Research Article

Genetic variability and selection for laticiferous system characters in *Hevea brasiliensis*

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Abstract

Six laticiferous system characters were investigated in 22 three-year-old, half-sib rubber tree [*Hevea brasiliensis* (Willd. ex Adr. de Juss.) Muell.-Arg.] progenies, evaluated at three sites (Votuporanga, Pindorama and Jaú, all in the São Paulo State, Brazil). The traits examined were: average rubber yield (Pp), average bark thickness (Bt), number of latex vessel rings (Lv), average distance between consecutive latex vessel rings (Dc), density of latex vessels per 5 mm per ring averaged over all rings (Dd) and the diameter of the latex vessels (Di). The joint analysis showed that site effect and progeny x sites interaction were significant for all traits, except Lv. Estimates of individual heritabilities across the three sites were high for Bt; moderate for Lv, Pp and Dc; low for Dd and very low for Di. Genetic correlations in the joint analysis showed high positive correlations between Pp and the other traits. Selecting the best five progenies would result in genetic gains of 24.91% for Pp while selecting best two plants within a progeny would result in a Pp genetic gain of 30.98%.

Key words: *Hevea brasiliensis*, rubber yield, laticiferous traits, genetic parameters.

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Introduction

The rubber tree [*Hevea brasiliensis* (Willd. ex Adr. de Juss.) Muell.-Arg.] is a perennial crop which has a long generative and testing cycle for individual trees in that it normally takes about four to five years for one generative cycle (excluding a seven to ten years of evaluation period for perennial performance) and about 20 to 30 years for one testing cycle from the time of cross-pollination (Tan, 1987).

The economic product of the tree is latex (a cytoplasmic fluid from the laticiferous cells), which can be continually extracted from the tree by repeatedly slicing off a thin layer of trunk bark in a process called "tapping". Latex is typically contained in tubes and cells collectively known as laticifers, branched or unbranched tubular structures which in many species form a very complex laticiferous system by anastomosis between tube. (Gomez, 1982).

In principle, studying the biometrical genetics of the laticiferous system should shed light on the pattern of inheritance in rubber trees, one potentially useful aspect of such a study being that it could assist breeders in the choice of parents when planning breeding programs. Several workers (Tan, 1981; Gonçalves *et al.,* 1999, Costa *et al.*, 2002) have concluded that yield variation can be largely accounted for by additive genetic variance.

The purpose of our present study was to provide further estimates of heritabilities and genetic gains for the laticiferous system (bark thickness, number of latex vessel rings, distance between consecutive latex vessel rings, density of latex vessels per 5 mm averaged over all rings) and rubber yield in trees at three different sites and also to determine genetic and phenotypic associations between these traits.

Material and Methods

Plant material and site locations

Our sample consisted of 22 three-year-old progenies obtained from open-pollinated seeds of clones phenotypically selected from a *H. brasiliensis* population of Asian origin. The following parental clones were selected:

AVROS 49, AVROS 255, AVROS 352, AVROS 363, AVROS 1328, AVROS 1126, C 228, C 259, C 297, C 318, GT 127, GT 711, PB 49, PB 86, PB 5/63, PR 107, RRIM 513, RRIM 600, Tjir 1 and Tjir 16.

The progeny tests were set up at three different regional poles on the plateau region of the Brazilian state of São Paulo, these poles belonging to the São Paulo state Agribusiness Technology Agency (APTA).

The Center-west Regional Pole, is at Jaú (22°17' S, 48°34' W; altitude 580 m) where the soil is a Koandiudox and the topography is flat and well-drained. An Aw (Köppen) climate predominantes in this region which has a well-defined dry season, an annual mean temperature of 21.6°, a mean annual rainfall of about 1.344 mm and an average humidity of about 70% with extremes of 77% in February (summer) and 59% in August (winter).

The Center-north Regional Pole is at Pindorama (21°13' S; 4°856' W; altitude 560 m) where the soil is Paleudox. The climate is tropical, with a wet summer and a dry winter period. Mean monthly temperatures vary from 16.6 to 28.9°C, and annual mean rainfall is 1,390 mm. The period from October to April usually has favorable precipitation for growth and production. Rainfall deficit and low temperatures occur from May to September.

The Northwest Regional Pole at Votuporanga (20°25' S; 49°50' W; altitude 450 m) has a Paleudalf soil and tropical climate with a hot wet summer and a dry winter with low temperatures and rainfall. Mean monthly temperature varies from 20 to 25 °C and annual mean rainfall from 1,087 to 1,537 mm. The winter drought varies from four to six dry months, with an average water deficiency of 180 mm.

