

Multivariate Bayesian analysis for genetic evaluation and selection of *Eucalyptus* in multiple environment trials

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ABSTRACT: Forest plantations are strong allies in preserving natural resources, providing social and economic benefits. The plantations carried out in the coming years will be vital to meet the growing demand for forest products. To ensure the continuity of genetic progress and the good results achieved with the improvement of forest species, statistical methods that accurately selects superior genotypes are desirable. Multi-trait multi-environment trials are preferred over single-trait single-environment trials, since they can exploit the covariance between traits and environments, increasing the analysis's prediction power. The Bayesian multi-trait multi-environments approach (BMTME) combines the cited advantages with the parsimony of Bayesian statistics promoting a more informative data analysis. Thus, the aims of this study were to estimate genetic parameters, evaluate genetic variability, and select eucalyptus clones through BMTME models. To this end, a data set with 215 eucalyptus clones evaluated in four environments for diameter at breast height and Pilodyn penetration was used. The Markov Chain Monte Carlo algorithm was applied to estimate the variance components and genetic parameters and to predict the genotypic values. The Smith-Hazel index was used to simultaneously achieve gains with selection for both traits. The BMTME approach provided high accuracies, being a good strategy to the evaluation of multiple environmental trials of *Eucalyptus* for breeding purposes.

KEY WORDS: quantitative genetics, multi-environment trials, genotype × environment interaction, *Eucalyptus* spp., forest tree breeding.

INTRODUCTION

The search for increasing wood productivity is a driving force on tree improvement researches (Jansson et al. 2017). In Brazil, the genus *Eucalyptus* has more than 7.5 million ha planted with its species (IBGE 2019), mainly intended to produce cellulose, wood, and energy (Ramalho et al. 2021). The international pulp trade and the intense search for renewable energy sources have increasingly motivated the establishment of eucalyptus plantations in new areas (Fonseca et al. 2010). In this sense, eucalyptus breeding programs have sought to identify more efficient genetic evaluation methods to increase yield and quality of traits of industrial interest (Alves et al. 2020).

A constant concern in eucalyptus breeding is the genotype × environment interaction (GEI). In practice, there is a great divergence between the productivity indices in different environments, attesting to the presence of the GEI (Elli et al. 2019). This differential behavior is mainly related to different edaphoclimatic conditions across locations (Binkley et al. 2017). In countries with continental dimensions like Brazil (8, 547, 403 km², according to IBGE 2021), where the crop is cultivated

in many regions, this concern is reinforced. Therefore, conduct multi-environment trials (MET) is crucial to study the GEI, ensuring the crop's genetic progress.

Frequently, the eucalyptus breeding objective is to improve two or more traits (growth, wood quality, resistance/tolerance to biotic and abiotic stresses) simultaneously. However, when genetic selection is based on several traits, which may be genetically correlated due to pleiotropic genes and/or gametic phase imbalance, selection bias may occur if these traits are analyzed individually (Pollak et al. 1984). In this case, the use of the multi-trait best linear unbiased prediction (BLUP) tends to be more efficient since it considers a greater amount of data and uses the genetic and residual correlations between traits (Alves et al. 2018; Montesinos-López et al. 2019). In this context, the index proposed by Smith (1936) and Hazel (1943) can be used, considering the BLUPs. This index is suitable because it uses a linear combination of the considered traits, weighted by a weight established by the breeder.

The Bayesian inference has been used, with advantages, in the genetic evaluation of eucalyptus (Mora and Serra 2014; Davies et al. 2017; Valenzuela et al. 2019). The Bayesian inference offers greater flexibility when compared to the frequentist inference, allowing incorporate the uncertainties in the inference process and the generation of accurate results, even in the face of small samples (Silva et al. 2020; Peixoto et al. 2021).

This study aimed to test the null hypothesis, which states that there is no genotypic variability on the population to simultaneously achieve gain with selection for both diameter at breast height (DBH) and Pilodyn penetration (PP). Additionally, this study desired to estimate genetic parameters, evaluate genetic variability, and select eucalyptus clones through Bayesian inference.

