

ARTICLE

Estimation of genetic parameters in rubber progenies

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Abstract - This study was designed to evaluate the genetic variability, the potential for rubber yield and secondary traits of rubber tree progenies at three locations in the state of Sao Paulo. The experiments were conducted in a randomized block design with 22 progenies and 6 replications. At the age of three years, the progenies were evaluated for rubber yield, girth growth and total number of latex vessel rings. The results showed the existence of genetic variability among progenies for each location separately as well as between locations, with differences in the progeny performance for the traits. The individual heritabilities calculated for rubber yield, girth growth and total number of latex vessel rings (0.30, 0.63 and 0.29, respectively), associated with high genetic gains with selection for the traits studied at each site, showed that the populations can be considered suitable for the rubber breeding program, provided that an appropriate selection procedure is used.

Key words: Hevea, genetic variance, linear mixed model.

INTRODUCTION

The breeding of rubber tree (*Hevea brasiliensis* (Willd. ex Adr. de Juss.) Muell.-Arg.) is based mainly on generating plants with high yield potential, followed by other secondary traits that contribute to the desirable increase in yield potential (Gonçalves et al. 2001). However, the time to produce and test new genotypes would require at least 20-30 years, until the final recommendation. These aspects have caused breeders to study possibilities of reducing the rubber tree selection cycle (Priyadarshan et al. 2009).

Quantitative information is based on the level of genetic variation, on the type of gene action and on the heritability of economically important traits. It is useful to determine the difficulty of selection and find strategies to overcome these problems, and in a broader context, it extends the knowledge on the genetic and reproductive behavior of the involved species (Gonçalves et al. 2006).

Estimating genetic parameters provides information about the nature of gene action involved in the trait inheritance and underlies the establishment of breeding plans. Thus, quantitative genetics, in general, explains almost all

phenomena involved in genetic breeding (Vencovsky and Barriga 1992). Studies of genetic variances and genetic gain in the juvenile plant stage can maximize genetic gains while shortening the breeding cycle (Adams et al. 2007).

This study was designed to evaluate the genetic variability, the potential for rubber yield and secondary traits in rubber progenies at three locations in the State of São Paulo.

MATERIAL AND METHODS

The study was conducted using 22 rubber half-sib progenies from superior parental clones, derived from genotypes introduced from Southeast Asia in 1952, at the Agronomic Institute (IAC). The experiments were conducted in three regional centers of the São Paulo Agency of Agribusiness Technology (APTA), in the municipalities of Jaú, Pindorama and Votuporanga, representing different regions of rubber cultivation in the State of São Paulo (Table 1). The experiments were conducted in a randomized block design with 22 treatments, 6 replications and 10 plants per plot (spacing 1.5 x 1.5 m).

The rubber yield (RY) was obtained by the modified early Hamaker Morris-Mann test (HMM) for three-year-old seed-

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lings (Tan and Subramaniam 1976), based on the average dry rubber yield of 20 consecutive tappings per plant. The tapping panel was opened 15 cm above the ground, using a 1/2S d/3 ET 2.5% (i.e., half-spiral tapping every three days, stimulation with 2.5% ethephon), with a total of 25 tappings, discarding the first five tapping samples that corresponded to the adaptation of the panel.

The girth growth was determined (GG, in cm) at 50 cm from the ground with a measuring tape. The total number of latex vessel rings (NR) was counted by examining radial longitudinal sections.

Analysis of variance

Analysis of individual variance

The studied variables referring to the data of each assessment of each site were analyzed using the mathematical model that considers all effects except the mean as random, expressed as:

$$Y_{ijk} = \mu + p_i + b_j + e_j + d_{ijk}, \text{ where}$$

Y_{ijk} : observation of plant k in replication j , in progeny i ; μ : the general mean; p_i : random effect of the i -th variable of the progeny ($i = 1, 2, \dots, p$); b_j : effect of replication j ($j = 1, 2, \dots, b$); e_j : effect of experimental error associated with progeny i of plot j ; d_{ijk} : deviation inherent to plant k ($k = 1, 2, \dots, n$) within plot ij .

