Brazilian Journal of Genetics, 19, 1, 105-111 (1996)
(Revista Brasileira de Genética)

Estimates of genetic parameters and correlations of juvenile characters based on open pollinated progenies of *Hevea*

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ABSTRACT

An investigation of 10 characters was conducted in three-year old open pollinated progenies of rubber tree [*Hevea brasiliensis* (Willd. ex Adr. de Juss.) Müell. Arg.]. The experiment included 17 families replicated in five blocks of ten tree rows. The characters studied were: average yield according to Hamaker-Morris-Mann test, virgin bark thickness, total number of latex vessel rings, overall density of latex vessels per ring per five square millimeters of bark, average diameter of latex vessels, average distance between consecutive latex vessel rings, average leaf area, crown form and stem circumference. Heritability as well as genotypic, phenotypic and environmental correlations among characters were estimated. Heritability values from progeny analysis data ranked from 0.08 (average distance between consecutive latex vessel rings) to 0.82 (average yield). Positive genetic correlations were found between average yield and characters of the laticiferous system. No relationship was found between average yield and stem circumference. Crown form and average yield were related (r = 0.55493), indicating that trees with high yield tend to have better crown form. No phenotypic correlation was found between average yield and total number of latex vessel rings, average leaf area, average diameter of latex vessels and average distance between consecutive latex vessel rings.

INTRODUCTION

Estimates of genetic parameters for various characters in juvenile half-sib progenies of rubber tree [*Hevea brasiliensis* (Willd. ex Adr. de Juss.) Müell. Arg.] have been reported by Paiva *et al.* (1982) and Moreti *et al.* (1994) in Brazil and full-sib progenies by Tan *et al.* (1975) and Tan and Subramaniam (1976). A knowledge of the association of quantitative characters, especially of yield and its attributes, would be important in order to develop suitable selection criteria and identify early selection parameters for *Hevea* breeding programmes. The magnitude of these responses can be predicted if the genetic correlation of two traits and their heritabilities are known (Falconer, 1981).

MATERIAL AND METHODS

The experiment was done at the Pindorama Experimental Station, State of São Paulo, Brazil

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Table I - Overall yield means following Hamaker-Morris-Mann test (MY), stem circumference (SC), average leaf area (LA), petiole length (PL), crown form (CF), virgin bark thickness (BT), total number of latex vessel rings (LV), overall density of latex vessel per ring per five square millimeters of bark (DV), average diameter of latex vessels (DL) and distance between consecutive latex vessel rings (AD) in seventeen half-sib progenies of rubber tree.

