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Research Article

Genetic variation in growth traits and yield of rubber trees (*Hevea brasiliensis*) growing in the Brazilian state of São Paulo

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Abstract

Analysis of variance and covariance was preformed on growth traits (stem girth, bark thickness, total height gain and rubber yield) of 22 open-pollinated progenies of the rubber tree *Hevea brasiliensis* from an Asian *Hevea* collection introduced to Agronomic Institute (Instituto Agronômico, Campinas, São Paulo, Brazil; IAC) in 1952. This progeny trial was replicated at three sites in São Paulo state and it was found that at three years from sowing there was statistically significant variation for girth, bark thickness, height and rubber yield. An individual test sites, values of individual plant heritability for girth ranged from $\hat{h}_i^2 = 0.36$ to $\hat{h}_i^2 = 0.89$ whereas values for heritability for progeny means ranged from $\hat{h}_i^2 = 0.77$ to $\hat{h}_i^2 = 0.87$. These moderate and high heritabilities suggest that a combination of progeny and within-progeny selection would be effective at increasing girth in this population at individual sites. Across sites, values of individual-plant heritability for girth ranged from $\hat{h}_i^2 = 0.36$ to $\hat{h}_i^2 = 0.47$, whereas values for heritability of progeny means girth ranged from $\hat{h}_{\bar{x}}^2 = 0.77$ to $\hat{h}_{\bar{x}}^2 = 0.87$. There were high positive genetic correlations between increased girth and bark thickness suggesting that breeding aimed at increasing girth would also increase bark thickness and possibly height.

Key words: Hevea brasiliensis, rubber tree, heritability, genetic parameters.

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Introduction

Given the long breeding and selection cycle of the rubber tree *Hevea brasiliensis* (Willd. Adr. ex Juss.) Muell.-Arg. the possibility of testing and selection at an early stage of growth in order to improve traits in adult trees is an important consideration in most breeding programs. Early testing provides the opportunity to shorten the length of the breeding cycle and increase average genetic gains per year (*i.e.* single-stage early selection).

Several immature stage studies have been conducted to try to understand the variation in genetic and environmental variances in species such as *Hevea* (Ho, 1972, 1976, 1979; Marques and Gonçalves, 1990; Gonçalves *et al.* 1996, 1998a, 1998b; Moreti *et al.* 1994; Boock *et al.* 1995; Costa *et al.* 2000a, 2000b), such studies having especially helped in the development of methods for predicting the levels in variability, heritability and genotype caused by environmental interactions and genetic and phenotypic correlations.

The effectiveness of early selection depends largely on the early-mature correlation and the heritability of juvenile traits. In addition, genotype by environment interaction in the field tests will reduce the effectiveness of early selection and also early-mature genetic correlations. It is well know that performance of genotypes relative to each other may vary with testing environments. Genotype by environment interaction is important in many aspects of a breeding program (Bridgwater and Stonecypher, 1978). Interaction in the field trials affects mature selection and also early selection, so when evaluating the effectiveness of early selection it is imperative to determine whether or not the genotype by environment interaction among sites has a meaningful impact on early mature genetic correlation.

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The aim of this study was to provide further estimates of heritability of girth, total height gain, bark thickness and rubber yield in young *H. brasiliensis* trees and to determine the genetic and phenotypic associations between these traits. In this study emphasis was placed on the level of genetic variability, heritability and genotype by environment interactions as well as genetic and phenotypic correlations and their implications on the selection and breeding of *Hevea*.

Material and Methods

Plant material, field-testing and assessment

The study involved 22 open-pollinated *Hevea brasiliensis* (Willd. Adr. ex Juss.) Muell.-Arg. progenies that were randomly sampled from a base population of more than 100 Asian clones held at the Agronomic Institute (Instituto Agronômico, Campinas, São Paulo, Brazil; IAC) since 1952 (Gonçalves, 2002).

The *H. brasiliensis* seeds were sown in the autumn in polyethylene bags (12 x 18 x 18 cm) filled with a mixture of 70% humus and 30% sand, the seedlings remaining in these pots during the first six months of the growing season before being planted in the field at three sites (Votuporanga, site A; Pindorama, site B; and Jaú, site C) in the Brazilian state of São Paulo (Table 1). Throughout this paper, each experimental site is represented by a letter (A, B, C) and combinations of sites by a combination of letters. At each site a randomized complete block experimental design was used with three replications and ten-tree row plots with a spacing of 1.5 x 1.5 m between trees at sites A and C and 2 x 2 m at site B (to facilitate mechanical weeding), although for the analysis we assumed that the spacing between trees was the same at all three sites because the spacing differences were small and the trees were not competing with each other for space since the trials only considered trees with a maximum age of three years.

