on all sites. Inspection of Figure 1 shows that clones 4, 8 and 9 fall into the former category and clones 3 and 24 into the latter.

Table 7 shows the average basic density of the 26 clones over the four sites, the coefficients of linear regression of clone means against site means, and the associated coefficients of determination. Regression coefficients varied from  $-0.002$  to  $1.989$ , and coefficients of determination from zero to  $93.4\%$ .

Malan and Verryn (1996) suggested that genotypes can be classified as having average stability (regression coefficients between  $0.8$  and  $1.2$ ), below average stability (regression coefficients greater than  $1.2$ ) or above average stability (regression coefficients less than  $0.8$ ). In this case eight clones (numbers 1, 3, 4, 5, 10, 11, 16 and 18) showed average stability, nine clones (numbers 7, 8, 9, 14, 15, 17, 20, 22 and 25) below average stability and nine clones (numbers 2, 6, 12, 13, 19, 21, 23, 24 and 26) above average stability.

Despite the wide range of regression coefficients, only one ( $\beta = 0.202$ , clone 24) was significantly different from 1, and only five coefficients of determination were greater than  $90\%$  (Table 7). This suggests that for most clones the predictable component of the observed genotype  $\times$  environment interactions (estimated by the regression coefficient) is much smaller than the unpredictable component (estimated by the deviations from the regression). It appears that, for this group of clones on these four sites, it is generally not possible to predict the basic density of wood produced at one site from its value at another site.

### Estimates of heritability

In spite of the significant clone  $\times$  site interaction, estimates of broad sense heritability of basic density were high:  $h^2 = 0.96$  for five clones grown on two sites

**Table 5** Results of analysis of variance of wood basic density of *Eucalyptus* clones (one tree of each of 26 clones on four sites). \*\* $P \leq 0.01$

Source	DF	SS	MS	F	P
Clone	25	0.1160390	0.0046416	8.03	**
Site	3	0.0301055	0.0100352	17.36	**
Error	75	0.0433540	0.0005781		
Total	103	0.1894985			

**Table 6** Spearman's rank correlation coefficients between sites; 26 *Eucalyptus* clones ranked in decreasing order of wood basic density at each site. ARA - Aracruz; SBA - Southern Bahia; SM1 - São Mateus 1; SM2 - São Mateus 2. \*\* $P \leq 0.01$

	SM1	SM2	ARA
SBA	0.712**	0.727**	0.690**
SM1		0.601**	0.650**
SM2			0.560**

**Table 7** Mean basic density of 26 *Eucalyptus* clones over four sites, coefficients of linear regression ( $\beta$ ) of clone basic density on site mean basic density, coefficients of determination ( $R^2$ ) and the results of group regression analysis (F is significant if is significantly different from 1). \* $P \leq 0.05$ ; Ns – not significant

Clone	Mean basic density ( $\text{g} \cdot \text{cm}^{-3}$ )	$\beta$	$R^2$ (%)	F
1	0.486	0.843	60.7	Ns
2	0.483	0.552	43.9	Ns
3	0.456	0.989	90.8	Ns
4	0.553	0.890	92.4	Ns
5	0.539	1.173	89.5	Ns
6	0.532	0.719	53.0	Ns
7	0.500	1.571	91.2	Ns
8	0.562	1.207	74.2	Ns
9	0.577	1.618	87.1	Ns
10	0.492	0.879	93.1	Ns
11	0.519	0.986	37.9	Ns
12	0.518	0.628	5.4	Ns
13	0.485	-0.026	0.1	Ns
14	0.523	1.440	40.3	Ns
15	0.536	1.757	35.3	Ns
16	0.469	1.004	71.9	Ns
17	0.502	1.911	69.7	Ns
18	0.530	1.145	93.4	Ns
19	0.463	-0.002	$\leq 0.1$	Ns
20	0.505	1.779	89.4	Ns
21	0.521	0.665	53.0	Ns
22	0.508	1.350	34.0	Ns
23	0.471	0.347	44.6	Ns
24	0.436	0.202	36.7	*
25	0.485	1.611	54.0	Ns
26	0.527	0.720	80.9	Ns

(Table 4) and  $h^2 = 0.64$  for 26 clones grown on four sites (Table 5). In a literature survey, Raymond (1995) concluded that the basic density of *Eucalyptus* wood was under reasonably strong genetic control. Individual tree heritability ranged from 0.05 to 0.84 (mean 0.57) in 16 estimates presented in 13 publications, while family heritability ranged from 0.45 to 0.91 (mean 0.65) in 13 estimates presented in 10 papers (Raymond, 1995).