MATERIAL AND METHODS

Experimental design and genetic material

The data used in this study refer to evaluation of a clonal test of eucalyptus, implemented in September 2007, in four experimental areas of the CMPC company, which are located in the state of Rio Grande do Sul, Brazil (Supplementary Table 1). In each experimental area, a trial in a randomized complete block design was established, with 215 clones (Supplementary Table 2) in single tree plots and 30 replications. Trees were planted at a spacing of 3.5 × 2.6 m.

The experiment consisted of performance evaluation of 22,295 3-year-old individuals regarding DBH (cm) and PP (mm). DBH was obtained using a diameter tape and PP by a Pilodyn device. The Pilodyn device uses the information of many previous laboratory tests to estimate the wood density. Its operation consists of inserting a 2.5-mm metallic pin into the wood and measuring the inversely proportional relationship between the depth of penetration and the hardness of the wood (Hasníková and Kuklík 2013). For PP evaluation, two measurements were made at the height of 1.3 m in the Northern and Southern cardinal directions of each tree, and the average value was used for the statistical analysis.

Statistical analyses

The Bayesian multi-trait multi-environment model was given by Eq. 1:

$$y = Xs + Zg + Wi + Qb + e \quad (1)$$

in which: y : the vector of phenotypic data; s : the vector of environment effects (systematic), added to the overall mean; g : the vector of genotypic effects (random), in which $g \sim N(0, \Sigma_g \otimes I)$; i : the vector of GEI effects (random), in which $i \sim N(0, \Sigma_i \otimes I)$; b : the vector of block effects (random), in which $b \sim N(0, \Sigma_b \otimes I)$; e : the vector of residuals (random), in which $e \sim N(0, \Sigma_e \otimes I)$. X , Z , W , and Q : the incidence matrices for the effects s , g , i , and b , respectively.

In this model, Σ_g is the unstructured genotype covariance matrix, Σ_i is the unstructured GEI covariance matrix, Σ_b is the unstructured block covariance matrix, Σ_e is the unstructured residual covariance matrix, I is an identity matrix with order appropriated to the respective effect, and \otimes is the Kronecker product. More information about covariance structures can be found in Mrode (2014) and Resende et al. (2014).

The Markov Chain Monte Carlo (MCMC) algorithm was used to estimate the variance components, genetic parameters and genotypic values via MCMCglmm R package (Hadfield 2010). The MCMC generates 1,000,000 cycles, with burn-in of 200,000 and thin of 10, resulting in 80,000 effectives samples. The convergence was checked by the Geweke criterion and by the Raftery and Lewis convergence criterion (Raftery and Lewis 1992) implemented in the boa R package (Smith 2007).

It was assumed that Σ_g , Σ_i , Σ_b , and Σ_e follow an inverted Wishart distribution WI, with hyperparameters ν and V (Sorensen and Gianola 2007). The hyperparameters for all prior distributions were selected to provide non-informative (flat) prior distributions, since this information is not available. For the systematic effects (s), a uniform prior distribution was established. Furthermore, the parameters g , i , b , e , Σ_g , Σ_i , Σ_b , and Σ_e were estimated by the joint posterior distribution (Eq. 2):

$$P(g, i, b, e, \Sigma_g, \Sigma_i, \Sigma_b, \Sigma_e | y_{ij}) \propto (y_{ij} | g, i, b, e, \Sigma_g, \Sigma_i, \Sigma_b, \Sigma_e) \cdot P(g, i, b, e, \Sigma_g, \Sigma_i, \Sigma_b, \Sigma_e) \quad (2)$$

The full model was compared with the reduced models by the deviance information criterion (DIC) (Spiegelhalter et al. 2002), which is a generalization of the Akaike information criterion (AIC), given by (Eq. 3):

$$DIC = D(\theta) + 2pD \quad (3)$$

in which: $D(\theta)$: a point estimate of the deviance obtained by replacing the parameters with their posterior mean estimates in the likelihood function; pD : the effective number of parameters in the model.

