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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.

Key words: Multiple-trait individual-tree mixed model, combined approach, genetic parameters, accuracy, *Eucalyptus grandis*.

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; $\hat{h}_t^2$ heritability for trait *t*; $\hat{r}_a$ additive genetic correlation; ***r***, theoretical accuracy of the predicted breeding values; LD, linkage disequilibrium.

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*** 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 compete 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 2,026 trees. A random sample of 187 trees originating from 131 families were genotyped with a range of 1 to 3 trees per family. The total number of phenotyped trees with at least one genotyped half-sib was 1,650 (see Table 1 for the summary).

[Insert **Table 1** about here]

2.2. *Molecular data*

The 187 randomly selected trees were genotyped by 2,816 DArT molecular markers selected from an operational array with 7,680 [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):**

$$\boldsymbol{y} = \boldsymbol{X}\boldsymbol{\beta} + \boldsymbol{Z}_r\boldsymbol{r} + \boldsymbol{Z}_a\boldsymbol{a} + \boldsymbol{e} \tag{1}$$

where the vector $\boldsymbol{y}$ contains the phenotypic data; $\boldsymbol{\beta}$ is the vector of fixed effects for the nineteen genetic groups formed according to provenance; $\boldsymbol{r}$ is the vector of random replicate effects, $\boldsymbol{a}$ is the vector of random additive genetic effects of individual trees (i.e., breeding values); and $\boldsymbol{e}$ is the vector of random residuals; $\boldsymbol{X}$, $\boldsymbol{Z}_r$ and $\boldsymbol{Z}_a$ are incidence matrices relating the observations ($\boldsymbol{y}$) to the model effects $\boldsymbol{\beta}$, $\boldsymbol{r}$ and $\boldsymbol{a}$, respectively. The vector $\boldsymbol{e}$ is distributed as $\boldsymbol{e} \sim N\left(\boldsymbol{0}, \boldsymbol{I}\sigma_e^2\right)$ and σ_e^2 is the error variance. For the pedigree-based approach, the vector $\boldsymbol{a}$ was assumed distributed as $\boldsymbol{a} \sim N\left(\boldsymbol{0}, \boldsymbol{A}\sigma_a^2\right)$ where σ_a^2 is the additive genetic variance and $\boldsymbol{A}$ is the average numerator relationship matrix derived from the pedigree information and containing the additive relationships among all trees: 164 mothers without records plus 2,026 offspring with data in $\boldsymbol{y}$.

2) Multiple-trait mixed model (MT):

$$\begin{bmatrix} y_i \\ y_j \end{bmatrix} = \begin{bmatrix} X_i & 0 \\ 0 & X_j \end{bmatrix} \begin{bmatrix} \beta_i \\ \beta_j \end{bmatrix} + \begin{bmatrix} Z_{ri} & 0 \\ 0 & Z_{rj} \end{bmatrix} \begin{bmatrix} r_i \\ r_j \end{bmatrix} + \begin{bmatrix} Z_{ai} & 0 \\ 0 & X_{aj} \end{bmatrix} \begin{bmatrix} a_i \\ a_j \end{bmatrix} + \begin{bmatrix} e_i \\ e_j \end{bmatrix} \tag{2}$$

where $\boldsymbol{y}_i$ and $\boldsymbol{y}_j$ are the vectors of individual tree observation for traits *i* and *j*. The matrices $\boldsymbol{X}_i \oplus \boldsymbol{X}_j$, $\boldsymbol{Z}_{ri} \oplus \boldsymbol{Z}_{rj}$, and $\boldsymbol{Z}_{ai} \oplus \boldsymbol{Z}_{aj}$ related the observation to the means of the genetic groups in $\left[\beta_i' \middle| \beta_j'\right]$, the replicate effects in $\left[\boldsymbol{r}_i' \middle| \boldsymbol{r}_j'\right]$, and the individual breeding value in $\left[\boldsymbol{a}_i' \middle| \boldsymbol{a}_j'\right]$ for trait $t = i, j$. The vector $\left[\boldsymbol{e}_i' \middle| \boldsymbol{e}_j'\right]$ 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:

