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Genetic control of coppice regrowth in *Eucalyptus* spp.

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Abstract

Forest companies prefer a coppice system as a silvicultural strategy owing to its economic and sustainability advantages compared to developing new plantations for second rotations. However, studies aiming to determine the selection of superior genetic material for this management strategy are scarce. In this study, we evaluated five clonal tests of *Eucalyptus* spp. located in Itatinga and Angatuba, São Paulo State, Brazil, to determine the genetic correlations and control of productivity for regrowth management in two rotations. The volume (m^3) and survival of the *Eucalyptus* spp. clonal tests were determined for the two rotations at 5.5 years of age. The experiments were carried out in a randomized block design with six replicates, five plants per plot, and unbalanced treatments. The heritability in the normal scale ($\hat{h}_n^2$) for the survival ranged from 0.056 to 0.11, the heritability in the broad sense ($\hat{h}_g^2$) ranged from 0.205 to 0.334, and the genotypic correlation was positive and high (0.71-0.86), and statistically significant to the genetic means for the two rotations. The ranking of the best clones in the second rotation was similar (76 %) to their ranking in the first selection. Thus, for the evaluated material, there was no need for the second measurement to obtain accurate selection when managing a coppice system.

Keywords: : *coppice, quantitative genetics, tree breeding, urograndis*

Introduction

Trees of the *Eucalyptus* genus have a high commercial value because of characteristics like trunk straightness, elevated growth rates, the possibility of vegetative propagation, good mechanical wood quality, and adaptation to diverse climatic conditions (Eldridge et al., 1993). The *Eucalyptus* species in Brazil present the highest productivity and the lowest rotation time in the world (IBÁ, 2017).

Some Brazilian forest companies have begun to use a coppice system as a silvicultural practice, which consists of retaining sprout growth for the second rotation, in *Eucalyptus* plantations. This system is more economical (Guedes et al., 2011; Crous and Burger, 2015) and sustainable (Takahashi et al., 2009; Gabrielle et al., 2013; Zhou et al., 2017) than establishing new plantations. In forest plantations, the coppice system can only be used with species that re-sprout from the epicormic buds present on the trunk after a clear-cut. This silvicultural system presents a high rate of initial growth compared to the first rotation because of a range of factors, including organic and inorganic sources available to stumps and an already formed root system that facilitates initial plant growth (Reis and Kiminns, 1986; Reis and Reis, 1991; Whittock et al., 2003).

However, in some cases, the volume of production in the second rotation is lower than that observed in the first rotation (Ribeiro et al., 1987; Fontenele et al., 2018). This is associated with many factors, such as the season and height of cutting, the number of sprouts retained, the health of the stump,

location of the plantation, and genetic material (Ribeiro et al., 1987; Higa and Sturion, 1997; Perrando and Corder, 2006).

Estimating genetic parameters can be understood as the search for methods to determine the genetic mechanisms underlying quantitative traits and the kind of selection that must be used in breeding programs (Vencovsky, 1969). The genetic control of traits can be assessed by using the estimates of the genetic parameters obtained from the mean or variance components (Falconer and Mackay, 1996).

Owing to the scarcity of the genetic information on the regrowth capacity of *Eucalypts*, this study aimed to estimate the genetic control of productivity for coppice systems in the *Eucalyptus* spp. clones and answer the following questions: (i) are there any genetic correlations between the observed productivities of the first and the second rotation coppice systems? (ii) is clonal selection necessary for the second rotation?

Materials and Methods

Experimental material

The data used for this experiment include the measurements taken before the forest plantation clear-cut for the first and second rotations of five clonal tests (Table 1) that were parts of independent experiments belonging to the Duratex S/A forest company. Therefore, the clones and species evaluated were not necessarily the same in all different locations, making it impossible to perform analysis across the sites. The species used in the experiments were *Eucalyptus grandis* W. Hill ex Maiden (from Coffs Harbour), *Eucalyptus saligna* Sm. (undefined provenance), *Eucalyptus urophylla* S.T. Blake (from the Island Flores), and the hybrid *E. urophylla* × *E. grandis* (*E. urograndis*). The clonal test was established using a randomized block design, with linear plots of five trees, six blocks, and different number of treatments (Table 1). The experiments were established in the municipalities of Itatinga and Angatuba, São Paulo State. According to the Köppen and Geiger (1936) classification, the climate of the study area was classified as Cfa: humid, temperate with hot summers, annual average temperatures of 19.1 °C and 19.9 °C, and annual average rainfalls of 1,308 mm and 1,215 mm for Itatinga and Angatuba, respectively. Four of the study areas presented the soil classified as typic dystrophic Red-Yellow Latosols with a sandy, medium texture, and the fifth area presented dystrophic Red Latosol with a clayey texture.