The estimation of variances was based on the plot means at each location, as recommended by Steel and Torrie (1980). The variances within plots (σ_d^2) were calculated using data of individual plants, and the means of these plot variances were considered as the respective mean squares. The other estimates of variance components were computed by the mathematical expectation of mean squares.

Combined analysis of variance

The combined analysis of variance was performed according to the mathematical model that considers the local and genotypes as random effects (Vencovsky and Barriga 1992):

$$Y_{ijlm} = \mu + b_{j/k} + p_i + a_k + (pa)_{ik} + e_{ijk} + d_{ijkl}, \text{ where,}$$

μ : general mean; p_i : effect of the j -th progeny ($i = 1, 2, \dots, p$); a_k : effect of the k -th location ($k = 1, 2, \dots, a$); $(pa)_{ik}$: interaction effect of the j -th progeny with the k -th location; e_{ijk} : effect of experimental error of the plots, d_{ijkl} : deviation inherent to plant l of progeny i , in replication j at location k .

The expected mean squares [E (MS)], considering the model for combined analysis in randomized blocks, were based on Cruz and Regazzi (2004).

Table 1. Descriptive variables of the experimental sites of progeny testing in the State of São Paulo

Descriptive variables	Locations		
	Jaú	Pindorama	Votuporanga
Spacing (m)	1.5 x 1.5	1.5 x 1.5	1.5 x 1.5
Planting density	1 row x 10 plants 10 plants plot ⁻¹	1 row x 10 plants 10 plants plot ⁻¹	1 row x 10 plants 10 plants plot ⁻¹
Experimental design	RBD ¹	RBD ¹	RBD ¹
Number of replications	6	6	6
Altitude (m)	580	560	450
Latitude (S)	22° 17'	21° 13'	20° 25'
Longitude (W)	48° 34'	48° 56'	49° 59'
Temperature (annual mean)	21.6°	21°	22.3°
Annual rainfall (mm) (annual mean)	1.344	1.390	1.480
Soil Type	Ferralsol	Acrisol	Lixisol
Terrain	Flat	Flat	Flat

¹ Randomized block design

Estimates of genetic and phenotypic parameters

The estimates of variance components were obtained by the methodology of mixed linear model Reml/Blup (restricted maximum likelihood and best linear unbiased prediction), according to the procedure proposed by Resende (2002a).

The genetic-statistical software Selegen-Reml/Blup (Resende 2002b) was used. The following genetic parameters were estimated from the individual location analyses:

$$\hat{h}_a^2 = \frac{4\hat{\sigma}_p^2}{4\hat{\sigma}_p^2 + \hat{\sigma}_e^2 + \hat{\sigma}_d^2} \quad (\text{Individual narrow-sense heritability});$$

$$\hat{c}^2 = \frac{\hat{\sigma}_e^2}{4\hat{\sigma}_p^2 + \hat{\sigma}_e^2 + \hat{\sigma}_d^2} \quad (\text{Correlation due to the common environment of the plot});$$

$$\hat{h}_{mp}^2 = \frac{\hat{\sigma}_p^2}{\hat{\sigma}_p^2 + \hat{\sigma}_e^2/b + \hat{\sigma}_d^2/(nb)} \quad (\text{mean heritability of the progenies});$$

$$\hat{\sigma}_f^2 = 4\hat{\sigma}_p^2 + \hat{\sigma}_e^2 + \hat{\sigma}_d^2 \quad (\text{Individual phenotypic variance});$$

$$CV_{g_i}(\%) = \sqrt{\frac{4\hat{\sigma}_p^2}{\bar{x}}} \cdot 100 \quad (\text{Coefficient of individual genetic variation});$$

$$CV_{e_i}(\%) = \sqrt{\frac{\hat{\sigma}_e^2}{\bar{x}}} \cdot 100 \quad (\text{Coefficient of environmental variation among plots});$$

$$\hat{h}_g^2 = \frac{\sigma_p^2}{((\sigma_d^2/nba) + (\sigma_e^2/ba) + (\sigma_{pa}^2/a) + \sigma_p^2)} \quad (\text{Heritability of progeny mean across locations, where:}$$

$\hat{\sigma}_p^2$: genetic variance among progenies;

$\hat{\sigma}_d^2$: residual variance within plots;

$\hat{\sigma}_e^2$: environmental variance among plots.