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

where σ^2_{aii} and σ^2_{ajj} are the additive genetic variances of traits *i* and *j*, respectively; and σ_{aij} is the additive genetic covariance between traits *i* and *j*. The residual vector is distributed as:

$$\begin{bmatrix} \boldsymbol{e}_i \\ \boldsymbol{e}_j \end{bmatrix} \sim N\left(\begin{bmatrix} 0 \\ 0 \end{bmatrix}, \boldsymbol{I} \otimes \begin{bmatrix} \sigma^2_{eii} & \sigma_{eij} \\ \sigma_{eji} & \sigma^2_{ejj} \end{bmatrix} \right)$$

where σ^2_{eii} and σ^2_{ejj} are the residual variance of trait *i* and *j*, respectively; and σ_{eij} is the residual covariance between traits *i* and *j*.

In the combined approach, the $\boldsymbol{A}$ matrix of the previous mixed models (1), and (2) was replaced by the combined pedigree- and marker-based pairwise relationship $\boldsymbol{H}$ matrix of the same dimension as the pedigree-based matrix.

The inverse of the relationship matrix that combines pedigree and genomic information ($\boldsymbol{H}^{-1}$) was derived by Misztal et al. [12], Legarra et al. [13], Aguilar et al. [21], and Christensen and Lund [14], and calculated following closely to Cappa et al. [16] as:

$$\boldsymbol{H}^{-1} = \boldsymbol{A}^{-1} + \begin{bmatrix} \boldsymbol{0} & \boldsymbol{0} \\ \boldsymbol{0} & \lambda\left(\boldsymbol{G}^{-1} - \boldsymbol{A}_{22}^{-1}\right) \end{bmatrix}$$

where λ scales differences between genomic and pedigree-based information, $\boldsymbol{G}^{-1}$ is the inverse of the genomic-based relationship matrix and $\boldsymbol{A}_{22}^{-1}$ is the inverse of the pedigree-based relationship matrix for the genotyped individuals ($\boldsymbol{A}_{22}$). The weighting factor λ was set to 1.0 for all models [16].

The genomic relationship matrix $\boldsymbol{G}$ was constructed from the dominant DArT markers following the formula suggested by Resende et al. [40]:

$$\boldsymbol{G} = \frac{\left(\boldsymbol{M} - \boldsymbol{P}\right)\left(\boldsymbol{M} - \boldsymbol{P}\right)'}{\sum_k p_k\left(1 - p_k\right)}$$

where p_k is the frequency of the code 1 at locus k, $\boldsymbol{M}$ is a $n \times m$ matrix (n = number of genotyped trees, m = number of DArT markers) that specifies the genotypes expressed as 0/1 denoting the absence/presence of the DArT marker, and $\boldsymbol{P}$ is a matrix containing p_k in the kth column. The $\boldsymbol{G}$ matrix was scaled to have the same diagonal and off-diagonal averages as the corresponding $\boldsymbol{A}$ matrix following closely the work of Christensen et al. [18]. See further details about the scale of $\boldsymbol{G}$ matrix in Cappa et al. [16].

Restricted maximum likelihood (REML, [41]) was used to estimate variances and covariances and to predict the breeding values and their corresponding standard errors in the mixed models Eqs. [1] and [2], and were obtained with the ASReml program [42], which uses the average information algorithm described by Gilmour et al. [43].

Two genetic parameters were compared: 1) heritability for each trait; and 2) genetic correlations between traits. The heritability of trait t (for t = DBH, TH or SS) was estimated as $\hat{h}_t^2 = \hat{\sigma}_{att}^2 / \hat{\sigma}_{att}^2 + \hat{\sigma}_{ett}^2$, where $\hat{\sigma}_{att}^2$ is the estimated additive genetic variance of trait t, and $\hat{\sigma}_{ett}^2$ is the estimated residual variance of trait t. Meanwhile, the additive genetic correlation between trait i and j was calculated as $\hat{r}_a = \hat{\sigma}_{aij} \Big/ \sqrt{\hat{\sigma}_{aii}^2\,\hat{\sigma}_{ajj}^2}$.