Planting for the first rotation was realized in 2001 for all tests and measurements before forest clear-cut were conducted in 2007 for the first rotation and in 2012 for the second rotation. Two sprouts per individual were retained for all plants, except for the plants located next to the individuals that failed to re-sprout, for which three sprouts were retained.

The individual volume was estimated using volumetric equations provided by the company. The measurement of diameter at breast height (DBH) and total height was performed using a diameter calliper and hypsometer, respectively. Survival was evaluated for both rotations in each site.

Table 1

Clonal tests of *Eucalyptus* spp. evaluated at 5.5 years of age in each rotation, with their respective number of treatments (clones) and spacing. Experiments 1, 2, 3, and 4 were established in Itatinga, SP, and experiment 5 in Angatuba, SP.

	Species/number of treatments				
Experiment	*E. grandis*	*E. urograndis*	*E. saligna*	*E. urophylla*	Spacing (m)
1	20	1	2	1	4.5 × 1.33
2	20	15	0	0	4 × 1.2
3	23	8	0	11	4.5 × 1.33
4	11	1	0	11	4.5 × 1.33
5	33	3	1	19	4 × 1.5

Statistical analysis

We estimated the components of variance for volume and survival for both measurements in each site, using the variance analysis and the following addictive model:

$$y = X\beta + Zg + Wb + e,$$

where *y* is a vector of measurements at two different rotations for each tree, *β* is the vector of block effects (fixed), *g* is the vector of clone effects, *b* is the effects of clone x rotation interaction, and *e* is the vector of residual effects with normal and homoscedastic distribution; *g, b,* and *e* are random effects; *X, Z,* and *W* represent the incidence matrices for the respective effects.

The analysis was performed using the software R (R Core Team 2018) and the mixed-model statistical package *lme4* (Bates et al., 2015). In this package, we used the lmer function to estimate the variance components by restricted maximum likelihood (REML).

Genetic parameter estimates

The following components of variance were estimated: genetic variance among clones ($\hat{\sigma}_g^2$), residual variance ($\hat{\sigma}_e^2$), clone × rotation variance ($\hat{\sigma}_{gr}^2$), and phenotypic variance ($\hat{\sigma}_f^2 = \hat{\sigma}_g^2 + \hat{\sigma}_e^2 + \hat{\sigma}_{gr}^2$). From the variance components, we obtained:

a) Heritability in the broad sense: $\hat{h}_g^2 = \dfrac{\hat{\sigma}_g^2}{\hat{\sigma}_f^2}$

b) For survival, the heritability in the normal range and broad sense: $h_n^2 = h_{0/1}^2 [p(1-p)]/z^2$ (Dempster and Lerner, 1950); where $h_{0/1}^2$ is the binomial heritability in the broad sense, *p* is the frequency of phenotype; and *z* is the order of the standard normal curve corresponding to the probability *p* .

c) Experimental variation coefficient: $\widehat{CV}_{exp} = \dfrac{\sqrt{\hat{\sigma}_e^2}}{\hat{m}}$; where $\hat{m}$ is the mean.

d) Genetic variation coefficient: $\widehat{CV}_g (\%) = \dfrac{\sqrt{\hat{\sigma}_g^2}}{\hat{m}} * 100$; where $\hat{m}$ is the mean volume.

For survival, the heritabilities were estimated at the binomial scale and later transformed to the standard scale. This transformation is only applicable when the heritabilities are less than or equal to 0.3, which was the case in our study (Van Vleck, 1971; Lopes et al., 2000).