Selective accuracy $c(\hat{r}_{aa})$ obtained by the square root of the progeny mean heritability.

RESULTS AND DISCUSSION

The individual values of mean squares, as well as the means and coefficient of experimental variation for rubber yield (RY), the total number of latex vessel rings (NR) and girth growth (GG), referring to the individual and combined analyses, are shown in Tables 2 and 3, respectively.

The means for NR were highest in Jaú (3.16), followed by Pindorama (3.06) and Votuporanga (2.98). Mean for GG varied little between locations (8.68 cm in Jaú, 10.36 cm in Pindorama and 11.84 cm Votuporanga). For the means of RY, substantial differences were observed between Jaú (0.89 g) compared to Pindorama (0.48 g) and Votuporanga (0.43 g). The values obtained are consistent with those found for rubber yield by Costa et al. (2000). These data indicate that the plant material of Jaú may be more productive and maximize genetic gains in the sequence of the breeding program. The combined means of all locations were 2.65 for NR, 9.61 cm for GG, and 0.33 g for RY.

The genetic variability was evidenced by the significant effects at 1% probability for all traits at the three locations,

Table 2. Means, mean squares of analysis of variance and experimental coefficients of variation (CVe %) for the variables rubber yield (RY), girth growth (GG), and total number of latex vessel rings (NR), based on of 22 progenies of rubber assessed at three locations in the State of São Paulo

Location	Variable	Mean square			Mean	CVe (%)
		Progeny	Residue	Plot		
Jaú	RY (g)	0.0752*	0.0431	0.3017	0.8895	23.3354
	GG (cm)	13.2372**	1.5234	7.7883	8.6875	14.2071
	NR	0.7979**	0.1725	0.6730	3.1629	13.1313
Pindorama	RY (g)	0.0649**	0.0084	0.0569	0.4812	23.3354
	GG (cm)	15.1054**	1.9661	11.8144	10.3560	13.5397
	NR	0.5021**	0.1118	0.6808	3.0595	10.9304
Votuporanga	RY (g)	0.0338**	0.0066	0.0544	0.4339	18.7647
	GG (cm)	15.0810**	1.6513	13.4889	11.8427	10.8509
	NR	0.1794**	0.1124	0.5682	2.9823	11.2393

* p < 0.05; ** p < 0.01

Table 3. Mean square values, experimental coefficient of variation (CVe%) and overall average obtained for rubber yield (RY), girth growth (GG) and total number of latex vessel rings (NR), based on the combined analysis of 22 rubber progenies at three locations in the State of São Paulo

Source of variation	df	Mean squares		
		RY (g)	GG (cm)	NR
Progeny	21	0.1391	36.6339**	1.2674**
Locations	2	0.6773	375.0637**	0.2525
Progenies x locations	42	0.0973**	3.9974*	0.5647**
Residue	315	0.0452	2.2038	0.2711
Mean		0.3303	9.6144	2.6465
CVe (%)		64.3610	15.4407	19.6740

* p < 0.05; ** p < 0.01

except for RY (Jaú), with a significant difference at 5% probability, indicating less variability among progenies for rubber yield in Jaú than at the other locations. These results are consistent with those found by Gonçalves et al. (2005) and Martins et al. (2000) in a study conducted for the trait rubber yield at the same experimental locations, confirming the possibility of using the genotypes established with individual selection within progenies.

The mean square effects of the progenies, of the locations and of the genotype-environment interaction (Table 3) were significant at 1% probability for GG only, indicating that for this variable, the progeny performance at the three locations is different. For NR and RY, the mean square effects were not significant, showing that the progenies did not differ, although there was interaction with the environment. The significant mean square effect of the genotype - environment interaction indicates the need to conduct region-specific breeding programs, to obtain genotypes better adapted to soil and climatic conditions, ensuring high yields. Gonçalves et al. (2009a) found significant effects at 1% probability in a

study with progenies at more than one location. The results of test evaluating the genotype can be used to select and recommend clones adapted to a particular agro-climatic condition if the differences can be defined according to environmental factors (Gonçalves et al. 2003).