Table 1 - Planting of 22 open-pollinated *Hevea* progenies at three sites in the Brazilian state of São Paulo. The Hevea seedlings were planted at all sites in 1994 using a randomized block design, a planting density of 1 row x 10 plants (10 plants/plot) and six replicates.

Remarks	Sites		
	Votuporanga (site A)	Pindorama (site B)	Jaú (site C)
Spacing (m)	1.5 x 1.5	2 x 2	1.5 x 1.5
Total area (ha)	0.28	0.53	0.28
Elevation above mean sea level (m)	450	467	450
Latitude and longitude	20°25'S; 49°50'E	21°13'S; 48°56'E	22°17'S; 48°34'E
Annual mean temperature (°C)	23.7	22.7	21.6
Annual mean rainfall (mm)	1,300	1,390	1,344
Soil type	Paledalf	Landiudox	Paleudox
Terrain	Flat undulating	Flat	Flat

Field assessments of traits (height, stem girth, bark thickness and rubber yield) were first made in the autumn (April in the Southern Hemisphere) of 1995 when the seedlings were one year old (five leaf whorl stage) with subsequent assessments when the trees were two and three years old.

Girth (G; centimetres) was measured 10 cm from ground level when the trees were one (G1), two (G2) and three (G3) years old.

Rubber yield (Yr; grams) was determined by the Hamker-Morris-Mann test (HMM) according to the method of Tan and Subramanian (1976). Briefly, 30 half-spiral tapping were made on alternate days (1/2S d/2) 15 cm from the ground and yield recorded by cup coagulation with the 'coagula' being air-dried for two-months until constant weight, the performance of each tree being expressed in grams per tapping.

Virgin bark plugs were removed from the trunk 20 cm above ground level on the opposite side of the tapping panel for latex vessel determination and the thickness of the bark (Bt; millimetres) was measured using microscopy.

The final height of each tree was measured when the trees were three years old and expressed as total height gain (Hg; centimetres).

Data analysis

At individual sites, the following random-effects model was used:

$$Y_{ijl} = \mu + r_i + g_j + gr_{ij} + w_{ijl}$$

where: Y_{ijl} = observation on the lth plant in the jth progeny planted in the ith replication; μ = general mean; r_i = effect due to ith replication, IND (0, $\hat{\sigma}^2_r$; g_j = effect due to the jth progeny, IND (0, $\hat{\sigma}^2_g$); gr_{ij} = effect due to replication by progeny interaction, IND (0, $\hat{\sigma}^2_{gr}$); w_{ijl} = within progeny effect an error associated with an observation on the lth plant in jth progeny planted in the ith replication, IND (0, $\hat{\sigma}^2_w$).

Except for the general mean, all effects on the right-hand side of the model were considered random, additive, independent, and normally distributed with a mean of zero and their respective variances (in parentheses). The analysis of variance (ANOVA) for this model is shown in Table 2.

For combined site analysis, the following random-effects model was used:

$$Y_{ijl} = \mu + s_l + r_{i(l)} + g_i + gs_{jl} + e_{ij(l)} + w_{k(l)ij},$$

where: Y_{ijl} = observation on the kth plant in the jth progeny planted in the ith replication within the lth test site; μ = general mean; s_l = effect due to the lth test site, IND (0, $\hat{\sigma}^2_s$); $r_{i(l)}$ effect due to the ith replication within the lth test site, IND

Table 2 - Analysis of variance (ANOVA) degrees of freedom (df) and expected mean square (E.M.S.) equations for the single site and combined site models for estimating the variance due to differences among plants within plots in a rubber tree progeny trial at three sites in the Brazilian state of São Paulo.