Further model comparison was provided by the theoretical accuracy ($\boldsymbol{r}$) of the predicted breeding values, which was calculated using the following expression: $\boldsymbol{r} = \sqrt{1 - \mathrm{PEV} \Big/ \left(\left(1 + F_i\right)\hat{\sigma}_a^2\right)}$. The acronym PEV stands for 'prediction error variance' of predicted breeding values, and are calculated as the square of the standard error, and F_i is the inbreeding coefficients of tree *i*. After that, we estimated the expected gain in accuracy of a tree's breeding value for an individual using a linear regression on the trait (DBH, TH or SS), the model (ST or MT), the approach (pedigree-based ***A*** or combined ***H***), and the group to which the tree belongs (parents or offspring).

3. Results

3.1. *Additive genetic relationship matrices*

The pairwise relationship coefficients for the genotyped trees derived from the pedigree- ($\boldsymbol{A}_{22}$) and the genomic-based (***G***) relationship matrix and for genotyped and non-genotyped trees derived from the pedigree- (***A***) and combined pedigree-genomic (***H***) relationship matrix, are presented in Fig. S1. When relationships were estimated from the pedigree ($\boldsymbol{A}_{22}$ and ***A***), expected relationships between individuals from this breeding population were very sparse with only three relationship classes: 0, 0.25, and 0.50. As expected, a large number of pairwise relatedness coefficients from pedigree were zero. On the contrary, realized relationships obtained from the DArT markers (***G*** and ***H***) showed a continuous distribution with relationship values from -0.04 to 0.13 between mothers, from -0.15 to 0.38 between offspring, and from -0.09 to 0.75 between mother and offspring. Moreover, as noted early Cappa et al. [16] using the same dataset, the combined relationship matrix ***H*** diffused the information from genomic markers to non-genotyped offspring and mothers, while, as expected, offspring from mothers with non-genotyped offspring did not produce any additional information. For example, several pairs of mothers assumed unrelated in ***A***, with a coefficient equal to zero, while appeared as related in the combined matrix ***H***, with coefficients that varying from -0.04 to 0.13.

3.2. *Heritability estimates and additive genetic correlations between traits*

Heritability estimates and additive genetic correlations from the pedigree- (***A*** matrix) and combined (***H*** matrix) approaches are presented in Table 2. The combined approach yielded higher heritability estimates (0.161 *vs*. 0.152 for TH and 0.337 *vs*. 0.317 for DBH), except for SS (0.230 *vs*. 0.199). The additive genetic correlations based on the ***A*** matrix were strongly positives between the two growth traits (0.892, DBH-TH), and negative and weak between the two growth traits and stem straightness (-0.146 for DBH-SS, and -0.077 for TH-SS). However, last two estimates had large high standard errors, and were did not significantly different from zero. The genetic correlations based on the ***H*** matrix were 0.913, -0.228, and -0.140 for DBH-TH, DBH-SS, and TH-SS, respectively. However, only the correlation between TH and SS did not differ significantly from zero, thus, including genomic information produced stronger (positive or negative) genetic correlations and reduced the standard errors in two out of the three correlations estimates.

[Insert **Table 2** about here]

3.3. ***Accuracy of predicted breeding values***

The impact of including genomic information in a combined approach and leveraging other correlated traits in a multiple-trait analysis on the prediction accuracy of breeding values was also evaluated (Table 3). The percentages of the expected difference in accuracies for mother and offspring between the pedigree-based and combined approaches for single- and multiple-trait models, and between single-trait and multiple-trait models for the pedigree-based and combined approaches are summarized in Fig. 1.