The individual genetic parameters are shown in Table 4, and the genetic parameters of the combined analysis in Table 5. The individual heritability estimates (\hat{h}_a^2) at the three locations were 0.30, 0.63 and 0.29 for RY, GG and NR, respectively. These values are considered moderate to high, indicating that the environment has little influence on the variables. The data show that the populations are suitable for the breeding program. In other words, genetic gains are expected by applying the appropriate selection procedure. These results are similar to those reported for rubber by Gonçalves et al. (2005) ($\hat{h}_a^2 = 0.30$ for NR), Costa et al. (2008) ($\hat{h}_a^2 = 0.54$ for GG) and Gonçalves et al. (2009b) ($\hat{h}_a^2 = 0.39$ for RY). The results obtained at the three locations are supportive for the rubber tree breeding program of the State of Sao Paulo. In general,

Table 4. Estimates of genetic parameters for rubber yield (RY), girth growth (GG) and total number of latex vessel rings (NR) based on the individual analyses of 22 rubber progenies evaluated at three locations in the State of São Paulo

Estimates	Jaú			Pindorama			Votuporanga		
	RY (g)	GG (cm)	NR	RY (g)	GG (cm)	NR	RY (g)	GG (cm)	NR
\hat{h}_a^2	0.0669 ± 0.0598	0.7448 ± 0.1420	0.4725 ± 0.1182	0.5449 ± 0.1567	0.5923 ± 0.1214	0.3295 ± 0.0962	0.3016 ± 0.1026	0.5585 ± 0.1205	0.0704 ± 0.0443
\hat{h}_{mp}^2	0.4269	0.8849	0.7838	0.8702	0.8698	0.7773	0.8039	0.8905	0.3738
\hat{h}_{ad}^2	0.0532	0.8849	0.7838	0.4959	0.8698	0.7773	0.2500	0.8905	0.3738
\hat{r}_{aa}	0.6534	0.9407	0.8853	0.9328	0.9327	0.8816	0.8966	0.9437	0.6114
c_p^2	0.0404	0.0710	0.1192	0.0396	0.0531	0.0554	0.0199	0.0189	0.0875
$\hat{\sigma}_a^2$	0.0214	7.8092	0.4170	0.0376	8.7595	0.2602	0.0181	8.9531	0.0447
$\hat{\sigma}_{parc}^2$	0.0129	0.7445	0.1052	0.0027	0.7847	0.0438	0.0012	0.3024	0.0555
$\hat{\sigma}_f^2$	0.3199	10.4851	0.8824	0.0691	14.7889	0.7896	0.0601	16.0296	0.6349
$\hat{\sigma}_e^2$	0.2856	1.9314	0.3603	0.0287	5.2447	0.4856	0.0408	6.7740	0.5347
G%	24.6893	65.4167	56.0274	66.5004	61.4871	35.7967	64.4489	57.1660	8.3382
CVgi (%)	16.4444	32.1669	20.4156	40.3154	28.5790	16.6724	31.0244	25.2660	7.0905
$\hat{\theta}$	0.7047	2.2641	1.5547	1.7276	2.1108	1.5253	1.6533	2.3285	0.6309

\hat{h}_a^2 : individual narrow-sense heritability; \hat{h}_{mp}^2 : heritability of the progeny mean; \hat{h}_{ad}^2 : additive heritability within the plot; \hat{r}_{aa} : accuracy; c_p^2 : coefficient of determination of the plot effects; $\hat{\sigma}_a^2$: additive genetic variance; $\hat{\sigma}_{parc}^2$: environmental variance between plots; $\hat{\sigma}_f^2$: individual phenotypic variance; $\hat{\sigma}_e^2$: residual variance; G%: selection gain; CVgi%: coefficient of individual genetic variation and $\hat{\theta}$: index of variation = CVgi%/CVe%.