The rubber tree seeds were collected at the Experimental Center of the Campinas Agronomic Institute (Instituto Agronômico Campinas (IAC), Campinas, São Paulo, Brazil), germinated in polyethylene bags at the three experimental stations and taken to their definitive planting locations when the seedlings had two leaf whorls. In the field the seedlings (henceforth called progenies) were planted according to a randomized complete block design with 22 progenies, five replications and 10 plants per plot spaced at 1.5 x 1.5 m in single rows. The progenies were assessed when they were three years old.

Measurements

Determination of rubber yield (Pp) was made using the principle of the Hamaker-Morris-Mann test (HMM) (Tan and Subramanian, 1976). For latex vessel determination, virgin bark sample plugs were removed from the trunk at a position 20 cm from the ground on the opposite side to that of the tappings panel. The traits examined were: Average bark thickness (Bt); number of latex vessel rings (Lv); average distance between consecutive latex vessel rings (Dc); density of latex vessels per 5 mm per ring averaged over all rings (Dd); and the diameter of the latex vessel

(Di), detailed procedures for these measurements having been described by Gonçalves *et al.* (1995).

Data analyses

Individual analyses of variance were carried out on the data for each plant. For the joint analysis of all the data sets we used a mathematical model which considered sites and progenies as random effects and was equivalent to the following equation described by Cruz and Regazzi (1994):

$$Y_{ijk} = \mu + r_k + p_i + a_j + pa_{ij} + e_{ijk}$$

where Y_{ijk} is the observed value of the ith progeny of the jth site in the kth replication; μ the general mean; r_k the effect of the kth replication; p_i the effect of the ith open-pollinated progeny; a_j the effect of the jth site, pa_{ij} the effect of the ith progeny ith and jth site and e_{ijk} the effect of the kth ortet within the ith progeny in the jth site replication.

The open-pollinated offsprings were assumed to be half-sibs. Components of variance due to replication within sites ($\hat{s}_b^2$), phenotypic variance due to differences among plants within progenies ($\hat{s}_w^2$), environmental variance among progenies ($\hat{s}_e^2$), genotypic variance among progeny means ($\hat{s}_g^2$), genotypic variance due to differences among plants within progenies ($\hat{s}_{gw}^2$) were calculated from the expectations of mean squares (Vencovsky and Barriga, 1992). All these analyses were performed using the 'Genes' computer program, Windows version (Cruz, 2001). The total phenotypic variance ($\hat{s}_{pt}^2$) was obtained using the expression:

$$\hat{s}_{pt}^2 = \hat{s}_w^2 + \hat{s}_e^2 + \hat{s}_g^2 + \hat{s}_b^2$$

Heritabilities

Heritabilities of individual plants h(h_i^2), within progeny (h_w^2), and among progeny means ($h_{\bar{x}}^2$) levels for each progeny test were estimated as:

$$h_i^2 = \frac{4\hat{s}_g^2}{\hat{s}_g^2 + \hat{s}_e^2 + \hat{s}_w^2}$$

$$h_w^2 = \frac{\hat{s}_{gw}^2}{\hat{s}_w^2}$$

$$h_{\bar{x}}^2 = \frac{\hat{s}_g^2}{MSP/\bar{n}r},$$

where $\bar{n}$ is the harmonic mean of the number of plants within plots, r the number of replications and *MSP* the mean square of the progenies.

The joint analysis heritability estimates for individual plants (h_i^2) and half-sib progenies mean ($h_{\bar{x}}^2$) were used according to Vencovsky and Barriga (1992), as follows:

$$h_i^2 = \frac{3\hat{s}_g^2}{\hat{s}_g^2 + \hat{s}_{ge}^2 + \hat{s}_e^2 + \hat{s}_w^2}$$

$$h_{\bar{x}}^2 = \frac{\hat{s}_g^2}{\hat{s}_g^2 + (\hat{s}_{ge}^2 / a) + (\hat{s}_e^2 / ar) + (\hat{s}_w^2 / ar\bar{n})},$$

where, $\hat{s}_{ge}^2$ is the variance due to genotypic-environment interaction, a the number of sites, r the number of replications and $\bar{n}$ the harmonic mean of the number of plants within a plot.

The coefficients of genotypic variation ($CV_g\%$) for individual and joint analyses were estimated using the formula described by Vencovsky (1983):

$$CV_g\% = 100\sqrt{\frac{\hat{s}_g^2}{\bar{x}}}$$

Similarly, the phenotypic and experimental variation coefficients were estimated, where $\bar{x}$ represents the general mean of the trait.