Source of variation	d.f.	M.S.	E.M.S.	F
	Single site analysis			
Replications	r - 1	MS_1	$(1/k)\hat{\sigma}_w^2 + \hat{\sigma}_{gr}^2 + g\hat{\sigma}_r^2$	MS_1/MS_3
Progenies	g - 1	MS_2	$(1/k)\hat{\sigma}_w^2 + \hat{\sigma}_{gr}^2 + r\hat{\sigma}_g^2$	MS_2/MS_3
Progenies x replications	(r - 1)(g - 1)	MS_3	$(1/k)\hat{\sigma}_w^2 + \hat{\sigma}_{gr}^2$	MS_2/MS_3
Within plot	N - rg	MS_4	$\hat{\sigma}_w^2$	
		Combined site analysis		
Replication/location	(r - 1)s	MS_1	$(1/k)\hat{\sigma}_w^2 + \hat{\sigma}_e^2 + g\hat{\sigma}_r^2$	MS_1/MS_5
Progenies	g - 1	MS_2	$(1/k)\hat{\sigma}_w^2 + \hat{\sigma}_e^2 + r\hat{\sigma}_{gs}^2 + rs\hat{\sigma}_g^2$	MS_2/MS_4
Sites	s - 1	MS_3	$(1/k)\hat{\sigma}_w^2 + \hat{\sigma}_e^2 + r\hat{\sigma}_{gs}^2 + g\hat{\sigma}_r^2 + gr\hat{\sigma}_s^2$	$(MS_3+MS_5)/(MS_1+MS_4)$
Progenies x sites	(g - 1) (s - 1)	MS_4	$(1/k)\hat{\sigma}_w^2 + \hat{\sigma}_e^2 + r\hat{\sigma}_{gs}^2$	MS_4/MS_5
Residual (mean)	ΣN_1	MS_5	$(1/k)\hat{\sigma}_w^2 + \hat{\sigma}_e^2$	
Within plot	ΣN_2		$\hat{\sigma}_w^2$	

$\hat{\sigma}_g^2$ = variance due to differences among progeny variances; $\hat{\sigma}_w^2$ = variance due to differences among plants within progenies; $\hat{\sigma}_s^2$ = variance due to differences among sites; $\hat{\sigma}_e^2$ = environmental variance among plots; $\hat{\sigma}_r^2$ = variance due to replication within sites; $\hat{\sigma}_{gs}^2$ = variance due to interaction of progenies and sites; s = number of replications; s = number of sites; g = number of progenies; k = harmonic mean of plants per plot; ΣN_1 = sum of the number of degrees of freedom of the individual plots residual; ΣN_2 = sum of the number of degrees of freedom of the individual analysis within plots.

$(0, \hat{\sigma}_r^2)$; g_i = effect due to the *i*th progeny, IND $(0, \hat{\sigma}_g^2)$; gs_{jl} = effect due to site by progeny interaction, IND $(0, \hat{\sigma}_{gs}^2)$; $e_{ij(l)}$ = residual, an effect due to replication-within-site interaction, IND $(0, \hat{\sigma}_e^2)$; $w_{k(l)ij}$ = within-progeny, an error associated with an observation on *k*th plant in the *j*th progeny planted in the *i*th replication within the *l*th test site.

The assumptions made for the single-site model hold for the combined-sites model. The ANOVA for the combined-sites model is shown in Table 2.

Differences in spacing between site B and the other two sites were ignored because at the time of measurement the plants were still far apart. Because the data were unbalanced the variances and covariances were analyzed using the 'Genes' computer program (Cruz, 2001).

Single-site heritabilities were estimated according to Falconer and Mackay (1996) using the following formulas:

$$\hat{h}_i^2 = \frac{4\hat{\sigma}_g^2}{\hat{\sigma}_w^2 + \hat{\sigma}_{gr}^2 + \hat{\sigma}_g^2} \quad \text{and} \quad \hat{h}_{\bar{X}}^2 = \frac{\hat{\sigma}_g^2}{\frac{1}{kr}\hat{\sigma}_w^2 + \frac{1}{r}\hat{\sigma}_{gr}^2 + \hat{\sigma}_g^2}$$

where $\hat{h}_i^2$ is the individual plant heritability, $\hat{h}_{\bar{X}}^2$ the heritability for the progeny means, r the number of replications and k the harmonic mean of the number of plants within plots. Heritabilities for combined sites were similarly estimated using the following formulas:

$$\hat{h}_i^2 = \frac{4\hat{\sigma}_p^2}{\hat{\sigma}_w^2 + \hat{\sigma}_e^2 + \hat{\sigma}_{gs}^2 + \hat{\sigma}_g^2} \quad \text{and}$$

$$\hat{h}_{\bar{X}}^2 = \frac{\hat{\sigma}_g^2}{\frac{1}{krs}\hat{\sigma}_w^2 + \frac{1}{rs}\hat{\sigma}_e^2 + \frac{1}{s}\hat{\sigma}_{gs}^2 + \hat{\sigma}_g^2}$$

Standard errors of individual tree heritabilities were calculated as described by Becker (1975) and standard errors of the heritabilities for progeny means according to Wright (1976).