BLUPs and correlation estimates

We obtained the best linear unbiased predictions (BLUPs) using the genetic values generated by the ranef function of the mixed-model lme4 package (Bates et al., 2015) in the R software (R Core Team, 2018). The correlations were estimated using the chart.correlation function of the Performance *Analytics* package (Peterson and Carl, 2018), which uses the Pearson coefficient of correlation by default. For this analysis, we considered the mean prediction of each clone in each rotation.

Results

The average survival was lower in experiments 4 and 5 (< 70 %) than the other experiments (84.6-90.3 %, Table 2). The heritabilities in the normal range and narrow sense were low in all experiments, ranging from 0.057 (experiment 4) to 0.112 (experiment 1).

Significant (1 % for LRT) differences among clones and clone × rotation interactions were detected for the volume in all five experiments (Table 3). However, no differences were detected in experiment 5 among clones and clone × rotation interactions for survival, but it was the only experiment with significant interaction between clones and rotation. This suggests that the clones presented different survival between rotations. The clone × block interactions were significant in all experiments for both traits (Table 4).

The residual variance ($\hat{\sigma}_e^2$: 0.018-0.029) was predominantly higher than the other variance components (Table 5). The heritability in the broad sense ($\hat{h}_g^2$) ranged from 0.190 (experiment 3) to 0.281 (experiment 1).

For selecting the best genetic material, the best linear unbiased prediction (BLUP) associated with the random effect of $\hat{\sigma}_g^2$ (g) was added to the BLUP associated with the random interaction between clones and rotation $\hat{\sigma}_{gr}^2$ (ge) plus the mean of their respective trait at each rotation (*u*). On average, 76 % of the clones selected in the first evaluation were also the best in the second rotation. This result was particularly evident in experiment 3, wherein nine of the top ten clones were also observed among the top ten in the second rotation, while in experiment 1, only five of the top ten were observed in the next rotation (Table 6).

Positive and high correlations were observed among the rotations in the coppice system for all experiments (Figure 1) when performed for the mean genetic values predicted for the clones in each rotation, corroborating the results presented in Table 6. The Pearson correlation coefficient was high (0.71-0.86), suggesting that such variation might help select clones in the first rotation for production after regrowth.

Table 2

Estimates of genetic parameters for the *Eucalyptus* spp. clones obtained from the combined analysis of survival for two rotations, each evaluated at 5.5 years of age. Experiments 1, 2, 3, and 4 were established in Itatinga, SP, and experiment 5 in Angatuba, SP.

Parameter	Experiments				
	1	2	3	4	5
$\hat{\sigma}_f^2$	0.122	0.085	0.129	0.224	0.168
$\hat{\sigma}_g^2$ (SE)	0.006 (0.0025)	0.002 (0.0012)	0.006 (0.002)	0.008 (0.004)	0.009 (0.003)
$\hat{\sigma}_{gr}^2$	0	0	0	0	0.026 (0.001)
$\hat{\sigma}_e^2$ (SE)	0.116 (0.004)	0.083 (0.002)	0.123 (0.0035)	0.216 (0.008)	0.158 (0.010)
$\hat{h}_{0/1}^2$ (SE)	0.048 (0.02)	0.029 (0.02)	0.048 (0.01)	0.035 (0.02)	0.048 (0.02)
$\hat{h}_n^2$	0.112	0.084	0.111	0.057	0.081
$\overline{CV}_g$(%)	8.9	5.5	9.3	13.6	14.2
$\overline{CV}_e$(%)	39.8	31.8	41.5	72.1	58.7
$\bar{x}(\sigma)$ %	85.5 (35.2)	90.3 (29.6)	84.6 (36.1)	64.5 (47.9)	67.8 (46.7)

$\hat{h}_{0/1}^2$: inomial heritability in the narrow sense; $\hat{h}_n^2$: heritability in the normal range in the narrow sense; $\overline{CV}_g$(%) : coefficient of genetic variation; $\overline{CV}_e$(%) : coefficient of experimental variation; $\bar{x}$: mean survival (standard deviation), SE: standard error.

Table 3

Analysis of deviance and likelihood ratio test (LRT) for the volume (m³) and survival of the *Eucalyptus* spp. clones and clone ×
rotation interactions in two rotations at 5.5 years of age. Experiments 1, 2, 3, and 4, were established in Itatinga, SP, and experiment 5 in Angatuba, SP.