Genetic gain from selection among progeny (G_g) and within progeny (G_w) levels was computed using Falconer and Mackay (1996) formulas:

$$G_g = \frac{k_1\hat{s}_A^2}{4\sqrt{\hat{s}_g^2 + (\hat{s}_e^2 / r) + (\hat{s}_w^2 / nr)}}$$

$$G_w = \frac{3k_2\hat{s}_A^2}{4\sqrt{\hat{s}_w^2}}$$

where k_1 is the among progeny selection intensity (45%) and k_2 the within progeny selection intensity (10%).

The genetic gains expressed as a percent of the among and within progeny means were estimated using the formula:

$$G_g\% = \frac{G_g}{\bar{x}}.100$$

$$G_w\% = \frac{G_w}{\bar{x}}.100,$$

where $\bar{x}$ is the general mean.

To examine the relationship among the yield traits of *Hevea* plants at different sites, genetic ($r_{g(xy)}$) and phenotypic ($r_{p(xy)}$) correlation coefficients were calculated according to Kempthorne (1966), as follows:

$$r_{g(xy)} = \frac{Cov_{g(xy)}}{\sqrt{\hat{s}_{gx}^2.\hat{s}_{gy}^2}}$$

$$r_{p(xy)} = \frac{Cov_{p(xy)}}{\sqrt{\hat{s}_{px}^2.\hat{s}_{py}^2}}$$

where $Cov_{g(xy)}$ and $Cov_{p(xy)}$ are the genotypic and phenotypic covariances for traits x and y respectively; $\hat{s}_{gx}^2$ and $\hat{s}_{px}^2$ are the genotypic and phenotypic variances for trait x; $\hat{s}_{gy}^2$ and $\hat{s}_{py}^2$ are the genotypic and phenotypic variances for trait y. Correlation analyses were performed using ver-

sion 1.0 of the 'Selegen' computer program (Resende and Oliveira, 1997).

The significance of these correlations was tested using the simple correlation table in Fisher and Yates (1971) for simple correlation for 5% and 1% probabilities. The genotypic and phenotypic correlation coefficients were tested using the degrees of freedom of the error.

Results and Discussion

Individual analysis of variance for all locations

With the exception of the number of latex vessel rings (Lv) in the Votuporanga population and the density of latex vessels per ring (Dd) and latex vessel diameter (Di) in both the Votuporanga and Pindorama populations, the six traits studied showed significant differences ($p < 0.05$ and $p < 0.01$) in the individual analyses of variance (Table 1). This suggests that differences were attributable to genetic causes and that selection within each *Hevea* population included in this study is possible. Average rubber yield (Pp) was 0.85 g per individual plant (ortet) the lowest Pp value was 0.61 g per ortet and occurred in the Votuporanga population while the highest Pp value was 0.99 g per ortet in the Pindorama population, 62% higher than in the Votuporanga population. At the three locations bark thickness (Bt) averaged 3.80 mm per ortet, the lowest average Bt value being 3.76 mm per ortet in the Jaú population and the highest 3.85 mm per ortet in the Votuporanga population, 3% higher than in the Jaú population.

The number of latex vessels (Lv) averaged 3.29 units per ortet, the lowest average Lv value being 3.05 units per ortet in the Votuporanga population and the highest 3.15 units per ortet in the Jaú population, 3% higher than in the Votuporanga population. Although the experimental sites were at similar latitudes, longitude and altitude in the São Paulo plateau region the performance of the progenies varied, suggesting the involvement of other environmental factors such as soil type, fertility and structure.

Joint analysis of variance

The joint analysis of variance showed highly significant ($p > 0.01$) differences among progenies for Pp, Bt, Lv and Dc (Table 2). These variations indicate good prospects for both selection program and general continuity in the *Hevea* genetic breeding program. The experimental coefficients of variation ($CV\%$) showed were high for Pp ($CV_e = 32.65\%$), moderately high for Lv ($CV_e = 12.18\%$) and Dc ($CV_e = 12.12\%$) and moderately low for Bt ($CV_e = 9.04\%$) and Di ($CV_e = 9.43\%$). These values express the intrinsic properties of the traits. These values agreed with similar estimates by Gonçalves *et al.* (1998), Moreti *et al.* (1994), Boock *et al.* (1995) and Costa *et al.* (2000a). Except for Lv, the effect of site was significant on all traits, indicating that they were affected by site variation under the conditions of the present study. The progeny-location inter-

Table 1 - Mean squares, coefficient of experimental variation ($CV_e\%$) and coefficient of genetic variation ($CV_g\%$) for six different traits of the bark laticiferous system in 22 three-years-old open pollinated *Hevea* progenies growing at three sites in the Brazilian State São Paulo.