Models with lower DIC should be preferred over models with higher DIC. The highest probability density (HPD) was calculated for each estimate.

Posterior means and standard deviations (SD) for the estimated variance components, genetic parameters and genotypic values were obtained from MCMC samples.

The broad-sense heritability (h_g^2) was estimated according to Resende et al. (2014), given by Eq. 4:

$$h_g^2 = \frac{\hat{\sigma}_g^2}{\hat{\sigma}_g^2 + \frac{\hat{\sigma}_i^2}{n} + \frac{\hat{\sigma}_e^2}{nr}} \quad (4)$$

in which: $\hat{\sigma}_g^2$: the phenotypic variance; $\hat{\sigma}_i^2$: the GEI variance; $\hat{\sigma}_e^2$: the residual variance; n : the number of environments; r : the number of blocks.

The selective accuracy ($r_{\hat{g}_{g_i}}$) was estimated according to Resende et al. (2014) (Eq. 5):

$$r_{\hat{g}_{g_i}} = 1 - s(g_i)/g_i \quad (5)$$

in which: $s(g_i)$: the standard deviation of the estimated genotypic value (g_i).

Genotypic correlation (Pearson correlation) between DBH and PP ($r_{i,j}$) was estimated by Eq. 6:

$$r_{i,j} = \frac{\hat{\sigma}_{g_{i,j}}}{\sqrt{\hat{\sigma}_{g_i}^2 \hat{\sigma}_{g_j}^2}} \quad (6)$$

in which: $\hat{\sigma}_{g_{i,j}}$: the estimated genotypic covariance between DBH and PP traits; $\hat{\sigma}_{g_i}^2$: the estimated genotypic variance for the trait BDH; $\hat{\sigma}_{g_j}^2$: the estimated genotypic variance for the trait PP.

Selection index and gains with selection

The genotypic values estimated by the BMTME model for each trait were used to compose the Smith (1936) and Hazel (1943) index. The index was constructed aiming to simultaneously select genotypes with higher DBH and lower PP values, given economic weights and phenotypic and genotypic covariance matrices. The index is given by Eq. 7:

$$b = P^{-1} G a \quad (7)$$

in which: b : the vector of index coefficients; P : the matrix of phenotypic (co)variance; G : the matrix of genetic (co)variance; a : the vector of economic weighting coefficients.

The genetic worth of an individual genotype (I) was calculated using the index coefficients previously calculated (Eq. 8):

$$I = b_1 X_1 + b_2 X_2 \quad (8)$$

in which: b_1 : the index coefficient for DBH; b_2 : the index coefficient for PP; X_1 : the individual genotype BLUPs for DBH; X_2 : the individual genotype BLUPs for PP.

The clones were ranked based on their I values, and five clones were selected for planting, which is the selection intensity recommended by Resende (2002), for unrelated clones in clonal tests. The gains with selection, in percentage, [GS(%)] were calculated for both traits, according to Resende (2015) (Eq. 9):

$$GS(\%) = \frac{M_{Si} - M_{0i}}{M_{0i}} * 100 \quad (9)$$

in which: M_{Si} : the overall mean of the estimated genotypic value for the selected genotypes, for trait i ; M_{0i} : the overall mean of the estimated genotypic value for the population, for trait i .

RESULTS AND DISCUSSION

According to the DIC, there was evidence that the full model (DIC = 191,085.4) was the one that best fits the data. The DIC for genotypic, GEI, and block effects were 191,252.1, 194,926.8, and 192,638.9, respectively. Therefore, there is room for genetic selection in the evaluated population for both traits. The chains (covariance components) reached convergence with 80,000 effective samples, according to the Geweke criterion (absolute values of the Z statistic between -1.96 and 1.96) and the Raftery and Lewis criterion (dependence factor below 5) for both traits (Table 1). The posterior density of the genotypic and block variances showed the appearance of the χ^2 distribution (of which the Wishart distribution is a generalization), and the posterior density of the GEI and residual variances presented the behavior of a normal distribution for both traits (Fig. 1).