The low-heritable trait (TH; h^2_A = 0.152 and h^2_H = 0.161) displayed the highest expected gains in accuracy of breeding values when using the multiple-trait combined (***H***) rather the pedigree-based (***A***) approach, even higher than those from the single-trait approach (Fig. 1; Table 3). The improvements for the most heritable trait (DBH; h^2_A = 0.317 and h^2_H = 0.337) were smaller, albeit the largest gains were under a single-trait model. However, these improvements were not observed for the trait SS (h^2_A = 0.230 and h^2_H = 0.199) where the accuracy of predicted breeding values from the combined approach was lower than from the pedigree-based approach. This reduction in accuracy was a consequence of the reduced estimation of the additive-genetic variance under the combined approach, most likely due to the underlying quantitative nature of the trait. In summary, the expected accuracies of breeding values were marginally higher for DBH and TH, and lower for SS when the ***H*** matrix was used in both multiple- and single-trait models (Table 3).

The expected gains in accuracy for the three studied traits were higher (from 0.06 to 3.78%) when we compared the single- and multiple-trait models with ***H*** matrix (and ***A*** matrix), especially for TH, the trait with the lowest heritability (h^2_H = 0.161) (Fig. 1; Table 3). Moreover, higher correlations between traits showed higher gains in accuracies for the multiple-trait combined approach as compared to the accuracies from the single-trait model. For example, with a correlation of 0.913 (between TH-DBH, Table 2) the average accuracy of breeding values for TH was 0.781 using the combined approach (Table 3); while with a correlation of -0.140 (between TH-SS, Table 2) the average accuracy decreased to 0.762, only marginally higher than the average accuracy under the single-trait model; (0.761; Table 3). In contrast, for the high-heritable trait (DBH), the differences in accuracies were marginal, decreasing from 0.796 to 0.795 (Table 3) when the correlation decreased from 0.913 (between DBH-TH) to -0.228 (between DBH-SS) (Table 2).

The results from the multiple-trait *vs*. single-trait for the pedigree-based approach were similar to those from the combined approach in terms of accuracy of predicted breeding values (Fig. 1; Table 3).

[Insert **Fig. 1** about here]

[Insert **Table 3** about here]

4. Discussion

Traditionally, the BLUP-predicted breeding values for the *E. grandis* INTA improvement program are obtained through the use of the classical pedigree-based single- or multiple-trait approach based on joint phenotypic and pedigree data [37,44]. This study demonstrated the utility of the joint use of a multiple-trait mixed model with phenotyping, and blending both pedigree and genomic information for the analysis of correlated traits. The joint use of multiple-trait models and genomic information by means of the combined approach is a simple and effective tool for estimating heritabilities and genetic and environmental correlations in forestry progeny testing trials. Our results suggest that the benefit of using the multiple-trait combined approach will be greater for data sets with traits with larger differences in heritability and genetic correlations between traits than in the one used herein. The multiple-trait combined models would also be advantageous to predict a trait when trees have been measured for other traits, especially in situations where missing information occurs due to, for example, tree damage or, practical and technical problems with data recollection.

4.1. *Genetic parameters*

Knowledge of genetic parameters is required to formulate breeding strategies as well as predicting parents and offspring breeding values, and estimating gains from selection. Certainly, a key objective trait for eucalypts breeding is fast growth, typically measured by diameter and/or height. The present study's DBH and TH heritability estimates (Table 2) are similar to those previously reported for the same *E. grandis* population using the single-trait model with the ***A*** and ***H*** matrices [16] and to those reported by Marcó & White [37], Gapare et al. [45] and Harrand et al. [44] using the classical pedigree-based approach. However, heritability estimates for SS were higher than those reported by Marcó & White [37] using the ***A*** matrix and based on the categorical observed scale, possibly attributed to the normal score transformation used in our study. Cappa and Varona [46] observed that heritability estimates based on a transformation of categorical data to normal score are often higher than those based on the categorical observed scale.