Genetic and phenotypic correlation coefficients between traits were estimated from covariance and variance of respective traits as expressed in the following formulas:

$$r_{Axy} = \frac{\hat{\sigma}_{Gxy}}{\hat{\sigma}_{Gx} \cdot \hat{\sigma}_{Gy}} \quad \text{and} \quad r_{Pxy} = \frac{\hat{\sigma}_{Pxy}}{\hat{\sigma}_{Px} \cdot \hat{\sigma}_{Py}},$$

where, r_{Axy} is the genetic and r_{Pxy} the phenotypic correlation coefficients between any two traits, $\hat{\sigma}_{Gxy}$ the genetic and $\hat{\sigma}_{Pxy}$ the phenotypic covariances between any two traits, and $\hat{\sigma}_{Gx}$, $\hat{\sigma}_{Gy}$, $\hat{\sigma}_{Px}$ and $\hat{\sigma}_{Py}$ are the genetic and phenotypic standard deviations of individual traits. Standard errors of correlation coefficients were estimated according to Robertson (1959).

Results

Girth increase

At three years old (G3) the mean girth of the trees were as follows: site A mean tree girth was 25.9 cm, with the largest girthed tree being 13% above and the smallest girthed tree 31% below the mean; site B mean tree girth was 22 cm, with the largest girthed tree being 21% above and the smallest girthed tree 18% below the mean; site C mean tree girth was 17.8 cm, with the largest girthed tree being 17% above and the smallest girthed tree 23% below the mean (percentages rounded).

The girth progeny variances were statistically significant for all the years (*i.e.* G1 to G3) at all test sites (Table 3). As a percentage of the total variance, progeny variance at site A increased from 14% for G1 to 15% for G3 and at site B it varied from 13% for G1 to 17% for G3 but showed no clear trend at site C (20% for G1, 22% for G2 and17% for G3). Across sites, progeny variance decreased from about 9% of the total variance for G1 to 4% for G2 and 1% for G3.

Heritability estimates for girth (Table 3) showed trends similar to those for progeny variance, decreasing at site A between G1 and G2 but increasing between G2 and G3, while at site B heritability increased with plant age and declined with plant age at site C. Across sites, heritability for individual plant girth increased between the same ages. On the other hand, heritability for progeny means girth remained constant between G1 and G2 and then increased between ages G2 and G3. Generally, except for G2 at site A ($\hat{h}_i^2 = 0.44$), the heritability for individual plant girth was greater than $\hat{h}_i^2 = 0.50$ whereas the heritability for progeny means was greater than $\hat{h}_i^2 = 0.75$. At all sites and across sites, the standard errors of individual plant heritability estimates for girth were less than or equal to 50% of the heritability estimates. Standard errors of heritability estimates for progeny means were less than 25% of heritability estimates.

Rubber yield, bark thickness and height growth

The average rubber yield (Yr) was 0.62g at site A, 0.99g at site B and 0.94g at site C. The Yr progeny variance was statistically significant at the three sites, being about 5% at site A, 16% at site B and 8% at site C (Table 4). The Yr progeny variance by replication interaction for site A was low compared to sites B and C and the standard error of individual plant heritability at the site A was 50% of the heritability value

Mean bark thickness (Bt) was 3.75 mm at site A, 3.85 mm at site B and 3.76 mm at site C. As a percentage of the total Bt variance the Bt progeny variance was statistically significant at the three sites, being about 15% at site A, 25% at site B and 17% at site C. Generally, heritability estimates for individual plant Bt were higher than $\hat{h}_i^2 = 0.50$, and those of progeny means exceeded $\hat{h}_i^2 = 0.70$ (Table 4). Standard errors of heritabilities for individual tree Bt were slightly greater than 50% of heritability estimates. On the other hand, the standard error was almost equal to the heritability estimate at site C.