Progenies	MY g	SC cm	LA cm^2	PL cm	CF grade	BT mm	LV no.	DV no.	DL μ	AD μ
AVROS 49	0.51 ± 0.05[1]	7.52 ± 0.60	265.34 ± 12.54	18.51 ± 0.71	1.30 ± 0.02	4.02 ± 0.11	3.04 ± 0.14	41.56 ± 2.10	13.36 ± 0.56	251.46 ± 13.33
AVROS 255	0.56 ± 0.07	8.21 ± 0.73	314.45 ± 16.02	18.26 ± 0.73	1.37 ± 0.03	3.88 ± 0.14	2.86 ± 0.13	43.61 ± 2.62	14.39 ± 0.73	293.02 ± 17.59
AVROS 352	0.43 ± 0.07	7.60 ± 0.82	335.69 ± 13.92	19.96 ± 0.54	1.40 ± 0.03	3.33 ± 0.09	3.02 ± 0.11	45.22 ± 2.24	14.33 ± 0.69	288.48 ± 14.47
AVROS 1328	1.49 ± 0.22	7.98 ± 1.16	224.42 ± 21.01	18.15 ± 1.47	1.40 ± 0.06	3.62 ± 0.18	3.19 ± 0.22	50.57 ± 2.99	16.43 ± 1.12	278.25 ± 23.44
GT 127	1.22 ± 0.10	8.39 ± 0.77	287.09 ± 14.09	18.17 ± 0.59	1.35 ± 0.03	4.04 ± 0.17	2.92 ± 0.17	41.61 ± 2.13	14.37 ± 0.72	270.73 ± 18.19
GT 711	0.68 ± 0.07	8.16 ± 0.71	268.22 ± 12.20	16.59 ± 0.53	1.33 ± 0.02	4.05 ± 0.13	2.56 ± 0.11	43.83 ± 2.06	12.83 ± 0.54	301.91 ± 15.94
PB 49	0.91 ± 0.09	8.43 ± 0.70	315.11 ± 16.83	17.78 ± 0.73	1.32 ± 0.02	4.20 ± 0.16	2.61 ± 0.12	38.94 ± 2.20	13.34 ± 1.00	279.75 ± 14.56
PB 86	0.55 ± 0.09	8.26 ± 0.87	326.52 ± 22.40	19.49 ± 0.90	1.31 ± 0.03	4.16 ± 0.26	2.75 ± 0.15	45.48 ± 2.21	11.95 ± 0.83	303.15 ± 31.11
PB 5/63	0.85 ± 0.10	8.45 ± 0.70	327.09 ± 14.02	18.62 ± 0.50	1.34 ± 0.03	4.42 ± 0.14	2.53 ± 0.11	36.27 ± 1.54	12.65 ± 0.75	271.75 ± 16.99
PB 107	0.41 ± 0.05	7.79 ± 0.68	323.14 ± 19.09	17.23 ± 0.74	1.28 ± 0.02	3.70 ± 0.08	2.40 ± 0.09	36.11 ± 1.69	12.48 ± 0.51	330.47 ± 20.61
RRIM 509	0.58 ± 0.09	7.60 ± 0.71	300.02 ± 14.44	19.41 ± 0.75	1.34 ± 0.03	3.69 ± 0.11	2.40 ± 0.12	39.22 ± 1.93	12.71 ± 0.68	264.67 ± 15.04
RRIM 513	0.81 ± 0.11	8.74 ± 0.81	332.07 ± 13.52	19.51 ± 0.51	1.47 ± 0.05	4.03 ± 0.19	2.77 ± 0.16	47.50 ± 2.24	14.56 ± 0.95	295.19 ± 13.34
RRIM 526	0.98 ± 0.15	7.05 ± 0.61	326.42 ± 15.20	20.79 ± 0.63	1.43 ± 0.05	3.64 ± 0.14	2.68 ± 0.18	38.23 ± 2.95	10.47 ± 0.66	240.17 ± 24.68
RRIM 600	0.57 ± 0.07	7.79 ± 1.04	321.67 ± 27.45	19.12 ± 1.09	1.32 ± 0.03	3.54 ± 0.14	2.56 ± 0.12	37.60 ± 2.91	13.12 ± 0.89	272.30 ± 16.40
RRIM 606	0.89 ± 0.10	7.99 ± 0.66	325.77 ± 14.84	18.46 ± 0.47	1.34 ± 0.03	4.05 ± 0.13	2.73 ± 0.12	40.08 ± 1.65	13.50 ± 0.67	260.60 ± 13.54
Tjir 1	0.75 ± 0.07	7.98 ± 0.65	307.15 ± 13.31	20.88 ± 0.73	1.41 ± 0.03	4.31 ± 0.20	2.67 ± 0.12	38.43 ± 1.70	12.62 ± 0.53	275.69 ± 17.51
Tjir 16	0.49 ± 0.07	7.57 ± 1.07	318.30 ± 18.13	20.66 ± 1.06	1.27 ± 0.02	4.45 ± 0.17	2.40 ± 0.11	38.00 ± 2.34	11.31 ± 0.58	374.24 ± 28.36
LSD 0.05	0.27	2.20	60.73	2.73	0.11	0.50	0.50	9.28	3.27	61.42
LSD 001	0.36	2.92	80.68	3.63	0.15	0.66	0.70	12.33	4.34	81.61

[1]Standard error of the mean.

(21°11'25" latitude South). This region has a humid tropical climate with a mean yearly temperature of 21°C.

The trial included 17 three-year old half-sib progenies randomly selected on a populational basis from 100 asiatic clones (Table I). Each progeny was accommodated in a single row plot of 15 meters, with a spacing of 3.0 m among progenies and 1.5 m between plants. The experiment was carried out in a randomized block design, with five replications.

Yield determination was made using the principle of the Hamaker-Morris-Mann test (MY) (Tan and Subramaniam, 1976). Thirty tappings were made with a half-spiral alternate daily (1/2S 1/2d) tapping system at a height of 20 cm from the ground. Yield recording was done by cup coagulation. The "biscuits" were air dried for a two-month period until they gave constant weight. The results of each tree's performance were expressed in grams per tapping. Circumference measurements were taken at the same time at 20 cm height from the ground.