Strong genetic correlations were observed between growth traits (DBH and TH), indicating that selection for anyone would give a high correlated response to the other. These high and positive correlations confirm previous observations on *Eucalyptus* species (*e.g.* [45,47,48]) using the pedigree-based approach. However, low and negative genetic correlations were found between growth and stem straightness, an unfavorable state for breeding purposes. Although the precision of these estimates was somewhat low, the literature showed variable results for this relationship. For instance, in *E. grandis* and *Eucalyptus viminalis* Labill ssp. *viminalis* estimates of 0.37 to 0.80 and -0.09 to 0.70 were reported by Gapare et al. [45] and Cappa et al. [49], respectively.

In theory, genetic correlation from the classical pedigree-based analysis is expected to capture the expected genetic correlation, whereas marker-based analysis captures the realized genetic covariation that is traced by the markers [34]. Stem straightness appeared to be independent from height growth when the ***A*** matrix was fitted; however, a small and negative correlation is noted when the ***H*** matrix was implemented. Slightly higher and negative correlations were observed between DBH and SS when the ***A*** or ***H*** matrices were fitted (Table 2). Such differences in the genetic correlation between traits could be due to the different source from which the genetic correlation arises. In a recent study using the multiple-trait combined approach, Momen et al. [34] examined the impact of combining ***A*** and ***G*** matrices varying the weight assigned to each source of information from 0 (only ***A***) to 1 (only ***G***) on the genetic correlations between three traits measured in broiler chickens. These authors concluded that estimates of genetic correlations were affected by the weight placed on the source of information used to build the ***H*** matrix; however, the scaling was trait-dependent. When the pedigree-based method is used, the genetic correlation between traits arises mainly due to either a single gene or closely linked block of functionally related genes that have an effect on both traits (pleiotropy), or due to linkage disequilibrium (LD) between genes that affecting different traits [50]. Meanwhile, when marker-based methods are used, marker-QTL LD and LD relationships among markers intervene in the genomic correlation. According to Momen et al. [34] these estimates may also differ due to chance or other reasons, such as the extent of LD between markers and the unknown QTL, or LD between QTLs.

The observed lower standard errors for the genetic correlations obtained from the combined approach is in accordance with previous findings in animal breeding [33,51]. More precise genetic correlations may be explained by the fact that the relationship between relatives from pedigree and marker information are described more precisely than pedigree-based matrices, given that the former reflects the actual relationships that may deviate from their expectation because of Mendelian sampling (*e.g.* [52,53]).

4.2. *Multiple-trait models comparison between pedigree-based and the combined approach*

The difference between the pedigree-based and combined approach concerning the predicted accuracy of breeding values was evaluated in the context of a multiple-trait model. In general, the combination of the pedigree- and genomic-based matrices in a multiple-trait mixed model yielded higher expected accuracy than the pedigree-based approach (Table 3). Earlier studies using empirical data in animals [18,31,33,34] and forest trees [15] have also demonstrated the superiority of the multiple-trait combined prediction over the pedigree-based alternative. Aguilar et al. [31] indicated that the inclusion of genomic information using the combined approach resulted in approximately doubling the accuracy. In a recent study on white spruce, Ratcliffe et al. [15] found higher accuracies in offspring breeding values for increased genotyping efforts (0, 25, 50, 75, 100%) using a multiple-trait combined approach which ranged from 0.474 to 0.536 and 0.605 to 0.661 for height and wood density, respectively. Marker-based methods could achieve higher breeding values accuracies given that they are not only contributed by the expected genetic relationship between trees (as in the pedigree-based approach), but also by linkage disequilibrium (LD) and co-segregation to capture relationship at QTL [50].