Height growth (Hg) averaged 311 cm at site A, 261 cm at site B and 208 cm at site C. The Hg progeny variance was statistically significant both at all sites and across sites (Table 4), progeny variance being about 21% of the total variance at site A, 16% at site B and 22% at site C. Individual Hg plant heritability estimates were between $\hat{h}_i^2 = 0.62$ and $\hat{h}_i^2 = 0.89$ whereas those of the progeny means were between 0.76 and 0.87 (Table 4).

Table 3 - Site-related percentages of the variance components and heritabilities for increased girth in 22 open pollinated *Hevea* progenies growing at three sites (Votuporanga (A), Pindorama (B) and Jaú (C)) in the Brazilian state of São Paulo. Girth measured when the trees were one (G1), two (G2) and three (G3) years old.

Girth	Sites	Percentages of variance components							Heritabilities	
		$\hat{\sigma}^2_s$	$\hat{\sigma}^2_r$	$\hat{\sigma}^2_g$	$\hat{\sigma}^2_{gr}$	$\hat{\sigma}^2_{gs}$	$\hat{\sigma}^2_e$	$\hat{\sigma}^2_w$	h_i^2	$h_{\bar{X}}^2$
G1	A		3.18**	13.88**	11.66**			71.28	0.67 ± 0.11	0.77 ± 0.13
	B		5.11**	12.51**	10.53**			71.84	0.50 ± 0.06	0.80 ± 0.07
	C		0.98**	19.84**	15.03**			64.15	0.79 ± 0.08	0.83 ± 0.09
	Across	13.70	2.57	8.70**		3.71*	18.68*	52.62	0.41 ± 0.03	0.77 ± 0.06
G2	A		3.58**	11.04**	6.58**			78.79	0.44 ± 0.08	0.77 ± 0.10
	B		2.60**	15.45**	24.00**			57.94	0.61 ± 0.08	0.75 ± 0.09
	C		2.87**	22.37**	13.77**			60.98	0.89 ± 0.09	0.86 ± 0.09
	Across	10.10	3.00	4.36**		3.63*	13.02*	65.90	0.36 ± 0.03	0.80 ± 0.06
G3	A		1.06**	14.94**	1.56			83.29	0.56 ± 0.11	0.86 ± 0.13
	B		0.31*	16.70**	6.32**			76.66	0.67 ± 0.09	0.86 ± 0.11
	C		0.52**	16.75**	7.73**			75.00	0.67 ± 0.09	0.85 ± 0.10
	Across	13.10	3.19*	1.08		3.14*	11.70	67.73	0.4 ± 0.06	0.87 ± 0.12

* ($p < 0.05$); ** ($p < 0.01$); variance components are as follows: $\hat{\sigma}^2_s$ = variance due to differences among plants within progenies; $\hat{\sigma}^2_r$ = variance due to replication within sites; $\hat{\sigma}^2_g$ = variance due to differences among progeny; $\hat{\sigma}^2_{gr}$ = variance due to interaction of progeny and replication; $\hat{\sigma}^2_{gs}$ = variance due to interaction of progeny and site; $\hat{\sigma}^2_e$ = environmental variance among plots; $\hat{\sigma}^2_w$ = variance due to differences among plants within progenies; h_i^2 = individual plant heritability; $h_{\bar{X}}^2$ = heritability for progeny means.

Table 4 - Site-related percentages of variance components and heritabilities for rubber yield, bark thickness and height gain in 22 open-pollinated *Hevea* progenies growing at three sites (Votuporanga (A), Pindorama (B) and Jaú (C)) in the Brazilian state of São Paulo.