The measurements of flag leaf area (LA) and petiole length (PL) were taken after estimating the yield of each tree. The area of the flag leaf lamina was determinated in cm^2 using a Delta-T Devais apparatus connected to a computer with Dias Delta-T Image Analysis. The petiole length was measured using the length between the insertion of the leaflets and the stem.

Virgin bark samples were removed from the trunk as plugs at 20 cm height on the opposite side of the tapping panel. Bark samples were obtained from longitudinal and transverse sections and stained with Sudan III and osmic acid to determine the following characters:

- Total number of latex vessel rings (LV) (mean of three samples per tree).
- Overall density of latex vessels per ring per five square millimeters of bark (DV) averaged over all rings.
- Average diameter (μ) of the latex vessels (DL).
- Average distance (mm) between consecutive latex vessel rings (AD).
- Bark thickness (mm) (BT) measured from bark samples collected for the above characters.

Stem circumference was measured by the use of a steel tape at 0.50 m height from the ground (SC).

Crown form (CF) was scored. Crowns were evaluated on the basis of branch diameter, branch angle, branch length and general conformation. Scores ranged from 1 to 5. The best crown rated a score of 1 while the worst was scored 5. The mean for each character was determined for each progeny (Table I). Means of different progenies were compared using a protected LSD. Genotypic, phenotypic and environmental components of variance and covariance for each character were estimated from algebraic manipulation of the mean squares expectations of Table II (Vencovsky and Barriga, 1992).

To make biological interpretations of the components, the assumptions described by Dudley and Moll (1969) that the parents are random members of the genetic population and that experimental errors are independent were accepted. The variance among progenies was interpreted as one quarter of the additive genetic variance and narrow sense heritability (h^2) was calculated on an individual basis from the following formula: $h_i^2 = 4\sigma_p^2 / \sigma_p^2 + \sigma_{rp}^2 + \sigma_w^2$, where: σ_p^2 = variance due to differences among progenies = 1/4 σ_A^2 (σ_A^2 = additive genetic variance); σ_{rp}^2 = variance due to interaction of progenies and replication, and σ_w^2 = variance due to differences among trees within plots.

The standard error of the heritability estimates is essential to assess the precision of the estimates and was estimated by the formula S.E. (h^2) = $\sqrt{32 h^2 / nM}$ given by Falconer (1981), where: S.E. (h^2) = standard error of heritability; h^2 = heritability on an individual basis; n = number of individuals of one progeny and N = number of progenies.

Genetic coefficients of variation were estimated by the formula suggested by Vencovsky (1987) by dividing the square root of genotypic variance by the population mean and multiplying by 100.

The genotypic (rg_{ij}), phenotypic (rf_{ij}) and environmental (re_{ij}) correlations were worked out according to Kempthorne (1966) as follows:

$$(rg_{ij}) = (\sigma g_{ij}) / \sqrt{\sigma^2 g_i \cdot \sigma^2 g_j}$$

$$(rf_{ij}) = (\sigma f_{ij}) / \sqrt{\sigma^2 f_i \cdot \sigma^2 f_j}$$

Table II - Form of analysis used for estimating components of variance, covariance and heritability values in a three-year old open pollinated progeny test.

Source of variation	D.F.	Expected M.S.[1]	Expected M.C.P.[2]
Replications	r-1		
Progenies	p-1	$\sigma_{w/k}^2 + \sigma_{rp}^2 + r\sigma_p^2$	$\sigma w_{ij/k} + \sigma rp_{ij} + r\sigma p_{ij}$
Progenies x replications	(r-1)(p-1)	$\sigma_{w/k}^2 + \sigma_{rp}^2$	$\sigma w_{ij}/k + \sigma rp_{ij}$
Within plot	(N-rp)	σ_w^2	σw_{ij}

1) σ_w^2 = Variance due to differences among plants within plots.

σ_{rp}^2 = Variance due to interaction of progenies and replications.

σ_p^2 = Variance due to differences among progenies 1/4 σ_A^2 ·(σ_A^2 = additive genetic variance).

r = Number of replications.

k = Harmonic mean of plants per plot.

N = Total number of individuals in the trial.

p = Number of progenies.

2) σw_{ij} = Covariance among trees within plots of i and j traits.

σrp_{ij} = Covariance due to interaction of progenies and replications of i and j traits.