4.3. *Combined approach comparison between single- and multiple-trait models*

Bivariate genomic selection models have been already used in tree breeding populations [9,15]. However, this is the first study to investigate the benefit of using multiple-trait genomic models in forest tree breeding. Therefore, our second objective to quantifying the improvement that can be attained by the multiple- *vs.* single-trait model using a combined approach has been fulfilled. From our empirical *E. grandis* data, we found that the expected accuracy of breeding values was higher in a multiple-trait combined approach than in single-trait models, with a particularly high gain for low-heritability traits. Similar to the classical pedigree-based multiple-trait approach, traits with low-heritability can borrow/utilize information from correlated and high-heritability traits, achieving higher prediction accuracy [30]. Using the multiple-trait combined approach produced better breeding values prediction accuracies for several traits in a US Holstein [32], Danish Duroc pigs [17], Holstein dairy cattle [31], and oil palm [36] populations.

Our results indicated that higher correlations between traits produced improved accuracies for the multiple-trait combined approach when compared to the single-trait model (Table 2), confirming the importance of the absolute differences in the genetic correlation between traits in accuracy gain. In a simulation study, where the prediction accuracy was calculated as the correlation between observed and the predicted phenotype, Jia and Jannink [30] showed that for low-heritability (h^2= 0.1) the multiple-trait genomic selection approach greatly increased the prediction accuracy, but only when the genetic correlation between the related traits was higher than 0.7. Meanwhile, for a high heritable trait (h^2= 0.5), these accuracies remain stable across a range of genetic correlation of 0.1 to 0.9. Our findings are also in agreement with Calus and Veerkamp [54], who reported for an animal simulation study that the magnitude of accuracy increase was higher when the genetic correlation was higher than 0.5.

On average and across the three studied traits, the multiple-trait combined model produced higher gain in accuracy than those from the single-trait combined approach. However, these gains in accuracy were lower when we compared to the combined and pedigree-based approaches for the multiple-trait models. Therefore, the gain obtained by using the multiple-trait models was higher than those from the use of the genomic information. This may be due to the small number of genotyped trees (187 out of 2,026) and the relatively low number of marker assayed (2,816 DArT markers). Nonetheless, this empirical data set clearly demonstrated the benefits of multiple-trait combined approach in increasing the accuracy of breeding values.

Across single- and multi-trait models, the average accuracy of prediction of breeding values based on the pedigree and combined approaches were higher for mothers than the corresponding values for offspring (Table 3). However, there were a lower expected gain in accuracy for mothers than that for offspring (Fig. 1); i.e., the additional information generated by including the genomic information in the combined approach have a higher impact on the accuracies of the predicted breeding values of offspring than that of the mothers. These results are expected, given that mothers with numerous offspring generally have sufficient information from the phenotypic and pedigree data to achieve acceptable accuracies.

5. Conclusion

To our knowledge, this is the first study to investigate the potential benefit of the multiple-trait model that simultaneously makes full use of the pedigree and genomic information in forest breeding data. Our empirical study using *E. grandis* population suggests that it is possible to use the combined approach for estimating heritability and additive genetic correlation estimates in forest trees multiple-trait evaluations. Moreover, the results from this study highlighted the potential benefit in terms of gain in accuracy by implementing multiple-trait combined approach, even though the genotyping efforts used was low (less than 10% of the trees) and dominant bi-allelic DArT markers are less informative than the widely used co-dominant single-nucleotide polymorphisms (SNP) markers. As noted in earlier studies, the benefit of using multiple-trait combined analysis has been found to be more relevant for traits with low-heritability and high genetic correlations between traits. Here we considered a bivariate multiple-trait mixed model, but the method could easily be extended to a higher number of traits.

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Conflicts of interest

None.

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Figure Legend:

Fig. 1 Expected average percent increases of the accuracy of breeding values for mothers and offspring from a) the combined approach (***H*** matrix) with respect to the pedigree-based approach (***A*** matrix) by single-trait (ST) and multiple-trait (MT) individual-tree mixed model, and from b) the MT model with respect to the ST model by approach (***A*** and ***H***). In both cases, results are further classified by trait: diameter at breast height (DBH), total height (TH), and normal score of stem straightness (SS).

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.

		Mean (SD[a])		
	N° of records	**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.