Traits	Sites	Percentages of variance components							Heritabilities	
		$\hat{\sigma}_s^2$	$\hat{\sigma}_r^2$	$\hat{\sigma}_g^2$	$\hat{\sigma}_{gr}^2$	$\hat{\sigma}_{gs}^2$	$\hat{\sigma}_e^2$	$\hat{\sigma}_w^2$	h_i^2	$h_{\bar{X}}^2$
Rubber yield (Yr)	A		0.32	5.25**	7.26			87.16	0.22 ± 0.11	0.67 ± 0.18
	B		0.33	15.77**	6.76**			77.13	0.63 ± 0.21	0.86 ± 0.57
	C		0.50*	7.86**	11.42**			80.21	0.31 ± 0.19	0.50 ± 0.29
	Across site	5.65**		4.96**		4.48**	15.02*	69.88	0.21 ± 0.03	0.67 ± 0.36
Bark thickness (Bt)	A		0.45	14.90**	2.90			81.73	0.59 ± 0.32	0.85 ± 0.40
	B		0.38*	24.53**	4.72**			70.37	0.78 ± 0.40	0.98 ± 0.49
	C		0.65**	17.09**	11.28**			70.98	0.68 ± 0.53	0.83 ± 0.29
	Across site	11.92		9.52**		6.14**	11.65*	60.77	0.43 ± 0.11	0.77 ± 0.36
Height gain (Hg)	A		1.09**	21.45**	13.26**			64.19	0.85 ± 0.19	0.84 ± 0.33
	B		4.45**	15.58**	22.42**			57.56	0.62 ± 0.19	0.76 ± 0.31
	C		2.18**	22.44**	12.22**			63.15	0.89 ± 0.46	0.87 ± 0.40
	Across site	29.34**		4.20**		5.62**	20.73*	40.10	0.24 ± 0.12	0.57 ± 0.32

* ($p < 0.05$); ** ($p < 0.01$); variance components are as follows: $\hat{\sigma}_s^2$ = variance due to differences among plants within progenies; $\hat{\sigma}_r^2$ = variance due to replication within sites; $\hat{\sigma}_g^2$ = variance due to differences among progeny; $\hat{\sigma}_{gr}^2$ = variance due to interaction of progeny and replication; $\hat{\sigma}_{gs}^2$ = variance due to interaction of progeny and site; $\hat{\sigma}_e^2$ = environmental variance among plots; $\hat{\sigma}_w^2$ = variance due to differences among plants within progenies; h_i^2 = individual plant heritability; $h_{\bar{X}}^2$ = heritability for progeny means.

Genotype by environment interaction

Analysis of variance showed that the genotype by environment (GE) interaction was statistically significant for G1, G2, G3, Yr, Bt and Hg (Table 3 and 4). Generally, the GE interaction variance slightly decreased from G1 to G2 and G2 to G3. Genetic correlations between sites were high. Very low Pearson's correlation coefficients for progeny means (Table 5) also indicate the existence of high GE interaction between pairs of test sites.

Genetic and phenotypic correlations

Age to age genetic and phenotypic correlations for girth were between $\hat{r} = 0.79$ and $\hat{r} = 0.97$ at individual sites and $\hat{r} = 0.96$ to $\hat{r} = 0.99$ across sites. At all three sites and across sites, genetic correlations were slightly greater than the corresponding phenotypic correlations (Table 6). At individual sites and across sites, genetic and phenotypic correlations between increased girth and rubber yield were between $\hat{r} = 0.15$ and $\hat{r} = 0.92$ with few exceptions, genetic correlations between girth and rubber yield being greater than the corresponding phenotypic correlations (Table 6). At site A, bark thickness was positively genetically correlated with girth ($\hat{r}_{Axy} = 0.60$ to $\hat{r}_{Axy} = 0.71$) and rubber yield ($\hat{r}_{Axy} = 0.20$). The phenotypic correlations for bark thickness with girth and rubber yield at this site were also positive but weak. Across sites, rubber yield did not correlate genetically or phenotypically with girth, bark thickness or height gain.

Table 5 - Genetic and Pearson's correlation coefficients between sites for six *Hevea* traits in 22 open-pollinated progenies of *Hevea* growing at three sites (Votuporanga (A), Pindorama (B) and Jaú (C)) in the Brazilian state of São Paulo. Girth measured when the trees were one (G1), two (G2) and three (G3) years old.

	Site A and B		Site A and C		Site B and C	
Traits	$\hat{r}_g$	$\hat{r}_f$	$\hat{r}_g$	$\hat{r}_f$	$\hat{r}_g$	$\hat{r}_f$
Girth						
G1	0.5401**	0.1770	0.7826**	0.3341	0.8616**	0.2803
G2	0.7062**	0.1842	0.8547**	0.2860	NA	0.1323
G3	0.7692**	0.4721*	0.8953**	0.4828*	0.9928**	0.4706*
Other traits						
Rubber yield (Ry)	0.6563**	0.3422	0.9445**	0.2454	0.7728**	0.0667
Bark thickness (Bt)	0.8901**	0.5907**	0.3920	0.2679	0.5254*	0.2320
Height gain (Hg)	0.1056	0.0881	0.8311**	0.3829	0.2223	0.1785

*($p < 0.5$); ** ($p < 0.01$), $\hat{r}_g$ = genetic correlation, $\hat{r}_f$ = Pearson's correlation for progeny means.