Sites	Traits[1]	Analysis of variance mean square values[2]				Mean	$CV_e\%$	$CV_g\%$
		Replications (R)	Progenies (P)	P x R	Within plot			
Votuporanga	Pp	0.4452	0.8770**	0.2853	0.2688	0.61	7.67	20.62
	Bt	1.5492	5.9193**	0.8562	0.6588	3.85	8.27	8.99
	Lv	0.8551	1.6018n.s.	1.1226	0.5879	3.05	12.12	3.54
	Dc	0.0095	0.0449**	0.0108	0.0085	0.32	11.37	9.02
	Dd	31.2553	73.3875n.s.	77.1367	40.8389	46.30	6.63	-
	Di	105.3573	17.5892n.s.	20.1426	14.2827	19.00	9.21	-
Pindorama	Pp	0.5372	7.0787**	1.0143	0.5807	0.99	34.91	34.84
	Bt	1.5766	11.9116**	0.9609	0.6098	3.80	8.80	12.12
	Lv	1.2880	4.3488**	1.0368	0.6771	3.06	11.44	10.34
	Dc	0.0102	0.0378**	0.0138	0.0082	0.32	12.67	6.82
	Dd	149.8487	105.5731n.s.	104.7621	46.4484	45.03	7.78	0.28
	Di	27.0902	34.7806n.s.	28.5751	12.6741	17.16	10.79	2.05
Jaú	Pp	0.7282	0.9959*	0.4954	0.2529	0.94	28.75	16.68
	Bt	2.2674	8.1624**	1.3206	0.5676	3.76	10.58	9.83
	Lv	32.7214	6.6046**	1.5609	0.6762	3.15	13.92	10.22
	Dc	0.0217	0.0354*	0.0104	0.0475	0.25	13.87	8.75
	Dd	267.8469	140.5422**	49.4823	21.4847	43.74	5.60	3.10
	Di	133.1510	48.3380**	25.8348	9.9836	17.52	10.08	3.84

*p < 0.05; **p < 0.01; n.s. = not significant.
[1]Key (units in parenthesis): Pp = rubber yield (g); Bt = bark thickness (mm); Lv = number of latex vessel rings; Dc = average distance (µm) between consecutive latex vessel rings (based on all rings); Dd = density of latex vessels per 5mm per ring, averaged over all rings; Di = diameter (µm) of latex vessels.
[2]Degrees of freedom were: 5 for replication, 21 for progeny and 105 for residual for all traits.

Table 2 - Estimates of variance due to replication within sites ($\hat{s}_b^2$), genetic variance among progeny means ($\hat{s}_g^2$), environmental variance among progenies ($\hat{s}_e^2$), phenotypic variance within progenies ($\hat{s}_w^2$), genotypic variance due to differences among plants within progenies ($\hat{s}_{gw}^2$), heritabilities of individual plants ($\hat{h}_i^2$), among progeny means ($\hat{h}_{\bar{x}}^2$), and within progeny ($\hat{h}_w^2$) levels for five different laticiferous system in 22 three-years-old open-pollinated *Hevea* progenies growing at three sites in the Brazilian State of São Paulo.

Sites	Variances components	Traits[1]					
		Pp	Bt	Lv	Dc	Dd	Di
Votuporanga	$\hat{s}_b^2$	0.0010	0.0374	-	-	-	0.4687
	$\hat{s}_g^2$	0.0109	0.1201	0.0116	0.0008	-	-
	$\hat{s}_e^2$	0.0022	0.0234	0.0648	0.0003	4.4387	0.7091
	$\hat{s}_w^2$	0.2688	0.6588	0.5879	0.0084	40.8390	14.2827
	$\hat{s}_{gw}^2$	0.0484	0.3602	0.3487	0.0025	-	-
	$\hat{h}_i^2$	0.2249	0.5987	0.3700	0.3463	-	-
	$\hat{h}_{\bar{x}}^2$	0.6748	0.8554	0.2991	0.7586	-	-
	$\hat{h}_w^2$	0.1802	0.5468	0.0593	0.2940	-	-
Pindorama	$\hat{s}_b^2$	-	0.0032	0.0013	-	0.2402	-
	$\hat{s}_g^2$	0.1187	0.2125	0.0653	0.0005	0.0158	0.1241
	$\hat{s}_e^2$	0.0509	0.0409	0.0426	0.0007	6.8339	0.9061
	$\hat{s}_w^2$	0.5807	0.6098	0.6771	0.0082	46.4484	12.6941
	$\hat{s}_{gw}^2$	0.3562	0.6375	0.1960	0.0014	0.0475	0.3424
	$\hat{h}_i^2$	0.6328	0.9848	0.3329	0.2007	0.0012	0.0337
	$\hat{h}_{\bar{x}}^2$	0.8567	0.9143	0.7616	0.6347	0.0077	0.1784
	$\hat{h}_w^2$	0.6133	1.0456	0.2895	0.1712	0.0010	0.0293

Table 2 (cont.)