Table 2. Heritability and genetic correlation estimates from the multiple-trait model determined by pedigree-based relationship matrix (***A***) (above diagonal) and the combined genomic and pedigree-based relationship matrix (***H***) (below diagonal). Approximate standard errors are in parenthesis.

Trait	h^2_A[a]	h^2_H[a]	**DBH**[b]	**TH**[b]	**SS**[b]
DBH[b]	0.317 (0.071)	0.337 (0.073)	-	0.892 (0.057)	-0.146 (0.175)
TH[b]	0.152 (0.053)	0.161 (0.055)	0.913 (0.051)	-	-0.077 (0.219)
SS[b]	0.230 (0.062)	0.199 (0.058)	-0.228 (0.174)	-0.140 (0.222)	-

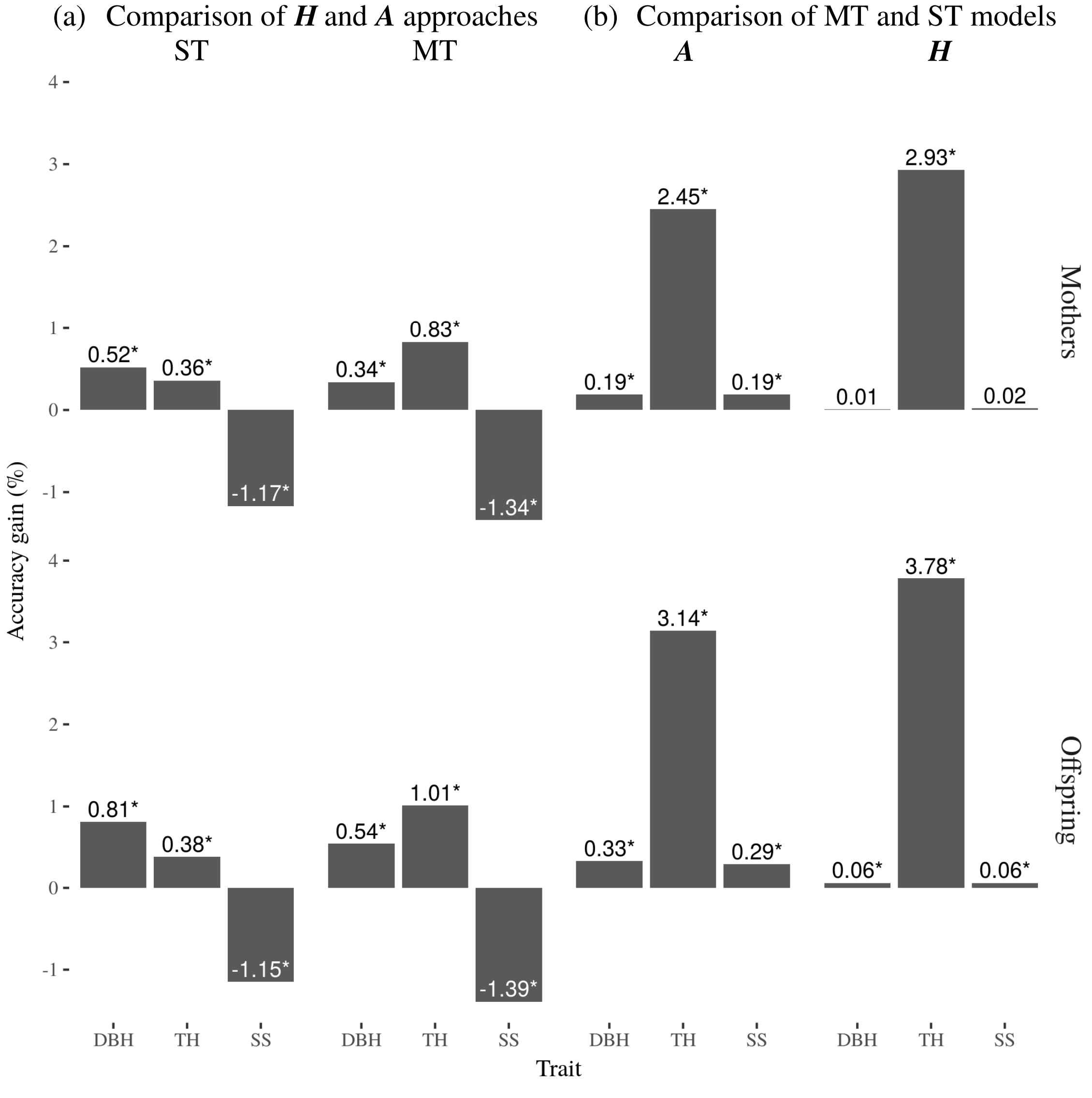
[a] The heritability estimates for each trait and approach are the average of the corresponding estimates from the two bivariate models in which the trait participates.