Table 6 - Site-related genetic ($\hat{r}_a$) and phenotypic ($\hat{r}_p$) correlations between traits (rubber yield (Yr), bark thickness (Bt) and height gain (Hg)) in 22 open-pollinated progenies of *Hevea* growing at three sites (Votuporanga (A), Pindorama (B) and Jaú (C)) in the Brazilian state of São Paulo. Girth measured when the trees were one (G1), two (G2) and three (G3) years old.

Traits	Site A		Site B		Site C		Across sites	
	$\hat{r}_a$	$\hat{r}_p$	$\hat{r}_a$	$\hat{r}_p$	$\hat{r}_a$	$\hat{r}_p$	$\hat{r}_a$	$\hat{r}_p$
G1 & G2	0.8838 ± 0.01	0.8174	0.9792 ± 0.04	0.4253	0.9552 ± 0.01	0.7089	0.9897 ± 0.01	0.7623
G1 & G3	0.7863 ± 0.04	0.7465	NA	0.4455	0.90 ± 0.03	0.7197	0.9940 ± 0.18	0.7140
G2 & G3	0.8689 ± 0.02	0.7560	0.8908 ± 0.02	0.6891	NA	0.7272	0.9694 ± 0.05	0.8088
G1 & Yr	0.1950 ± 0.15	0.1148	0.7908 ± 0.32	0.3533	0.7561 ± 0.16	0.3891	0.5271 ± 0.20	0.3565
G2 & Yr	0.1535 ± 0.11	0.1087	0.3650 ± 0.01	0.4700	0.9282 ± 0.13	0.4635	0.4524 ± 0.25	0.4176
G3 & Yr	0.4107 ± 0.07	0.3030	0.4444 ± 0.17	0.4422	0.7925 ± 0.15	0.3690	0.5239 ± 0.11	0.4655
G1 & Bt	0.7060 ± 0.15	0.5618	0.8138 ± 0.21	0.3761	0.9162 ± 0.21	0.5950	0.8097 ± 0.16	0.6468
G2 & Bt	0.7096 ± 0.11	0.5836	0.8024 ± 0.31	0.5941	NA	0.5432	0.8483 ± 0.11	0.7252
G3 & Bt	0.6184 ± 0.10	0.6345	0.7126 ± 0.20	0.5981	0.9209 ± 0.12	0.7361	0.7788 ± 0.88	0.7145
G1 & Hg	0.7514 ± 0.09	0.5843	0.7135 ± 0.02	0.8216	0.9163 ± 0.16	0.6888	0.7990 ± 0.29	0.5255
G2 & Hg	0.9121 ± 0.01	0.7920	0.8215 ± 0.16	0.7110	NA	0.7039	0.8259 ± 0.17	0.5788
G3 & Hg	0.7700 ± 0.05	0.5673	0.6203 ± 0.12	0.5841	0.9208 ± 0.11	0.6865	0.8491 ± 0.16	0.5074
Yr & Bt	0.2045 ± 0.29	0.2319	0.4010 ± 0.09	0.4149	0.3112 ± 0.20	0.1792	0.4367 ± 0.17	0.3752
Yr & Hg	0.1081 ± 0.23	-0.0218	0.0108 ± 0.33	-0.0991	0.8545 ± 0.22	0.3014	0.4010 ± 0.14	0.2045
Bt & Hg	0.5385 ± 0.53	0.4952	-0.4021 ± 0.35	-0.1544	0.6833 ± 0.12	0.5047	0.4420 ± 0.42	0.3370

NA = not applicable (values greater than 1.0).

Discussion

Performance at individual sites and across sites

At all sites, there was a significantly large progeny by replication for G1, G2 and height. High progeny by replication interaction was also reflected in significantly large residual variances across sites. This high progeny by replication interaction could have been the result of within site heterogeneity in soil and moisture, and their influence on the microclimate of the rubber trees (Bataglia *et al.,* 1998).