Table 5. Estimates of genetic parameters for rubber yield (RY), girth growth (GG), and total number of latex vessel rings (NR), based on the combined analysis of 22 progenies of rubber assessed at three locations of the State of São Paulo

Parameters	RY (g)	GG (cm)	NR
\hat{h}_i^2	0.011646 ± 0.0058	0.023506 ± 0.0071	0.013844 ± 0.0057
\hat{h}_g^2	0.4158	0.6309	0.4644
\hat{r}_{aa}	0.6448	0.7943	0.6815
c_p^2	0.097	0.158	0.201
c_{int}^2	0.018	0.001	0.001
$\hat{\sigma}_g^2$	0.0052	0.3590	0.0113
$\hat{\sigma}_{parc}^2$	0.0433	2.4168	0.1640
$\hat{\sigma}_{int}^2$	0.0083	0.0195	0.0011
$\hat{\sigma}_f^2$	0.4478	15.2746	0.8171
$\hat{\sigma}_e^2$	0.3911	12.4793	0.6406
G%	12.9624	6.2272	4.5387
CVg%	8.8231	5.8084	3.4665
$\hat{\theta}$	0.1371	0.3762	0.1762

\hat{h}_i^2 : broad-sense heritability; \hat{h}_g^2 : heritability of the mean genotypes; \hat{r}_{aa} : accuracy of genotype selection; c_p^2 : coefficient of determination of the plot effects; c_{int}^2 : coefficient of determination of the effects of genotype-environment interaction; $\hat{\sigma}_g^2$: genotypic variance; $\hat{\sigma}_{parc}^2$: environmental variance among plots; $\hat{\sigma}_f^2$: individual phenotypic variance; $\hat{\sigma}_e^2$: residual variance; G%: genetic gain; CVg (%): coefficient of genotypic variation; $\hat{\theta}$: index of variation = CVg%/CVe%.

low individual heritabilities are common for quantitative traits and, as a rule lead to a moderate level of heritability of progeny means (Resende 2002a). According to Falconer (1987), heritability is not a property of one trait only, but also of the population and the circumstances of the environments to which the plants are exposed. The heritability value may be altered if any of the components of genetic and phenotypic variances is changed.

The results of the average heritability of progenies (\hat{h}_{mp}^2) were moderate to high (0.37 to 0.89), indicating that selection may be more effective using the information of the progenies. These findings agree with data on rubber published elsewhere (Costa et al. 2000, Gonçalves et al. 2005).

The individual heritability in the broad sense (\hat{h}_i^2) of the combined analysis (Table 5) was low for all traits (0.014, 0.024, 0.012 for NR, GG and RY, respectively). These values were lower than those resulting from the individual analysis, indicating a greater effect of environment on progenies. The values of the progeny mean heritability (\hat{h}_g^2) were moderate to high: RY 0.42, GG 0.63, and 0.46 for NR.

The selective accuracy of progenies (\hat{r}_{aa}) showed values of 0.61 for NR (Votuporanga) and 0.94 for GG (Jaú) in the individual analysis (Table 4), and 0.64 for RY, 0.79 for GG and 0.68 for NR (Table 5). The value obtained for yield of the rubber progenies was consistent with that determined by Costa et al. (2000).

The accuracy is an estimate of the correlation between the real and the predicted genetic value. It is an important component of genetic progress, and can be improved by a more appropriate testing, maintaining the same size of the experiment, but changing the number of plants per plot and replications, to maximize genetic gain (Resende 2002a). According to Rocha et al. (2006), the coefficient of determination of the plot effects (c_p^2) quantifies the variability within the block, i.e., a high magnitude of this coefficient means high variability between plots. In reliable experiments with perennial crops, this ratio should be approximately 10% of the total phenotypic variation within the block (Resende 2002a). Thus, only for NR (Jaú) a (c_p^2) value considered high (12%) was found for individual analysis and the highest (20%), for combined analysis, followed by GG (16%) and RY (9%). The coefficient of determination of the effects of genotype-environment interaction (c_{int}^2) showed values below 2% for all traits, indicating low relevance of this interaction and high correlation of the progeny performance across the locations, which is desirable for breeding.