There are fewer published estimates of broad sense heritabilities of basic density, but those which exist are comparable with the results of the present study. Thus the heritability of basic density estimated from nine clones of *Eucalyptus* growing on one site in Brazil was 0.90 (Bertolucci et al., 1992), and heritability estimated from data for the same clones on three sites was 0.92 (Demuner et al., 1993). There were strong genetic correlations between basic density and cooking and pulp characteristics (Bertolucci et al., 1992).

### Implications for tree improvement strategies

There is no consensus among tree breeders (or agricultural crop breeders) on the best way of detecting genotype  $\times$  environment interactions or the way they should be handled in breeding programmes. The number of methods available for detecting genotype  $\times$  environment interactions can be a deterrent to analysis, since breeders have too many options to consider (Romagosa and Fox, 1993), and



the methods may give contradictory results. Crop breeders continue to debate the merits of breeding for general and specific adaptation and of selection in optimum and stress environments (Romagosa and Fox, 1993). Tree breeders are facing similar questions as they complete the first generation of tree improvement programmes, in which selection has usually been for general adaptation over a range of sites (Matheson and Cotterill, 1990).

A number of authors have pointed out the need to assess the practical importance of genotype  $\times$  environment interactions before drawing up breeding strategies (Pswarayi et al., 1997; Matheson and Cotterill, 1990). This is obviously desirable, but there is little evidence that the techniques available for estimating the effects of interactions on breeding programmes (see Matheson and Raymond, 1984) are used routinely.

Pswarayi et al. (1997) found that, of the five methods used to analyse data on wood density of *Pinus elliotti*, only one (analysis of variance) detected statistically significant family  $\times$  site interactions. They concluded that interactions were of little practical importance. McDonald et al. (1997) reached a similar conclusion when they found that, although family  $\times$  site interactions for pilodyn pin penetration in *Eucalyptus globulus* ssp. *globulus* were significant, they only accounted for 3% of the total variance.

For the same set of environments, family  $\times$  environment interactions are expected to be less pronounced than clone  $\times$  environment interactions because the mixture of genotypes within families provides a measure of genetic buffering. In the set of *Eucalyptus* clones assessed in the present study, analysis of variance showed clone  $\times$  site interactions to be statistically significant even for five clones on two sites (Table 4). Regression analysis suggested that interactions were unpredictable, and there were marked differences in stability between clones (Table 7). The loss of potential genetic gain resulting from these clone  $\times$  site interactions (C, see Matheson and Raymond, 1984) may be as high as 20%. On the other hand, interactions accounted for less than 4% (adjusted  $R^2$  statistic) of the variance in basic density of 26 clones on four sites (Table 5), rank correlations between sites were all significant (Table 6), and it was possible to identify clones which produced wood of consistently high or low basic density on the four test sites (Figure 1).

Basic density is positively correlated with many of the mechanical properties of solid wood. If tree breeders want to improve these properties, should they identify clones which give the highest wood density on a particular site type (i.e. select for specific adaptation)? Or should they select for general adaptation and identify clones which produce wood of above average (but not necessarily the highest) density on a range of sites?

These are difficult questions to answer, not least because the environmental factors which affect basic density are not well understood. This means that environments cannot be well-defined and may not be repeatable, conditions which Matheson and Cotterill (1990) consider essential if genotypes are to be matched to sites. Even if these conditions can be met, the costs of selecting and testing clones for specific adaptation can only be justified if they are outweighed by the commercial benefits of propagating and growing them. Ideally, decisions about selection strategies should be made only after the economic objectives of breeding programmes have been correctly defined and the relative importance of density in determining the mechanical properties of interest has been determined (Borralho and Cotterill, 1994). Such decisions cannot be made by breeders alone; they should be taken in consultation with wood users.

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