Table 1. Convergence diagnostic by Geweke and Raftery & Lewis criteria for the variance components for diameter at breast height (DBH) and Pilodyn penetration (PP) for selection of eucalyptus in a multiple environment trial.

Convergence criterion	Variance component				
	Trait	$\hat{\sigma}_g^2$	$\hat{\sigma}_i^2$	$\hat{\sigma}_b^2$	$\hat{\sigma}_e^2$
Geweke	DBH	0.64	1.31	-0.83	0.09
	PP	-0.5	1.14	0.22	0.64
Raftery & Lewis	DBH	1.01	1.01	1.01	1
	PP	0.99	1.03	1	1

$\hat{\sigma}_g^2$: genotypic variance; $\hat{\sigma}_i^2$: genotypes × environments interaction variance; $\hat{\sigma}_b^2$: block variance; $\hat{\sigma}_e^2$: residual variance.

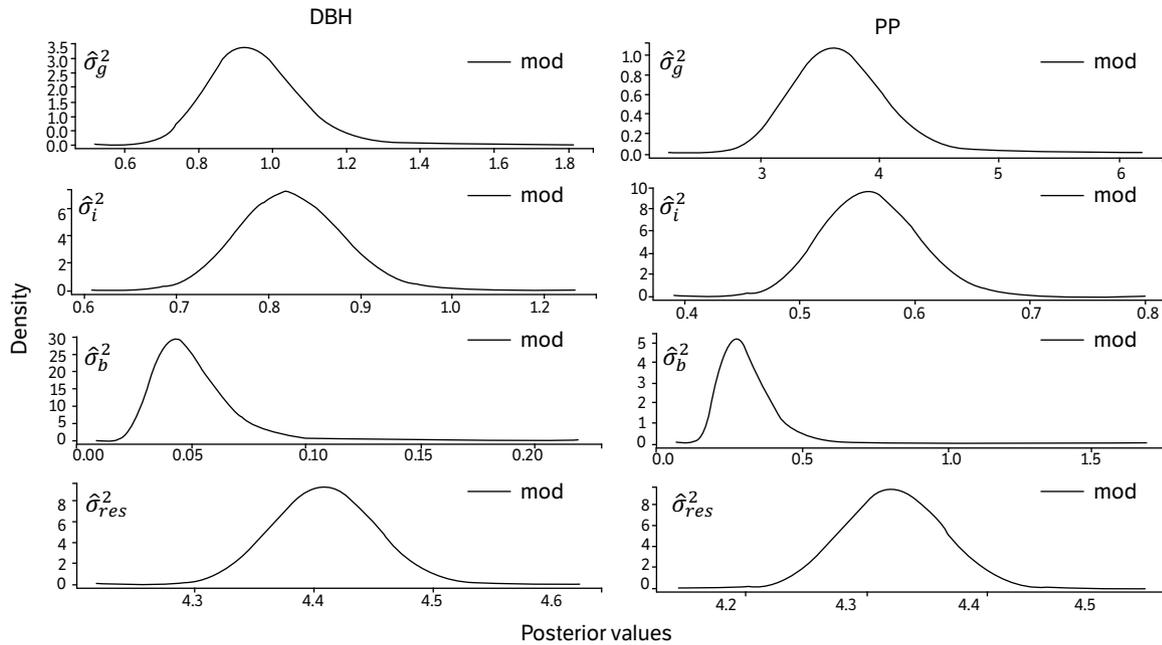


Figure 1. Posterior density of the variance components for diameter at breast height (DBH) and Pilodyn penetration (PP) for selection of eucalyptus in a multiple environment trial.