In this study, all traits at individual sites and G2, G3, Yr and Bt showed high within-progeny variability as reflected by the high percentages of within progeny variance. This high variability among trees in open pollinated progenies might be an indicator of many effective pollen parents (Gonçalves *et al.,*1999)

Heritabilities and their implications

With three exceptions individual plant heritabilities estimated in this study were less than $\hat{h}_i^2$ = 0.3 and heritabilities for progeny means were equal to or greater than 0.5 for all traits. Therefore, heritability values especially for individual trees were on the lower side. Nevertheless, heritabilities estimated in this study were within the range of those estimated in other studies of *Hevea*. For example, except for two cases where heritabilities of $\hat{h}_i^2$ = 0.14 and $\hat{h}_i^2$ = 0.48 were estimated, Costa *et al.* (2000c) found that heritabilities for individual plant girth exceed $\hat{h}_i^2$ = 0.30. Other reported heritability values for girth in *Hevea* include $\hat{h}_i^2$ = 0.32 (Moreti *et al.*, 1994) and $\hat{h}_i^2$ = 0.47 (Boock *et al.*, 1995; Gonçalves *et al.*, 1999). The low values for individual plant heritability in our study could be attributable to large progeny by replication interaction and within progeny variances compared with the progeny variances. Likewise, large values of progeny by site interaction, residual- and within-progeny variances (especially for girth) reduced individual plant heritabilities across sites.

Implications of the genetic correlations

High age-to-age genetic correlations between girths at age one and three suggest that selection for fast growing rubber trees can be done early in the life of the tree. However, two years is too short a time to make significant changes in progeny ranks with plant age for the tested progenies, and caution should be exercised when interpreting such genetic correlations because they might be lower when longer intervals are involved. Gonçalves *et al.* (1998b), for example, found that for *Hevea* the genetic correlation for girth at 12 and 96 months was $\hat{r}_g$ = 0.37 while the value for girth at 48 and 96 months was $\hat{r}_g$ = 0.86, indicating that the ranking of genotypes at 12 months was different from the ranking of the same genotypes at 96 months of age. In one case, however, Tan (1987) observed a correlation of $\hat{r}_g$ = 0.77 between rubber yield (Yr) at a nursery stage and rubber yield at five years of age. Age-to-age genetic correlation is important in early selection and should therefore, be monitored in future assessments of these progeny tests.

The high positive genetic correlations between increased girth and bark thickness (Bt) suggests that selection for increased girth would result in plants with thick virgin bark, which might be favorable for *Hevea* because thicker virgin bark would minimize the incidence of wounding known to affect the yield productivity of later panels. The strong association between increased girth and bark thickness means that breeders can select for thick bark to improve girth growth without suppressing height gain, *i.e.* one way of improving bark thickness would be to select for increased girth rather than height gain.

In our study, height gain (Hg) was positively genetically correlated with rubber yield and bark thickness at site C. Considering the size of the standard errors, the positive (site A) and negative (site B) genetic correlations between height gain and rubber yield and bark thickness at sites B, C and across sites were negligible (Table 5). On the other hand the phenotypic correlations show a universal picture of the relationship between height gain and bark thickness. All the three sites and across sites phenotypic correlations show that height gain had low positive correlations with bark thickness. This supports the argument of Marques and Gonçalves (1990) that in *Hevea* height gain has no causal relationship with rubber yield related traits.

In summary, our major findings were as follows: a) Heritability values for girth growth were moderately high on individual sites and low across sites, so to achieve sufficient genetic gain in increased girth a combination of progeny and within-progeny selection would be require; b) Girth exhibited a genotype by environment GE interaction which was almost entirely due to the different ranking of progenies across sites, which means that in São Paulo state breeding Asian *Hevea* populations for increased girth would require the development of site specific genotypes as opposed to regionally adapted ones; and c) There were high positive genetic correlations between increased girth and bark thickness, suggesting that breeding to increase girth would increase bark thickness and possibly height gain. For *Hevea,* a high positive correlation between increased girth and bark thickness is favorable, since a thick bark is needed to minimize the incidence of wounding in the stem panel. However, if vigor became an option for these *Hevea* populations, increased girth would lead to a reduction in rubber yield due to the absence of correlation between girth and rubber yield.

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