Sites	Variances components	Traits[1]					
		Pp	Bt	Lv	Dc	Dd	Di
Jaú	$\hat{s}_b^2$	0.0016	0.0052	0.1752	0.0001	1.2043	0.5863
	$\hat{s}_g^2$	0.0248	0.1367	0.1040	0.0005	1.8414	0.4531
	$\hat{s}_e^2$	0.0360	0.0902	0.1095	0.0047	3.3970	1.9151
	$\hat{s}_w^2$	0.2529	0.5676	0.6762	0.0007	21.4848	9.9836
	$\hat{s}_{gw}^2$	0.0744	0.4100	0.3120	0.0014	5.5242	1.3593
	$\hat{h}_i^2$	0.3161	0.6881	0.4676	0.3279	0.2756	0.1467
	$\hat{h}_{\bar{x}}^2$	0.5026	0.8382	0.7637	0.7052	0.3479	0.4655
	$\hat{h}_w^2$	0.2941	0.7224	0.4615	0.3052	0.2571	0.1362
Joint analysis	$\hat{s}_g^2$	0.0261	0.0959	0.0294	0.0003	0.1521	-
	$\hat{s}_e^2$	0.0709	0.1173	0.1417	0.0013	8.3602	2.8492
	$\hat{s}_w^2$	0.3675	0.6121	0.6471	0.0058	36.2574	12.3201
	$\hat{s}_{ge}^2$	0.0241	0.0618	0.0334	0.0003	0.5609	0.2372
	$\hat{h}_i^2$	0.3243	0.3243	0.3036	0.1169	0.0100	-
	$\hat{h}_{\bar{x}}^2$	0.7586	0.7586	0.5654	0.5947	0.1513	-

[1]Key (units in parenthesis): Pp = rubber yield (g); Bt = bark thickness (mm); Lv = number of latex vessel rings; Dc = average distance (μm) between consecutive latex vessel rings (based on all rings); Dd = density of latex vessel per 5 mm per ring, averaged over all rings; Di = diameter (μm) of latex vessels.

action effect was also significant on all studied traits. According to Vencovsky (1969) the progeny x site interaction reflects the difference in viability among progenies and the correlation among materials for different traits.

Genetic and environmental parameters

The genotypic variation coefficient, ($CV_g\%$) expresses the amount of existing genetic variation as a percentage of the general mean (Table 1), and was higher for Pp and Bt followed by Lv in Pindorama (Pp = 34.84%, Bt = 12.12% and Lv = 10.34%), Jaú (Pp = 16.68%, Bt = 9.83% and Lv = 10.22%) and Votuporanga (Pp = 20.62%, Bt = 8.99% and Lv = 3.54%). These results confirmed the F test results for progeny differences and characterized these traits as being suitable for expressing the genetic variability of the population studied. These results also agree with those reported by Gonçalves *et al.* (1998) and Boock *et al.* (1995) for the same traits.

As a percentage of the total phenotypic variance based on individual plants ($\hat{s}_p^2$) the genetic variance components among progenies for Pp accounted for 3.85% in the Votuporanga population, 7.87% in the Pindorama population and 15.82% in the Jaú population (Table 2). As a percentage of phenotypic variance, the contribution of genotypic variance among progenies ($\hat{s}_g^2$) was 17.09% for Bt (bark thickness) and 16.45% for Lv (number of latex vessel rings) in Jaú and was substantially greater than the $\hat{s}_g^2$ values for Bt (14.30%) and Lv (1.75%) in Votuporanga. On the other hand, the $\hat{s}_g^2$ values for Bt (24.17%) and Lv (8.30%) were substantially greater in Pindorama and

smaller in Votuporanga. In addition, except for the joint analysis, genotypic variance components among progeny means were always higher than those for the environmental effects (Table 2).

Heritabilities

On individual plant level, Pp heritabilities ($\hat{h}_i^2$) moderately high for Votuporanga (0.22), Jaú (0.32) and Pindorama (0.63) while Bt ($\hat{h}_i^2$) values were all high in that they were 0.60 at Votuporanga, 0.69 at Jaú and 0.98 at Pindorama (Table 3). Our data agreed with that various authors (Costa *et al.*, 2000a, b; Gonçalves *et al.,* 1998, 1999; Boock *et al*., 1995*; Moreti* et al., 1994) who reported individual plant heritability values ($\hat{h}_i^2$) of 0.22 to 0.50 for Pp (rubber yield) and from 0.45 to 0.73 for Bt, indicating that both these traits have moderately high heritability estimates. Our results indicate that there was a large amount of genetic variability in our population. The Lv $\hat{h}_i^2$ values were relatively high on an individual basis (0.37 for Votuporanga, 0.33 for Pindorama and 0.47 for Jaú) and also for between progeny means (0.30 for Votuporanga, 0.76 for Pindorama and 0.76 for Jaú) and within progenies (0.06 for Votuporanga, 0.29 for Pindorama and 0.46 for Jaú). The Dd (density of latex vessels) $\hat{h}_i^2$ values were very low for Pindorama and Jaú on an individual basis (0.001 for Pindorama and 0.28 for Jaú) and also between progeny means (0.01 for Pindorama and 0.35 Jaú) and within progenies 0.001 for Pindorama and 0.26 for Jaú), these moderately low heritability estimates indicating that there is a need to