The HPD intervals demonstrated statistical significance for all random effects of BMTME model, since the intervals did not contain the zero value (Table 2). The HPD intervals ensure that the shortest possible interval with a given probability (e.g., 95%) for a given parameter was achieved (Chen et al. 2007). In complex cases, such the studied one, achieving the convergence of Bayesian models is easier compared to frequentist models (Resende and Rosa-Perez 2002).

Table 2. Estimates of variance components and genetic and non-genetic parameters for diameter at breast height (DBH) and Pilodyn penetration (PP) estimated through a Bayesian algorithm for selection of eucalyptus in a multiple environment trial.

Component/ parameter	DBH			PP		
	Lower	Mean	Upper	Lower	Mean	Upper
$\hat{\sigma}_g^2$	0.7276	0.9509	1.1888	2.9702	3.6685	4.4373
$\hat{\sigma}_i^2$	0.7176	0.8247	0.9364	0.4822	0.5624	0.6441
$\hat{\sigma}_b^2$	0.0238	0.0499	0.0824	0.1557	0.3028	0.4789
$\hat{\sigma}_e^2$	4.3250	4.4090	4.4919	4.2387	4.3221	4.4044
$\hat{\sigma}_p^2$	5.7940	6.2345	6.6995	7.8468	8.8558	9.9647
h_g^2	0.12	0.15	0.18	0.37	0.41	0.46
c_i^2	0.11	0.13	0.15	0.05	0.06	0.07
c_b^2	0.00	0.01	0.02	0.02	0.03	0.05
c_e^2	0.68	0.71	0.73	0.45	0.49	0.53
r_{gg}		0.89			0.97	
μ		13.61			18.77	
ρ_g			0.16			

$\hat{\sigma}_g^2$: genetic variance; $\hat{\sigma}_i^2$: genotypes × environments interaction (GEI) variance; $\hat{\sigma}_b^2$: block variance; $\hat{\sigma}_e^2$: residual variance; h_g^2 : broad-sense individual heritability; c_i^2 : coefficient of determination of GEI effects; c_b^2 : coefficient of determination of block effects; c_e^2 : coefficient of determination of residual effects; r_{gg} : selective accuracy; ρ_g : genotypic correlation.

According to Resende (2015), the heritability for DBH (0.15) and PP (0.41) were classified as moderate magnitude (Table 2). For DBH, similar results were found by Alves et al. (2020) using the same dataset under a frequentist approach, and by Vargas-Reeve et al. (2013) in a MET of *Eucalyptus cladocalyx* using Bayesian inference. For PP, slightly higher values were reported by Alves et al. (2020), and similar results were reported for *Eucalyptus* wood density under a Bayesian approach (Valenzuela et al. 2019).

The selective accuracy is an important statistical parameter for genotypic evaluation, because it reflects the correlation between predicted genotypic values and true genotypic values (Resende and Alves 2020). Therefore, values close to 1 are desired. The selective accuracies were classified as high (0.89) and very high (0.97) for DBH and PP, respectively (Resende and Alves 2020), similar to the ones reported by Alves et al. (2020). As proposed by Resende and Alves (2020), the genetic correlation between DBH and PP was classified as low magnitude (0.16) (Table 2), which means that selection aiming positive gains for one trait may not improve the performance of the other trait. There are discrepancies in genetic correlation between growth traits and density in *Eucalyptus* spp. (Nunes et al., 2017). It can be explained due to the natural genetic variation that exists in the evaluated populations and the differential gene expression for these traits.

Based on the Smith-Hazel index, it was possible to identify genotypes on the evaluated population that simultaneously increase DBH and reduce PP (Fig. 2), rejecting the study's null hypothesis. The expected gain with selection were 11.48 for DBH and -4.59% for PP, when the best five clones were selected for planting (Fig. 2), as recommended by Resende (2002). However, the weak correlation between DBH and PP provides much lower genetic gains than what could be achieved by direct selection (Resende 2015).