σp_{ij} = Covariance due to traits i and j.

$$(re_{ij}) = (\sigma e_{ij}) / \sqrt{\sigma^2 e_i \cdot \sigma^2 e_j}$$

where: σg_{ij}, σf_{ij} and σe_{ij} = genotypic, phenotypic and environmental covariances for traits i and j, respectively.

$\sigma^2 g_i$, $\sigma^2 f_i$ and $\sigma^2 e_i$ = genotypic, phenotypic and environmental variances for trait i.

$\sigma^2 g_j$, $\sigma^2 f_j$ and $\sigma^2 e_j$ = genotypic, phenotypic and environmental variances for trait j.

The significance of these correlations was tested using the table in Fisher and Yates (1981), for simple correlations for 5% and 1% probability. The genotypic and phenotypic correlations were tested with 15 degrees of freedom and environmental correlations were tested with the degrees of freedom of the error.

RESULTS AND DISCUSSION

Means and variations

The mean, range and coefficient of variation for each character are given in Table III. The differences among traits were significant for the characters studied. All the characters exhibited considerable range in their expression. The coefficient of variation was the highest for MY. DV, DL and LV also showed considerable experimental coefficient of variation. SC and CF had the lowest phenotypic coefficient of variation.

Variances and heritability

Genotypic, phenotypic and environmental variances for different characters are shown in Table IV. The phenotypic variance was taken as the sum of error and genotypic variance, while the latter was calculated by subtracting the error mean square from the progeny mean square and dividing the remainder by the number of replications (Vencovsky, 1987).

Wide range among genotypic coefficients of variation was observed, from 2.71% for CF to 36.93% for average yield.

The heritability estimates varied between 0.08 and 0.82 for the various characters, with the estimates being highest for SC and MY (Table IV). Heritability was lowest for AD ($h^2 = 0.07$) and DL ($h^2 = 0.12$). For the remaining characters it was not substantial.

Relationship studies

In general, genotypic correlations were slightly superior to phenotypic correlations. Both were superior to environmental correlations (Tables V, VI and VII).

Genetic correlations

As is clear from Table V, MY had a high negative correlation with LA and AD. High positive

Table III - Overall means, standard deviation, coefficient of variation %, and number of trees for characters of the three-year old open pollinated progenies of rubber trees.

Characters	Mean	Range	Units	Standard deviation	Coefficient of variation
Average yield (MY)	0.75	0.30 - 10.41	g.	4.26	28.62
Stem circumference (SC)	8.00	5.57 - 11.62	cm	4.00	15.93
Average leaf area (LA)	306.70	74.57 -849.66	cm	48.01	15.64
Petiole length (PL)	19.95	10.22 - 36.72	cm	2.16	11.41
Crown form (CF)	1.35	1.00 - 5.00	grade	0.09	6.51
Virgen bark thickness (BT)	3.50	1.85 - 7.30	mm	0.39	10.01
Total number of latex vessel rings (LV)	2.71	2.00 - 6.00	unit	0.42	15.35
Overall density of latex vessel per ring (DV)	41.31	15.00 - 85.00	unit	7.34	17.76
Average diameter of latex vessels (DL)	13.20	5.00 - 31.99	μ	2.58	19.56
Average distance between consecutive latex vessel rings (AD)	283.01	100.00 -730.00	μ	48.57	11.71

Table IV - Components of variance and heritability estimates and standard error for average yield following Hamaker-Morris-Mann test (MY), virgin bark thickness (BT), total number of latex vessel rings (LV), overall density of latex vessel per ring per five square millimeters of bark (DV), average diameter of latex vessel (DL), average distance between consecutive latex vessel rings (AD), crown form (CF), average leaf area (LA), stem circumference (SC) and petiole length (PL) in rubber tree progenies.