Trait	Deviance	Experiment				
		1	2	3	4	5
Volume (m³)	LRT$_{Clone}$	12.164*	35.091*	29.925*	12.028*	12.058*
	LRT$_{Clone \times Rotation}$	98.245*	12.794*	24.731*	26.134*	96.613*
Survival	LRT$_{Clone}$	10.332*	7.494*	17.798*	10.296*	2.361
	LRT$_{Clone \times Rotation}$	0	0.2178	0.017	0	124.975*

*: significant at 1% probability by LRT; LRT$_{Clone}$: likelihood ratio test of clone; LRT$_{Clone \times Rotation}$: likelihood ratio test of clone × rotation interaction.

Table 4

F test with Satterthwaite approximation for fixed effects (F$_{Clone \times Block}$) for the traits, volume (m³) and survival, of the *Eucalyptus*
spp. clones in two rotations at 5.5 years of age. Experiments 1, 2, 3, and 4 were established in Itatinga, SP, and experiment 5 in
Angatuba, SP.

	Volume (m³)	Survival
Experiments	P-value	P-value
1	0.0007	<0.0001
2	0.0052	<0.0001
3	<0.0001	<0.0001
4	<0.0001	<0.0001
5	<0.0001	<0.0001

Table 5

Estimates of genetic parameters for the *Eucalyptus* spp. clones obtained from the combined analysis of volume (m³) for two
rotations, each evaluated at 5.5 years of age. Experiments 1, 2, 3, and 4 were established in Itatinga, SP, and experiment 5 in
Angatuba, SP.

Parameter	Experiments				
	1	2	3	4	5
$\hat{\sigma}_f^2$	0.032	0.030	0.027	0.044	0.042
$\hat{\sigma}_g^2$	0.009 (0.0035)	0.007 (0.0019)	0.005 (0.0016)	0.011 (0.0049)	0.01 (0.0022)
$\hat{\sigma}_{gr}^2$	0.005 (0.0015)	0.001 (0.0005)	0.001 (0.001)	0.004 (0.004)	0.009 (0.004)
$\hat{\sigma}_e^2$	0.018 (0.0007)	0.022 (0.0007)	0.021 (0.0007)	0.029 (0.0014)	0.023 (0.0009)
$\hat{h}_n^2$	0.281 (0.08)	0.233 (0.05)	0.190 (0.05)	0.25 (0.10)	0.24 (0.08)
$\overline{CV}_g(\%)$	32.49	26.26	22.67	26.45	30.26
$\overline{CV}_e(\%)$	45.88	46.50	44.66	42.66	45.25
$\bar{x}(\sigma)$	0.295 (0.181)	0.322 (0.175)	0.327 (0.173)	0.403 (0.221)	0.332 (0.203)

$\hat{\sigma}_f^2$: phenotypic variance; $\hat{\sigma}_g^2$: quadratic component associated with genotypic variance; $\hat{\sigma}_{gr}^2$: variance of the clone x rotation interaction;
$\hat{\sigma}_e^2$: residual variance; $\hat{h}_n^2$: heritability in the broad sense for mean clones; $\overline{CV}_g(\%)$: coefficient of genetic variation; $\overline{CV}_e(\%)$: coefficient of
experimental variation; $\bar{x}$: mean volume (m³) (standard deviance).

Table 6
Best Linear Unbiased Prediction (BLUP) for volume based on the means of the clones from two rotations and ranking of the best *Eucalyptus* spp. clones at 5.5 years. Experiments 1, 2, 3, and 4 were established in Itatinga, SP, and experiment 5 in Angatuba, SP.