The trait GG had the highest additive genetic variance ($\hat{\sigma}_a^2$), and phenotypic variance ($\hat{\sigma}_f^2$) at the three study sites separately and together (Tables 4 and 5, respectively), suggesting the use of this trait in the prediction of genetic values of candidate plants for selection. Estimates of additive genetic variance were higher than the residual variance, indicating high genetic variability resulting in a high heritability value. The additive genetic variance is the key fraction to be determined, for being the main cause of similarity between relatives and functional determinants of the genetic traits of the population, and consequently, of their response to selection (Falconer 1981). Genetic variation and mainly its additive part shows, for a certain trait, the potential of a population for selection by economically important traits, which has ensured major advances in breeding, particularly for higher yields (Namkoong 1979).

The coefficients of individual additive genetic variability (CVgi %) ranged from low to high for all traits studied at the three locations and in the combined analysis. For NR, CVgi varied from 7.09% (Votuporanga) to 20.41% (Jaú), for GG from 25.29% (Votuporanga) to 32.47% (Jaú) and for RY from 40.32% (Pindorama) to 16.44% (Jaú). These values were consistent with those reported by Gonçalves et al. (2005) in progeny tests in the State of Sao Paulo.

The estimate of experimental variation at each location ranged from 10.85% (GG in Votuporanga) to 23.33% (RY in Jaú and Pindorama); in the combined analysis, the estimates were 19.67% for NR, 15.44% for GG and 64.36% for RY.

The high coefficient of variation for rubber yield indicates that the experimental data are subject to experimental errors, despite being within the normal standard for rubber tree (Costa et al. 2000, Gonçalves et al. 2003).

The relationship between the coefficient of genetic and experimental variation ($\hat{\rho}$) was high for most traits at all locations, varying from 0.63 for NR to 2.33 for RY, both in Votuporanga. The values of this relationship for combined data analysis were low (0.18, 0.38 and 0.14 for NR, GG and RY, respectively). Vencovsky (1987) stated that when this ratio tends to be ≥ 1 , the situation is favorable in the case of maize selection. This shows that for the selection tests, conditions are best for the traits at each location, with expectations of higher gains than when analyzed together.

The individual genetic gains (G%) at each location for RY varied from 24.69% (Jaú) to 66.50% (Pindorama), NR varied from 8.33% (Votuporanga) to 56.03% (Jaú) and GG ranged from 57.17% (Votuporanga) to 65.42% (Jaú). The values were high, indicating high genetic control, as evidenced by the individual heritabilities, suggesting these traits for the rubber tree improvement program. The genetic gain in the combined analysis was lower for all traits (4.54%, 6.23% and 12.96% for NR, GG and RY, respectively), compared to individual gains. This was due to the fact that the combined analysis addressed gains in improved genotypes for multiple locations simultaneously. However, the genotype-environment interaction reduces these gains. Gonçalves et al. (2009b) achieved selection gains of 8.20% for rubber yield in a combined analysis at the same experimental site.

CONCLUSIONS

The results showed the existence of genetic variability for each progeny and location, for the traits studied, demonstrating differences in the progeny performance across locations.

Individual heritability, associated with high genetic selection gains for the traits studied at each location, showed that populations may be considered appropriate for the rubber breeding program, provided an appropriate selection procedure is applied.

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Estimativa de parâmetros genéticos em progênes de seringueira

Resumo – *Avaliaram-se a variabilidade genética e o potencial de produção de borracha e de caracteres secundários em progênes de seringueira, em três locais do Estado de São Paulo. Os experimentos foram instalados em blocos ao acaso com 22 progênes e seis repetições. Aos três anos de idade, as progênes foram avaliadas quanto à produção de borracha, perímetro do caule e número total de anéis de vasos laticíferos. Houve variabilidade genética entre progênes em cada local, assim como entre locais, para os caracteres, demonstrando diferenças de comportamento das progênes. As herdabilidades individuais obtidas para produção de borracha, perímetro do caule e número total de anéis de vasos laticíferos (0,30, 0,63 e 0,29, respectivamente), associadas aos ganhos genéticos com seleção de altas magnitudes para os caracteres estudados em cada local, mostraram que as populações podem ser consideradas apropriadas para o programa de melhoramento genético da seringueira, aplicando-se procedimento adequado de seleção.*

Palavras-chave: Hevea, variância genética, modelo linear misto.

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