



Genomic-based multiple-trait evaluation in *Eucalyptus grandis* using dominant DArT markers



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ABSTRACT

We investigated the impact of combining the pedigree- and genomic-based relationship matrices in a multiple-trait individual-tree mixed model (a.k.a., multiple-trait combined approach) on the estimates of heritability and on the genomic correlations between growth and stem straightness in an open-pollinated *Eucalyptus grandis* population. Additionally, the added advantage of incorporating genomic information on the theoretical accuracies of parents and offspring breeding values was evaluated. Our results suggested that the use of the combined approach for estimating heritabilities and additive genetic correlations in multiple-trait evaluations is advantageous and including genomic information increases the expected accuracy of breeding values. Furthermore, the multiple-trait combined approach was proven to be superior to the single-trait combined approach in predicting breeding values, in particular for low-heritability traits. Finally, our results advocate the use of the combined approach in forest tree progeny testing trials, specifically when a multiple-trait individual-tree mixed model is considered.

1. Introduction

The magnitude of genetic gain is affected by several factors, including the accuracy of individuals' estimated breeding values and the extent of additive genetic variance present in the breeding population. The inclusion of genomic information in quantitative genetics analyses has resulted in improving the accuracy of individuals' predicted breeding value estimates [1]. Higher breeding values accuracy, through using the marker-based realized kinship (G matrix) in the mixed model equations (genomic best linear unbiased predictors –GBLUP–; [2]), have been demonstrated theoretically [3–5] and empirically [6–10] in several forest tree evaluation scenarios. In forest tree progeny testing trials, the large number of tested individuals makes genotyping the

entire population unmanageable for financial and logistical reasons, thus the option of restricting genotyping to only a subset of the testing population is favourable [11]. Recently, the single-step approach, which incorporates genomic information of a reduced set of individuals into the genetic evaluation of a larger un-genotyped progeny testing trials, was proposed by Misztal et al. [12], Legarra et al. [13], and Christensen and Lund [14], as a simple and efficient genetic evaluation method. In this approach, the pedigree and genomic information are combined to enhance individuals' genetic and genomic relationships information during the implementation of the individual-tree mixed model [15,16]. The simple combined method involves: (1) constructing the pedigree-based relationship A matrix of genotyped and non-genotyped individuals, (2) constructing the marker-based relationship G

Abbreviations: DBH, diameter at breast height; TH, total height; SS, stem straightness; ST, single-trait mixed model; DArT, Diversity Arrays Technology; MT, multiple-trait mixed model; h_t^2 , heritability for trait t ; r_a , additive genetic correlation; r , theoretical accuracy of the predicted breeding values; LD, linkage disequilibrium

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matrix of a sub-set of genotyped individuals, and (3) blending the pedigree and genomic matrices in the H matrix in the individual tree mixed model. Since the combined/blended approach uses the traditional BLUP mixed model equations, then extending to more complicated models used to fit the pedigree-based relationship matrices can be immediately implemented [17]. The combined approach has been widely applied in animal breeding with many successful applications including pigs [18], chickens [19,20], dairy cattle [21], dairy sheep [22], dairy goat [23], and beef cattle [24]. However, the use of the combined approach in forest genetic trial is scant [15,16,25] and somewhat limited as the analyses were restricted to single- rather than multiple-trait models. For instance, in a recent study using the same dataset used in the present study (see below), Cappa et al. [16] demonstrated that the combined approach is simple to implement in a traditional single-trait individual-tree mixed model and provided an easy extension to single-trait individual-tree mixed models with competition effects and/or environmental heterogeneity. However, this analysis did not consider the simultaneous evaluation of multiple traits as well as utilizing between the traits phenotypic and genetic correlations.

Multiple-trait mixed models result in improved prediction accuracies of breeding values as the information from correlated traits is incorporated in the analyses and traits with lower heritability benefit when analysed in combination with traits with higher heritabilities [26]. The increase in accuracy is dependent on the absolute difference between genetic and residual correlations between the traits, i.e., the larger the differences the greater the gain in accuracy [27]. Multiple-trait GBLUP approach has shown a higher accuracy of predicted breeding values than single-trait GBLUP in simulated [28,29] and empirical [30] scenarios in animal studies. Integrating marker information in multiple-trait models is possible in the combined approach [18,31–35], but has only been recently considered in plants (oil palm, [36]; white spruce, [15]). Ratcliffe et al. [15] used multiple-trait models but did not make comparisons with the single-trait models.

The objectives of this study are to compare the performance of: (1) the pedigree-based and the combined approaches using the multiple-trait models and (2) the single- and multiple-trait models using the combined approach. These comparisons were carried out using two growth attributes and stem straightness data from an open-pollinated *Eucalyptus grandis* breeding population. Genetic parameters (i.e., heritability, and additive genetic correlations) and expected gain in predicted breeding values' accuracy of parents and offspring were compared.

2. Materials and methods

2.1. Progeny trial data

A total of 164 open-pollinated families originating from native-forest (148) and two local land-race (16) of *Eucalyptus grandis* (Hill ex Maiden) growing in a progeny trial located at Gobernador Virasoro (lat. 28° 02' S, long. 56° 03' W alt. 105 m), northern Corrientes province, Argentina, and established by the National Institute of Agricultural Technology (Instituto Nacional de Tecnología Agropecuaria, INTA), provided the material for this study (see [37] for details). Briefly, the progeny trial was established as a randomized complete block design with 20 replications with one tree per plot at each replication. Five years from planting, trees were assessed for over the bark diameter at breast height (1.3 m above the ground level) (DBH, cm), total height (TH, m), and stem straightness (SS) assessed by a four-point subjective score after transformation to normal scores [38]. The study included phenotypic data (DBH, TH, and SS) from 2026 trees. A random sample of 187 trees originating from 131 families were genotyped with a range of 1–3 trees per family. The total number of phenotyped trees with at least one genotyped half-sib was 1650 (see Table 1 for the summary).