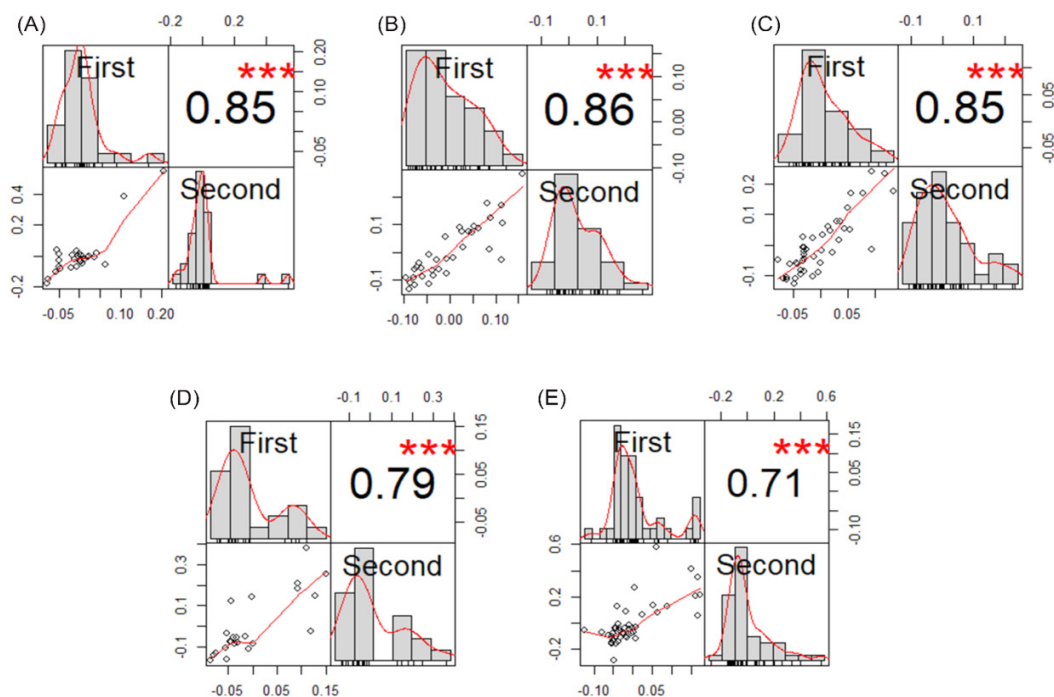| Ranking	Experiment 1				Experiment 2				Experiment 3				Experiment 4				Experiment 5			
	Rotation 1		Rotation 2		Rotation 1		Rotation 2		Rotation 1		Rotation 2		Rotation 1		Rotation 2		Rotation 1		Rotation 2	
	Clone	*g+ge+u*	Clone	*g+ge+u*	Clone	*g+ge+u*	Clone	*g+ge+u*	Clone	*g+ge+u*	Clone	*g+ge+u*	Clone	*g+ge+u*	Clone	*g+ge+u*	Clone	*g+ge+u*	Clone	*g+ge+u*
1	159	0.512	159	0.845	119	0.498	119	0.605	144	0.431	108	0.541	158	0.502	151	0.841	157	0.438	149	1.035
2	119	0.408	119	0.653	115	0.435	118	0.502	152	0.427	152	0.539	151	0.497	158	0.729	156	0.433	144	0.879
3	70	0.322	50	0.337	96	0.424	115	0.501	108	0.406	144	0.493	146	0.480	143	0.680	147	0.427	156	0.821
4	61	0.316	79	0.335	118	0.414	120	0.461	112	0.379	112	0.477	143	0.449	147	0.657	143	0.427	133	0.716
5	49	0.303	70	0.324	120	0.407	96	0.452	145	0.361	145	0.469	153	0.447	146	0.629	144	0.421	157	0.708
6	34	0.298	68	0.313	97	0.395	99	0.427	135	0.360	148	0.430	147	0.443	104	0.611	96	0.347	143	0.694
7	41	0.284	9	0.312	101	0.380	107	0.422	148	0.347	109	0.390	104	0.351	136	0.580	149	0.343	96	0.587
8	76	0.284	76	0.312	107	0.377	106	0.417	117	0.337	102	0.386	72	0.322	153	0.475	145	0.323	100	0.586
9	63	0.283	49	0.303	99	0.371	98	0.409	95	0.330	95	0.368	154	0.319	13	0.438	100	0.314	92	0.578
10	30	0.279	62	0.301	103	0.362	103	0.406	109	0.328	117	0.367	85	0.317	154	0.428	95	0.282	147	0.543

Figure 1
Estimates of genotypic correlations with volume in five experiments for the *Eucalyptus* spp. clones in two different rotations based on the Pearson correlation coefficient. Letters A, B, C, D, and E represent experiments 1, 2, 3, 4, and 5, respectively. ***P < 0.001. Experiments 1, 2, 3, and 4 were established in Itatinga, SP, and experiment 5 in Angatuba, SP.