Table 3 - Heritability coefficients for six different laticiferous system traits of 22 three-year-old open-pollinated *Hevea* progenies growing at three sites in the Brazilian State of São Paulo.

Site	Heritabilities	Traits[1]					
		Pp	Bt	Lv	Dc	Dd	Di
Votuporanga	Individual plants ($\hat{h}_i^2$)	0.2249	0.5987	0.3700	0.3463	-	-
	Progeny mean ($\hat{h}_{\bar{x}}^2$)	0.6748	0.8554	0.2991	0.7586	-	-
	Within progeny ($\hat{h}_w^2$)	0.1802	0.5468	0.0593	0.2940	-	-
Pindorama	Individual plants ($\hat{h}_i^2$)	0.6328	0.9848	0.3329	0.2007	0.0012	0.0337
	Progeny mean ($\hat{h}_{\bar{x}}^2$)	0.8567	0.9143	0.7616	0.6347	0.0077	0.1784
	Within progeny ($\hat{h}_w^2$)	0.6133	1.0456	0.2895	0.1712	0.0010	0.0293
Jaú	Individual plants ($\hat{h}_i^2$)	0.3161	0.6881	0.4676	0.3279	0.2756	0.1467
	Progeny mean ($\hat{h}_{\bar{x}}^2$)	0.5026	0.8382	0.7637	0.7052	0.3479	0.4655
	Within progeny ($\hat{h}_w^2$)	0.2941	0.7224	0.4615	0.3052	0.2571	0.1362
Pooled analysis	Individual plants ($\hat{h}_i^2$)	0.3243	0.3243	0.3036	0.1169	0.0100	-
	Progeny mean ($\hat{h}_{\bar{x}}^2$)	0.7586	0.7586	0.5654	0.5947	0.1513	-

[1]Key (units in parenthesis): Pp = rubber yield (g); Bt = bark thickness (mm); Lv = number of latex vessel rings; Dc = average distance (μm) between consecutive latex vessel rings (based on all rings); Dd = density of latex vessels per 5 mm per ring, averaged over all rings; Di = diameter (μm) of latex vessels.

increase the genetic variability for latex vessel density in these populations.

It is important to emphasize that these highly significant heritability estimates coupled with the large amount of variation observed within our rubber tree populations suggest that an effort to increase both yield and bark thickness through progeny selection would be rewarding.

Correlations

High and significant genetic and phenotypic correlations were found for Pp ($r_g = 0.94$, $r_p = 0.85$; both significant at $p < 0.01$) and Lv ($r_g = 0.76$, $r_g = 0.77$; both significant at $p < 0.01$) between Votuporanga and Jaú (Table 4).

There were high and significant Bt (bark thickness) and Lv (number of latex vessel rings) genetic (r_g) and phenotypic (r_p) correlations between the Votuporanga and Pindorama populations ($r_g = 0.59$ and $r_p = 0.89$ for Bt; $r_g = 0.65$, $r_p = 0.64$ for Pp. All significant at $p < 0.01$) but the correlations were low for the other traits (Table 4). The high correlations indicate that a single breeding program could satisfactorily serve both the Votuporanga and the Jaú populations. This assertions is valid for both rubber yield, num-

Table 4 - Genotypic (r_g) and phenotypic (r_p) correlations among Votuporanga (1), Pindorama (2) and Jaú (3) sites for rubber yield (Pp), bark thickness (Bt), number of latex vessel rings (Lv), average distance between consecutive latex vessel rings (Dc), density of latex vessels per ring (Dd), diameter of latex vessels (Di) in 22 three-year-old open-pollinated *Hevea* progenies growing at three sites in the Brazilian state of São Paulo. Site 1 = Votuporanga, site 2 = Pindorama, site 3 = Jaú.