Table 1

Summary statistics of the studied *Eucalyptus grandis* open-pollinated families including the number of genotyped and non-genotyped individuals and traits (diameter at breast height: DBH, total height: TH, stem straightness: SS) means and standard deviations.

	N° of records	Mean (SD ^a)		
		DBH (cm)	TH (m)	SS ^b (Scale 1–4)
Total of offspring in the pedigree	2026	18.85 (4.27)	18.87 (2.68)	2.30 (0.69)
Number of trees from mothers with genotyped offspring	1650	18.87 (4.24)	18.87 (2.65)	2.31 (0.69)
Number of offspring with genotype	187	20.81 (3.07)	20.57 (1.67)	2.16 (0.66)

^a Standard deviation.

^b based on original scale assessment data.

2.2. Molecular data

The 187 randomly selected trees were genotyped by 2816 DArT molecular markers selected from an operational array with 7680 [39] (Diversity Arrays Technology Pty Ltd., DArT P/L, Canberra, Australia). The selected markers showed call rate values > 0.8, reproducibility values > 0.97 (reproducibility of scoring between replicated target assays), and minor allele frequency (MAF) > 0.05.

2.3. Statistical models

The three assessed traits were analyzed using the following two individual-tree mixed models:

1) Single-trait mixed model (ST):

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}_r\mathbf{r} + \mathbf{Z}_a\mathbf{a} + \mathbf{e} \quad (1)$$

where the vector \mathbf{y} contains the phenotypic data; $\boldsymbol{\beta}$ is the vector of fixed effects for the nineteen genetic groups formed according to provenance; \mathbf{r} is the vector of random replicate effects, \mathbf{a} is the vector of random additive genetic effects of individual trees (i.e., breeding values); and \mathbf{e} is the vector of random residuals; \mathbf{X} , \mathbf{Z}_r and \mathbf{Z}_a are incidence matrices relating the observations (\mathbf{y}) to the model effects $\boldsymbol{\beta}$, \mathbf{r} and \mathbf{a} , respectively. The vector \mathbf{e} is distributed as $\mathbf{e} \sim N(\mathbf{0}, I\sigma_e^2)$ and σ_e^2 is the error variance. For the pedigree-based approach, the vector \mathbf{a} was assumed distributed as $\mathbf{a} \sim N(\mathbf{0}, \mathbf{A}\sigma_a^2)$ where σ_a^2 is the additive genetic variance and \mathbf{A} is the average numerator relationship matrix derived from the pedigree information and containing the additive relationships among all trees: 164 mothers without records plus 2026 offspring with data in \mathbf{y} .

1) Multiple-trait mixed model (MT):

$$\begin{bmatrix} \mathbf{y}_i \\ \mathbf{y}_j \end{bmatrix} = \begin{bmatrix} \mathbf{X}_i & \mathbf{0} \\ \mathbf{0} & \mathbf{X}_j \end{bmatrix} \begin{bmatrix} \boldsymbol{\beta}_i \\ \boldsymbol{\beta}_j \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_{ri} & \mathbf{0} \\ \mathbf{0} & \mathbf{Z}_{rj} \end{bmatrix} \begin{bmatrix} \mathbf{r}_i \\ \mathbf{r}_j \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_{ai} & \mathbf{0} \\ \mathbf{0} & \mathbf{Z}_{aj} \end{bmatrix} \begin{bmatrix} \mathbf{a}_i \\ \mathbf{a}_j \end{bmatrix} + \begin{bmatrix} \mathbf{e}_i \\ \mathbf{e}_j \end{bmatrix} \quad (2)$$

where \mathbf{y}_i and \mathbf{y}_j are the vectors of individual tree observation for traits i and j . The matrices $\mathbf{X}_i \oplus \mathbf{X}_j$, $\mathbf{Z}_{ri} \oplus \mathbf{Z}_{rj}$, and $\mathbf{Z}_{ai} \oplus \mathbf{Z}_{aj}$ related the observation to the means of the genetic groups in $\begin{bmatrix} \boldsymbol{\beta}'_i \\ \boldsymbol{\beta}'_j \end{bmatrix}$, the replicate effects in $\begin{bmatrix} \mathbf{r}'_i \\ \mathbf{r}'_j \end{bmatrix}$, and the individual breeding value in $\begin{bmatrix} \mathbf{a}'_i \\ \mathbf{a}'_j \end{bmatrix}$ for trait $t = i, j$. The vector $\begin{bmatrix} \mathbf{e}'_i \\ \mathbf{e}'_j \end{bmatrix}$ is the residual vector. The symbols \oplus and $'$ indicate the direct sum of matrices and the transpose operation, respectively. The vector of individual breeding values was assumed distributed as:

$$\begin{bmatrix} \mathbf{a}_i \\ \mathbf{a}_j \end{bmatrix} \sim N\left(\begin{bmatrix} \mathbf{0} \\ \mathbf{0} \end{bmatrix}, \begin{bmatrix} \sigma_{aii}^2 & \sigma_{aij}^2 \\ \sigma_{aji}^2 & \sigma_{ajj}^2 \end{bmatrix} \otimes \mathbf{A}\right)$$

where σ_{aii}^2 and σ_{ajj}^2 are the additive genetic variances of traits i and j ,

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