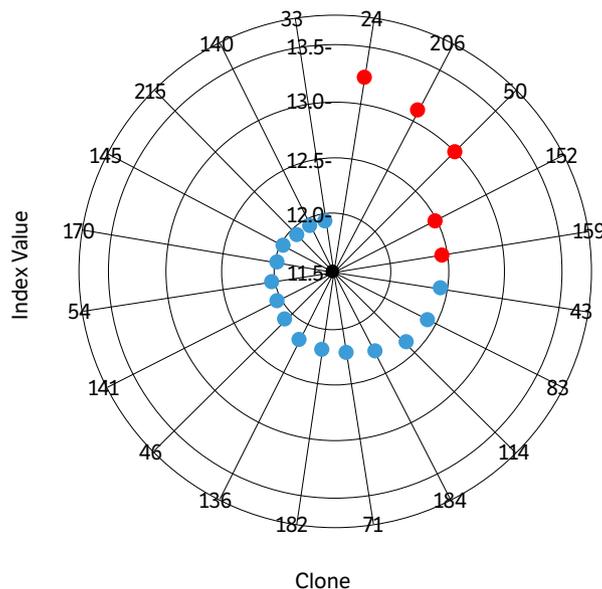


Figure 2. Ranking of the 20 clones by the Smith-Hazel index, aiming to increase diameter at breast height and decrease Pilodyn penetration for selection of eucalyptus in a multiple environment trial. The selected genotypes are represented by red circles.

Many authors pointed out the advantages of using multivariate analysis compared to the univariate one (Calus and Veerkamp 2011; Jia and Jannink 2012; Volpato et al. 2019), since considering the correlation between traits can better accommodate some non-genetic effects and help to elucidate the genetic control of a singular trait and the correlation between traits (Castro et al. 2013; Huang et al. 2015). The frequentist multi-trait BLUP method, proposed by Henderson and Quaas (1976), is broadly used for genetic evaluations of plant trials (Jia and Jannink 2012; Okeke et al. 2017; Mathew et al. 2018; Alves et al. 2019). On the other hand, the BMTME, despite its advantages, is still timidly used (Montesinos-López et al. 2019). In this study, the BMTME model proved to be very helpful for studying genetic and residual architecture for DBH and PP from MET of eucalyptus. The use of Bayesian inference for the evaluation of agricultural experiments is a trend in breeding programs (Schenkel et al. 2002; Waldmann et al. 2008; Silva et al. 2013; Junqueira et al. 2016; Peixoto et al. 2021), due to the improvement of computational power and novel methodological applications (Volpato et al. 2019). Therefore, the authors encourage the application of this methodology to other forest and agricultural crops.

CONCLUSION

The BMTME model provided high selective accuracies for DBH and PP. The genotypic variability presented in the evaluated population reveal that it can be used for selecting superior genotypes that simultaneously increase DBH and reduce PP values, rejecting the null hypothesis. The results gather by this work support the viability of the BMTME model for evaluation of MET of *Eucalyptus* for breeding purposes.

AUTHORS' CONTRIBUTION

Conceptualization: Ferreira, F. M. and Alves, R. S.; **Methodology:** Ferreira, F. M., Alves, R. S., Evangelista, J. S. P. C. and Chaves, S. F. S.; **Investigation:** Ferreira, F. M.; **Formal Analysis:** Ferreira, F. M., Alves, R. S., Evangelista, J. S. P. C. and Chaves, S. F. S.; **Writing – Original Draft:** Ferreira, F. M., Alves, R. S., Evangelista, J. S. P. C., Chaves, S. F. S., Silva, D. B. and Malikouski, R. G.; **Writing – Review and Editing:** Ferreira, F. M., Evangelista, J. S. P. C. and Chaves, S. F. S.; **Resources:** Resende, M. D. V., Bhering, L. L. and Santos G. A.; **Supervision:** Resende, M. D. V., Bhering, L. L. and Santos G. A.; **Data Curation:** Santos G. A. and Resende, M. D. V.