Discussion

The significant effects found for the survival trait in the four experiments (1, 2, 3, and 4) indicated that this trait varied according to the genetic material, whereas the opposite was seen for the interaction between clones and rotation, wherein the result was not significant for the same four experiments, indicating that rotation did not influence survival (Table 3).

The high average percentage of survival obtained in experiments 1, 2, and 3 (Table 2) is similar to that reported previously in the literature for *Eucalyptus* spp. clones at ages up to 7 years (Souza et al., 2012; Fontenele et al., 2018). The high average of survival allowed us to conclude that the materials are well adapted to the experimental environments 1, 2, and 3, and survival is not an essential trait for selection in this specific breeding program.

The heritability (in the normal scale) for survival was low in all experiments, according Stansfield (1974) heritability classification (low < 0.2, intermediary: 0.2-0.5; high > 0.5). Studying the clones of *E. grandis*, Osorio et al. (2001) observed similar values for survival heritability (0.11) in an experiment with similar averages of survival (close to 90 %).

The heritability ($\hat{h}_g^2$) value for volume was intermediate in all experiments, except for experiment 3, in which the heritability value was low.

For both traits (volume and survival), the residual coefficient of variation ($\widehat{CV}_e(\%)$) was very high (31.8-72.1 %). According to the classification of Mora and Arriagada (2016), values of $\widehat{CV}_e(\%) > 30$ % are usually indicative of poorly controlled experiments or problems in the data (Brown, 1998; Taylor et al., 1999). However, for field experiments, especially those with forest species, it is very common to find the values of $\widehat{CV}_e(\%)$ above 30 % (Moraes et al., 2015). It is important to emphasize that volume is an indirectly obtained trait, and therefore, it gathers both the measurement errors of the variables used in its estimation (diameter at breast height and height) as well as the errors of the estimate itself (residual error). This fact also helps in increasing the $\widehat{CV}_e(\%)$ estimates.

The coefficient of genetic variation ($\widehat{CV}_g(\%)$) for volume indicated high levels of genetic variability in all five experiments. These results can be explained by the fact that the trials present more than one *Eucalyptus* species, increasing the $\widehat{CV}_g(\%)$ value in each experiment. In most cases, the $\widehat{CV}_g(\%)$ values reported in the studies based on the pure populations of *Eucalyptus* spp. (Kageyama and Vencovsky, 1983; Santos et al., 2015; Henriques et al., 2017) were lower than those obtained in the studies on the hybrid populations (Moraes et al., 2014; Paludeto et al., 2017; Tambarussi et al., 2017a, b). Thus, the $\widehat{CV}_g(\%)$ value was increased probably because of the presence of two or more genomes in each population, resulting in high genetic variability.

In experiments 1 and 2, the top-ranked clones across both rotations were the same (clone 159 and 119, respectively). For all clones evaluated, the genetic values predicted in the second rotation were superior to those predicted in the first; this can be explained by the larger individual volume observed in the second clear-cut, given the retention of more than one sprout per tree, thereby increasing its volume considerably.

Gonçalves et al. (1997) studied clonal response in the second rotation based on the selection made in the first rotation for *E. grandis* half-sib families. They observed that compared to the first rotation, the gains were greater than 67 % of the expected gains if the selection was performed directly in the second rotation, indicating this strategy has a high level of accuracy. Nevertheless, the Pearson correlation results allowed us to infer that the clones selected in the first rotation would be the best in the coppice system. Thus, considering the lack of other studies that corroborate with one or another conclusion, a possible strategy is to perform a preliminary evaluation, considering the plant genetic material in both rotations, to understand the response to clonal selection in each breeding program.

Conclusions

A high and positive genotypic correlation exists between the productivities obtained for the coppice silvicultural system in the first and second rotations.

In the present breeding program, there was no need to perform a selection in the second rotation for the coppice system; this increased the efficiency and genetic gains in the breeding programs for this production system. Future studies are necessary to conclude the overall behaviour of clonal selection in coppice systems.

Conflict of Interest

The authors declare that they have no conflict of interest.

Acknowledgments

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