[b] See text for traits´ abbreviations

Table 3. Means and standard deviations of estimated theoretical accuracies for the predicted breeding values of mother and offspring based on the pedigree-based and combined approaches for diameter at breast height (DBH), total height (TH), and normal score of stem straightness (SS) in *Eucalyptus grandis* using single-trait (ST) and multiple-trait (MT) individual-tree mixed models. See text for models´ abbreviations.

Method of genetic evaluation	**DBH**			**TH**			**SS**		
	ST	**$\mathrm{MT}_{\mathrm{TH}}$**	**$\mathrm{MT}_{\mathrm{SS}}$**	**ST**	**$\mathrm{MT}_{\mathrm{DBH}}$**	**$\mathrm{MT}_{\mathrm{SS}}$**	**ST**	**$\mathrm{MT}_{\mathrm{TH}}$**	**$\mathrm{MT}_{\mathrm{DBH}}$**
Pedigree									
Mothers	0.851 ± 0.029	0.852 ± 0.029	0.851 ± 0.029	0.807 ± 0.023	0.827 ± 0.025	0.808 ± 0.023	0.828 ± 0.026	0.829 ± 0.024	0.828 ± 0.026
Offspring	0.788 ± 0.044	0.790 ± 0.045	0.789 ± 0.045	0.757 ± 0.026	0.773 ± 0.036	0.758 ± 0.027	0.771 ± 0.034	0.772 ± 0.031	0.771 ± 0.034
Average	**0.791 ± 0.045**	**0.793 ± 0.046**	**0.792 ± 0.046**	**0.759 ± 0.028**	**0.776 ± 0.037**	**0.760 ± 0.029**	**0.773 ± 0.036**	**0.775 ± 0.032**	**0.774 ± 0.036**
Combined									
Mothers	0.855 ± 0.029	0.855 ± 0.029	0.855 ± 0.029	0.810 ± 0.023	0.833 ± 0.025	0.810 ± 0.023	0.818 ± 0.025	0.818 ± 0.026	0.819 ± 0.025
Offspring	0.792 ± 0.047	0.793 ± 0.047	0.793 ± 0.047	0.759 ± 0.027	0.779 ± 0.039	0.760 ± 0.028	0.765 ± 0.031	0.765 ± 0.035	0.765 ± 0.031
Average	**0.795 ± 0.048**	**0.796 ± 0.048**	**0.795 ± 0.048**	**0.761 ± 0.029**	**0.781 ± 0.040**	**0.762 ± 0.030**	**0.767 ± 0.032**	**0.767 ± 0.037**	**0.767 ± 0.032**

Fig. 1 Expected average percent increases of the accuracy of breeding values for mothers and offspring from a) the combined approach (***H*** matrix) with respect to the pedigree-based approach (***A*** matrix) by single-trait (ST) and multiple-trait (MT) individual-tree mixed model, and from b) the MT model with respect to the ST model by approach (***A*** and ***H***). In both cases, results are further classified by trait: diameter at breast height (DBH), total height (TH), and normal score of stem straightness (SS).



* Significant expected percent increment with t-test ($p < 0.05$).