DATA AVAILABILITY STATEMENT

The data will be available upon request.

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SUPPLEMENTARY MATERIAL

Supplementary Table 1. Geographic location (GL) and annual climatic conditions (ACC) of each environment (E).

GL / ACC	CB	CP	FZ	SJ
Geographic coordinates	Latitude: 30°11'09" S	Latitude: 30°29'45" S	Latitude: 30°27'19" S	Latitude: 30°14'46" S
	Longitude: 52°00'10" W	Longitude: 52°19'35" W	Longitude: 52°39' 53" W	Longitude: 53°49'7" W
Altitude (m)	141	378	250	301
Average temperature (°C)	17.5	16	17	16.8
Absolute minimum temperature (°C)	-0.9	-1.7	-0.6	0.0
Absolute maximum temperature (°C)	32.3	30.7	33.3	34.7
Rainfall (mm)	1,422	1,564	1,368	1,133

CB: Minas do Leão, RS/Brazil (Forest Garden Cambará); CP: Encruzilhada do Sul, RS/Brazil (Forest Garden Capivara); FZ: Dom Feliciano, RS/Brazil (Forest Garden Fortaleza); SJ: Vila Nova do Sul, RS/Brazil (Forest Garden São João).

Supplementary Table 2. Hybrids of *Eucalyptus* evaluated in four environments: Minas do Leão, RS/Brazil (Forest Garden Cambará); Encruzilhada do Sul, RS/Brazil (Forest Garden Capivara); Dom Feliciano, RS/Brazil (Forest Garden Fortaleza); and Vila Nova do Sul, RS/Brazil (Forest Garden São João).

Two-way cross	Three-way cross	Four-way cross
<i>E. grandis</i> × <i>E. urophylla</i>	<i>E. urophylla</i> × (<i>E. grandis</i> × <i>E. urophylla</i>)	(<i>E. grandis</i> × <i>E. kirtoniana</i>) × (<i>E. robusta</i> × <i>E. tereticornis</i>)
<i>E. urophylla</i> × <i>E. maidenii</i>	<i>E. globulus</i> × (<i>E. grandis</i> × <i>E. urophylla</i>)	(<i>E. grandis</i> × <i>E. urophylla</i>) × (<i>E. urophylla</i> × <i>E. globulus</i>)
<i>E. pellita</i> × <i>E. grandis</i>	<i>E. grandis</i> × (<i>E. grandis</i> × <i>E. urophylla</i>)	
<i>E. grandis</i> × <i>E. maidenii</i>	<i>E. urophylla</i> × (<i>E. camaldulensis</i> × <i>E. grandis</i>)	
<i>E. grandis</i> × <i>E. dunnii</i>	<i>E. saligna</i> × (<i>E. grandis</i> × <i>E. urophylla</i>)	
<i>E. grandis</i> × <i>E. saligna</i>	<i>E. robusta</i> × (<i>E. grandis</i> × <i>E. urophylla</i>)	
<i>E. urophylla</i> × <i>E. saligna</i>	<i>E. grandis</i> × (<i>E. dunnii</i> × <i>E. grandis</i>)	
<i>E. urophylla</i> × <i>E. globulus</i>	<i>E. maidenii</i> × (<i>E. grandis</i> × <i>E. urophylla</i>)	
<i>E. grandis</i> × <i>E. globulus</i>	<i>E. saligna</i> × (<i>E. urophylla</i> × <i>E. grandis</i>)	
<i>E. globulus</i> × <i>E. tereticornis</i>	<i>E. urophylla</i> × (<i>E. grandis</i> × <i>E. globulus</i>)	
<i>E. urophylla</i> × <i>E. deanei</i>	<i>E. urophylla</i> × (<i>E. tereticornis</i> × <i>E. saligna</i>)	
<i>E. urophylla</i> × <i>E. tereticornis</i>	<i>E. urophylla</i> × (<i>E. urophylla</i> × <i>E. grandis</i>)	