	Pp				Bt		
Sites	Correlation types	2	3	Sites	Correlation types	2	3
1	r_g	0.6598**	0.9444**	1	r_g	0.5907**	0.2679ns
	r_p	0.6430**	0.8460**		r_p	0.8901**	0.3920ns
2	r_g	-	-0.1627ns	2	r_g	-	0.2320ns
	r_p	-	0.1091ns		r_p	-	0.5254*
	Lv				Dc		
Sites	Correlation types	2	3	Sites	Correlation types	2	3
1	r_g	0.0605ns	0.7569**	1	r_g	0.3733ns	0.1664ns
	r_p	-0.0088ns	0.7653**		r_p	0.4801*	0.6014ns
2	r_g	-	0.0841ns	2	r_g	-	0.2671ns
	r_p	-	0.6462**		r_p	-	0.5620**

Table 4 (cont.)

		Dd				Di	
Sites	Correlation types	2	3	Sites	Correlation types	2	3
1	r_g	-0.0202ns	0.0164ns	1	r_g	0.0006ns	0.0098ns
	r_p	0.0000	0.5473**		r_p	-0.0880ns	-0.1241ns
2	r_g	-	-0.1138ns	2	r_g	-	0.0393ns
	r_p	-	0.0000		r_p	-	-0.0019ns

*$p < 0.05$; **$p < 0.01$; ns = not significant.

ber of latex vessel rings, which can be checked by the genetic correlation between locations (Vencovsky and Barriga, 1992).

Genetic and phenotypic correlation coefficients obtained for Votuporanga and Pindorama had fairly strong genetic correlations for Bt ($r_g = 0.59$, $r_p = 0.89$; both significant at $p < 0.01$) and medium for Pp ($r_g = 0.66$, $r_p = 0.64$ both significant at $p < 0.01$) and Dc ($r_g = 0.37$, $r_p = 0.48$; r_p significant at $p < 0.05$). The highest values however, were smaller than those found for the coefficients between Pindorama and Jaú. As in the previous analysis, these results characterized the interaction for rubber yield, indicating that for these traits only one breeding program at one site will satisfy the needs of the other site involved.

In the joint analysis (Table 5) Pp and Dd had fairly strong positive genetic and phenotypic correlations ($r_g = 0.54$, $r_p = 0.56$; both significant at $p < 0.01$) suggesting that selection for one trait should lead to strong positive indirect responses in the other. This positive genetic association certainly needs to be verified by further studies across more sites. These findings for three-years-old progeny trials in São Paulo are the opposite to those reported for a one-year-old progeny study in the Amazon where Gonçalves *et al.* (1984) found adverse genetic associations between latex vessels density (Dd) and rubber yield (Pp) when selectively breeding *H. brasiliensis* for rubber production.

We observed high negative correlations between Lv and Dc ($r_g = -0.72$, $r_p = -0.63$; both significant at $p < 0.01$), these findings agreeing with the results reported for other sutdies involving progenies of the same age (Gonçalves *et al.* 1984)

Genetic correlation values (r_g) for both Bt (0.44) and Lv (0.43) were favorably associated with rubber production (Pp), and support the work of Gonçalves *et al.* (1999, 2004) who found phenotypic correlations of almost the same magnitude ($r_p = 0.42$ and 0.43).

Expected progress with selection

The estimated narrow sense heritabilities for rubber yield (Pp), bark thickness (Bt) and total number of vessel rings (Lv) varied between sites, with the Pp and Bt values being highest values at Pindorama which suggests that high genetic gains could be achieved for these traits at this site

Table 5 - Genotypic (r_g) and phenotypic correlations (r_p) for bark thickness (Bt), total number of latex vessel rings (Lv), average distance (mm) between consecutive latex vessel rings (Dc), density of latex vessels per 5mm per ring (Dd) and diameter of latex vessels (Di) in 22 three-year-old open-pollinated *Hevea* progenies growing at three sites in the Brazilian state of São Paulo. Values represent means for the three sites.

		Traits				
Traits	Correlation type	Bt	Lv	Dc	Dd	Di
Pp	r_g	0.4382*	0.4657*	0.3375ns	0.5425**	0.8628**
	r_p	0.4289*	0.4305*	-0.2941ns	0.5584**	0.7716**
Bt	r_g		0.3090ns	0.1263ns	0.3216ns	0.8263**
	r_p		0.2809ns	0.1170ns	0.2463ns	0.4690*
Lv	r_g			-0.7229**	0.4403**	0.5558**
	r_p			-0.6298**	0.3789	0.4500*
Dc	r_g				-0.2685ns	-0.0346ns
	r_p				-0.1506ns	0.0036ns
Dd	r_g					0.6542**
	r_p					0.7074**

*and ** significant at 5% and 1% probability, respectively
ns = not significant.