Characters	σ^2_p	σ^2_{rp}	σ^2_w	σ^2_A	h^2_i
MY (g)	30.3654	1.6061	116.2536	121.4616	0.8194 ± 0.244
BT (mm)	0.0715	0.0468	0.7648	0.2860	0.3239 ± 0.126
LV (un.)	0.0207	0.0942	0.5533	0.0830	0.1281 ± 0.079
DV (un.)	6.4246	35.5102	149.0015	25.6980	0.1367 ± 0.081
DL (μ)	0.5772	4.6894	13.7988	2.3080	0.1211 ± 0.076
AD (μ)	250.5917	643.8850	11.986.4380	1.002.3360	0.0778 ± 0.061
CF (deg)	0.0013	0.0038	0.0280	0.0054	0.1269 ± 0.096
LA (cm^2)	426.1729	948.1448	9.486.1978	1.704.6917	0.1570 ± 0.097
SC (cm)	1.2098	0.4234	14.5195	4.8392	0.3162 ± 0.151
PL (cm)	0.5362	1.8884	19.4534	1.1450	0.0980 ± 0.088

σ^2_p - estimate of component of variance among progenies.

σ^2_{rp} - estimate of component of variance of replication by progenies interaction.

σ^2_w - within plot variance.

σ^2_A - additive genetic variance.

h^2_i - narrow sense heritability on individual bases.

correlations were also observed with LV, DV and DL. Association of these characters with yield has been reported by Vasconcellos (1982), Ribeiro (1983), Alves (1985) and Gonçalves *et al.* (1984). LV and DL, LA, LV and DL had very strong and negative association with each other. LV and DL had a strong positive association and BT was negatively associated with DL. The association between MY and SC was non-significant.

Phenotypic correlations

All possible phenotypic correlations among the characters studied are given in Table VI. The association of MY and CF was the strongest among the characters. The associations of MY and the structural characters of the bark, viz., LV, DV, DL and AD were positive but not significant, indicating that MY was much more important than the structural characters of the bark. Vasconcellos (1982) and Gottardi *et al.* (1995) also reported low association between MY and LV, while Narayanan *et al.* (1974) and Gonçalves *et al.* (1984) reported strong positive association between MY and BT.

A positive association between MY and LV was also reported by Narayanan *et al.* (1974), Vasconcellos (1982), Ribeiro (1983) and Alves (1985). Apart from BT, DL showed a positive association with LV, indicating that plants with greater LV also had a larger DL.

The phenotypic association between LA and PL was high, indicating that large leaves in general have a long petiole.

SC did not show any association with any of the characters studied, indicating independent genetic control of vigor for all other characters studied. This also implies that high MY and high vigor could be combined in a single genotype.

Environmental correlations

The environmental correlation coefficients among characters under study are presented in Table VII. A positive correlation was noticed between MY and BT. However, MY showed low positive environmental correlation values with the other characters.

Generally, the association between a pair of characters is assessed on the basis of the error (environmental) component in the standard analyses of covariances (Fisher, 1954 and Snedecor, 1967). But when a number of varieties are included in the study a better idea of the relationships can be determined by partitioning the correlations into phenotypic, genotypic and environmental components. In the present investiga-

Table V - Genotypic correlations among average yield following Hamaker-Morris-Mann test (MY), stem circumference (SC), average leaf area (LA), petiole length (PL), crown form (CF), virgin bark thickness (BT), total number of latex vessel rings (LV), overall density of latex vessel per ring per five square millimeters of bark (DV), average diameter of latex vessels (DL) and average distance between consecutive latex vessel rings (AD) in seventeen half-sib progenies of the rubber tree.

Characters	SC	LA	PL	CF	BT	LV	DV	DL	AD
MY	-0.26232	-0.85262**	-0.28166	1.43940**	-0.03153**	0.76219**	0.54919*	0.83512**	-0.70299**
SC		0.32657	-0.98865	0.40405	0.53276*	-0.24607	0.10504	0.52611*	0.55261*
LA			-0.07782	-0.33279	-0.10583	-0.74493**	-0.65254**	-0.80805**	0.55822*
PL				0.94192**	-0.10105	0.09506	-0.10048	-0.86634**	-0.07432
CF					-0.52803*	0.51104	0.82836**	-0.05382	1.08733**
BT						-0.37491	-0.28366	-0.48378*	0.46619
LV							1.39989	0.79205**	-0.45558
DV								1.45295**	-0.30965
DL									0.08166

*P < 0.05; **P < 0.01.

Table VI - Phenotypic correlations among average yield following Hamaker-Morris-Mann test (MY), stem circumference (SC), average leaf area (LA), petiole length (PL), crown form (CF), virgin bark thickness (BT), total number of latex vessel rings (LV), overall density of latex vessel per ring per five square millimeters of bark (DV), average diameter of latex vessels (DL) and average distance between consecutive latex vessel rings (AD) in seventeen half-sib progenies of rubber tree.