(Table 3). The prediction of expected progress by selection between progenies assumed a selection intensity (Table 6) of 45% for all the traits, but the genetic gain values varied considerably for Pp and among the other laticiferous system traits and were especially high for the Bt trait. These values were within the limits obtained by other authors (Paiva *et al.,* 1994; Vasconcellos, 1985; Moreti *et al.*, 1994) and Book *et al.* (1995). The results also showed a tendency for greater gains when selection took place in Pindorama and Jaú. However, the expected progress in selection intensity for within progeny selection was only 10%, although here again the gain values varied considerably for Pp and among the other laticiferous system traits and were especially high for the Bt trait. These values were also within the limits obtained by other authors (Moreti *et al.,* 1994; Boock *et al.,* 1995; Costa *et al.*, 2002). The results showed a tendency for greater genetic gains when the within progeny selection took place in Pindorama and, to a lesser extent, Jaú.

Selection gains as a percentage of the between and within progeny means for the other laticiferous system traits such as latex vessel density (Dd) and latex vessels diameter(Di) were relatively low for all sites and somewhat lower than those reported by Boock *et al* (1995). These low expected gains probably resulted from low heritability estimates with high phenotypic variation in these traits. Zobel and Talbert (1984), however, pointed out that tree breeders can influence selection gains by controlling the environment by maximize heritability. Genetic gain could also be increased by employing an appropriate method of indirect selection (Falconer and Mackay, 1996).

Breeding strategies

Our results show that it is possible to develop a program for rubber tree improvement. Zobel and Talbert (1984) state that 'progeny plus within-family selection' method (*i.e.* selecting the best progenies and the best individuals within progenies) is the predominant form of selection used in most advanced generation tree improvement

Table 6 - Expected genetic gain from selection and percentage of the mean among (G_g) within (G_w) progenies and total (G_{test}) for six different traits of the laticiferous system in 22 three-year-old open-pollinated *Hevea* progenies growing at three sites in the Brazilian state of São Paulo.

Location	Trait[1]	From selection			In percent of the mean		
		G_g	G_w	G_{test}	G_g	G_w	G_{tot}^{2}
Votuporanga	Pp	0.1013	0.0801	0.1814	16.43	13.00	29.43
	Bt	0.4070	0.5636	0.9706	10.57	14.63	25.20
	Lv	0.3795	0.5778	0.9573	12.46	1.90	14.36
	Dc	0.0311	0.0346	0.0657	9.73	10.81	20.54
	Dd	-	-	-	-	-	-
	Di	-	-	-	-	-	-
Pindorama	Pp	0.4050	0.5936	0.9986	40.96	60.04	101.00
	Bt	0.5613	1.0369	1.5982	14.76	27.26	42.02
	Lv	0.2832	0.3025	0.5857	9.25	9.88	19.13
	Dc	0.0228	0.0197	0.0425	7.18	6.20	13.38
	Dd	0.0140	0.0088	0.0228	0.03	0.02	0.05
	Di	0.1889	0.1327	0.3216	1.10	0.77	1.87
Jaú	Pp	0.1636	0.1878	0.3514	17.34	19.90	37.24
	Bt	0.4299	0.6912	1.1211	11.43	18.38	29.81
	Lv	0.3579	0.4819	0.8398	11.34	15.27	26.61
	Dc	0.0176	0.0695	0.0871	7.03	27.71	34.74
	Dd	1.3872	1.5136	2.9008	3.17	3.46	6.63
	Di	0.5833	0.5464	1.1297	3.33	3.12	6.45
Average	Pp	0.2233	0.2872	0.5105	24.91	30.98	55.89
	Bt	0.4661	0.7639	1.2300	12.25	20.09	32.34
	Lv	0.3402	0.4541	0.7943	11.02	9.02	20.04
	Dc	0.0238	0.0413	0.0651	7.98	14.91	22.89
	Dd	0.7006	0.7612	1.4618	1.60	1.74	3.34
	Di	0.3861	0.3395	0.7256	2.21	1.94	4.15

[1]Key (units in parenthesis); Pp = rubber yield (g); Bt = bark thickness (mm); Lv = number of latex vessel rings; Dc = average distance (μm) between consecutive latex vessel rings (based on all rings); Dd = density of latex vessels per 5 mm per ring, averaged over all rings; Di = diameter (μm) of latex vessels. [2]G_{tot} = total genetic gain ($G_g + G_w$).

programs and we feel that this method should be adopted for improving rubber yield (Pb), bark thickness (Bt) and the number of latex vessel rings (Lv) in rubber trees growing in São Paulo. Since there was low significant genetic correlation between Pb, Bt and Lv indirect selection is not applicable so 'tandem selection' should be used in which rubber yield is improved first and Bt and number Lv afterwards when rubber production has reached a satisfactory level, although if the intentions is to improve rubber yield and bark thickness simultaneously an 'independent culling' method would be better.

Acknowledgments

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