Characters	SC	LA	PL	CF	BT	LV	DV	DL	AD
MY	-0.09413	-0.13675	-0.06721	0.55493*	-0.17806	0.18884	0.17474	0.21887	-0.23521
SC		-0.02244	-0.26464	0.05462	0.32649	-0.16383	0.06181	0.15375	0.38566
LA			-0.64546**	-0.13754	0.22594	-0.33120	-0.33957	-0.34763	-0.02675
PL				0.06763	0.15903	-0.06823	-0.13320	-0.20374	-0.14111
CF					-0.07031	0.40936	0.30667	0.51640*	0.06697
BT						-0.27602	-0.24815	-0.20082	0.10259
LV							0.45335	0.66639**	-0.33203
DV								0.40932	0.17268
DL									0.15879

*P < 0.05; **P < 0.01.

Table VII - Environmental correlations among average yield following Hamaker-Morris-Mann test (MY), stem circumference (SC), average leaf area (LA), petiole length (PL), crown form (CF), virgen bark thickness (BT), total number of latex vessel rings (LV), overall density of latex vessel per ring per five square millimeters of bark (DV), average diameter of latex vessels (DL) and average distance between consecutive latex vessel rings (AD) in seventeen half-sib progenies of rubber tree.

Characters	SC	LA	PL	CF	BT	LV	DV	DL	AD
MY	0.33707	0.23004	0.11583	0.20748	0.59149**	-0.01399	0.05412	0.05529	-0.10819
SC		-0.09813	-0.12409	0.14935	0.23272	-0.14009	0.05160	0.09036	0.33760**
LA			0.75317**	-0.22181	0.33723**	-0.27068*	-0.29414*	-0.10886	-0.10882
PL				-0.05518	0.22601	-0.08733	-0.13704	-0.20374	-0.14849
CF					-0.56382**	0.39374**	0.23225	0.58970**	-0.17129
BT						-0.26487*	-0.25067*	-0.15641	0.02748
LV							0.34022**	0.65438**	-0.31815*
DV								0.30369*	0.22703
DL									0.18194

*P < 0.05; **P < 0.01.

tion, the environmental correlation coefficients were generally lower than the phenotypic and genotypic components, except in a few cases. So it would appear that the environment does not appreciably influence the expression of these characters.

The significant environmental correlation between LV and CF and the negative environmental correlation between LV and SC would indicate that LV is influenced by the environment. This was also indicated by the high environmental variance for LV (Moreti *et al.*, 1994). In these progenies the best CF types had more LV and gave higher yields, though there were some CF progenies which did not bear correspondingly more LV.

ACKNOWLEDGMENTS

The authors wish to express their thanks to Mr. Edson Bernardes de Freitas for field work at Experimental Station of Pindorama, Mrs. Lígia Regina Lima Gouvêa and Rosimeiry Moreira Boschini for laboratory works and Miss Rosilei Felismino da Silva for the computer work. This work was supported by FAPESP. Publication supported by FAPESP.

RESUMO

Foram avaliados 10 caracteres juvenis de dezessete progênies de *Hevea brasiliensis* (Willd. ex Adr. de Juss.) Müell Arg. com o objetivo de identificar parâmetros de seleção precoce, para uso em futuros programas de melhoramento. Os caracteres estudados foram: produção média de borracha pelo teste Hamake-Morris-Mann (MY), espessura de casca virgem (BT), número total de vasos laticíferos (LV), densidade média dos vasos laticíferos em 5 mm^2 do anel (DV), diâmetro médio dos vasos laticíferos (DL), distância média entre os consecutivos anéis de vasos laticíferos (AD), área foliar (LA), forma da copa (CF), circunferência do caule (SC) e comprimento do pecíolo (PL). Correlações fenotípicas, genotípicas e ambientais entre os caracteres apresentaram melhores valores de herdabilidade. Os valores da análise de herdabilidade da progênie variam de h^2 = 0,08 (distância média entre os consecutivos anéis de vasos laticíferos) para h^2 = 0,82 (média de produção). A correlação genotípica entre MY e LV (rg = 0,76**), MY e LA (rg = -0.85*), Y e DL (rg = 0,83**) e MY e AD (rg = -0,70**) foi significativa ao nível de 1%. Não houve correlações fenotípicas entre MY e LV, LA, DL e AD.

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(Received June 24, 1993)