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Estimates of Genetic Parameters of Certain Characters in *Hevea brasiliensis*

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Summary. Heritability estimates of five quantitative characters, namely, yield, girth, girth increment, virgin bark and renewed bark thickness, of the breeding Phase III *Hevea* families have been obtained by variance component analyses. In general, the combined heritability estimates for various characters were low to moderate. The heritabilities of these characters based on female variance components, however, were high, suggesting that considerable improvement of each of the characters could be achieved in properly designed experiments.

Estimates of heritability for average yields (Range: 0.11 - 0.34) over different years showed that the first three years' yield was adequate for predicting estimates of genetic variance for the average of five years' yield.

Correlation studies on yield with other characters indicated considerable influence of environment, with genetic correlations accounting for about 0.07 to 0.36 in the characters studied.

Expected direct response to selection in yield and correlated response in yield to selection for girth at opening and virgin bark thickness have been calculated using three arbitrary values of selection intensity. The efficiency of the correlated response was found to be approximately half that of the direct response. However, the indirect selection for yield using virgin bark thickness appeared to be more favourable than that using the girth at opening favoured by earlier workers.

Introduction

The rubber breeding programme at the Rubber Research Institute of Malaysia (RRIM), begun in 1928 using controlled pollination, has progressed smoothly except for two interruptions, the depression in 1931-1936 and the second world war in 1942-1946. To evaluate the progress of this breeding programme, the annual programmes have been grouped into five phases: Phase I (1928-1931), Phase II (1937-1941), Phase III (1947-1958), Phase IV (1959-1965) and Phase V (1966-1973). The relationships between the materials used in the different phases are shown in Appendix A.

The earlier publications of this institute (Sharp, 1940, 1951; Ross, 1965; Ross and Brookson, 1966) compared the performance of progenies of the different crosses and recommended further exploitation of the best crosses. Such a study does not consider the quantitative genetic aspects of the crop. Only recently have a few researchers analyzed the same results using known biometrical models and suggested the mode of inheritance of some of the economic characters in *Hevea* (Simmonds, 1969; Gilbert et al., 1973; Nga and Subramaniam, 1974). Simmonds (1969) reported that the expected and the observed yields of the fifteen families produced in 1937 of the Phase II programme were highly correlated. He suggested that most of the differences between individual family yields could be accounted for by additive genetic variance. Nga and Subramaniam (1974) analyzed the same families using the North Carolina Modell II (Comstock and Robinson, 1952) and obtained high genetic variance for yield and girth. Gilbert et al. (1973), using the partial diallel design of Fyfe and Gilbert (1963), carried out an extensive analysis of the data of the Phase II and part of the Phase III breeding programmes. The authors concluded that:

(1) additive genetic variance accounted for most of the variations in yield and girth;
(2) inbreeding depression and unpredictable interaction occur when related parents are crossed;
(3) there is a high correlation between yield and girth;
(4) five years of yield recording is adequate for parental and family predictions.

Hence, high genetic variance would indicate that selection of progenies from specific crosses or open-pollinated polycrosses of unrelated parents with favourable characteristics should be effective in *Hevea* improvement.

The magnitude of genetic variance as expressed by heritability would vary according to the experimental population, mating systems and experimental design. In order to obtain a reliable estimate for genetic interpretation, it is essential to accumulate knowledge on this parameter (Dudley and Moll, 1969). This paper describes additional information on the heritability estimates of yield, girth, girth increment, virgin bark and renewed bark thickness using a different mating design. Meanwhile, attempts have also been made to study the corre-

lations between yield and other characters, the minimum yield measurements required to obtain a comparable heritability estimate and the feasibility of using correlated characters as selection criteria in order to obtain an indirect response in the most important character, yield.

Materials and Methods

Phase III breeding data involving a large number of progenies of diverse origin have been conveniently grouped into III A and B in this study. Separate analyses were carried out because two distinct tapping systems (Guest, 1940) were used to tap the trees of Phases III A and III B. In III A (1947-48) materials were tapped on half spiral on alternate daily system (S/2.d/2. 100%), while those in III B (1950-58) were tapped on half spiral third daily system (S/2.d/3.86%). It should be noted that data from the 1949 hand pollination programme were not included because the trees were not uniformly tapped by any particular tapping system.

Data from both phases were found to fit into the North Carolina Model I (N.C.M.1) of Comstock and Robinson (1952). Male parents were mated to several female parents with each female parent involved in one mating only, giving several progenies. The number of male parents, female parents and the progenies involved during the Phase III A were 4, 11 and 386, respectively. During Phase III B, records of 1,531 progenies from 11 male parents and 27 female parents were obtained (Appendix B).

Methods for pollination, germination of seeds, growth and planting of the progenies have been described before (Subramaniam et al., 1972). Briefly, hand pollination was made by emasculating the flowers and inserting the staminal column into female flower. To eliminate contamination by other pollens and prevent the staminal column falling out, the flowers were sealed with a plug of cotton wool smeared with a drop of latex. The seeds produced by hand pollination in Phase III were then germinated and planted in a nursery. After two years, the seedlings were topped and their stumps were transplanted to the field at the RRIM Experiment Station, Sungei Buloh. The progenies were planted in the form of a family block design, which is a modified randomised block design (Hutchinson and Panse, 1937). Each family was divided into equal portions and randomised in single tree plots within the replicated blocks. Seedlings of the 1956 and 1957 crosses, however, were directly planted into the field and cut back two years later, leaving the seedling stumps to grow in the field.

All the Phase III trees were tapped when about 70% of the trees (approximately six years old) reached a girth of 50.8 cm at a height of 55.9 cm from the ground. Only those trees with a girth of 50.8 cm or more were opened for tapping.

Yield (production of latex) was recorded fortnightly by coagulating the latex in a cup and drying and weighing the coagula. The average yield per tree per tapping for a year (g/tree/tapping) was obtained by dividing the total production of the coagula by the number of recordings for that particular year.

Girth of mature trees was measured at opening and, thereafter, annually. Virgin bark thickness was measured at opening by using a Carl Schlieper Gauge. Renewed bark thickness was obtained after four to five years of tapping.

Statistical Methods

Heritability Estimates from Hierarchal Matings

The model describing the sources of variation in the population was assumed to be:

$$Y_{ijk} = \mu + M_i + F_{ij} + e_{ijk}$$

where

Y_{ijk} the measurement of a character on the k^{th} progeny of the j^{th} female parent mated to the i^{th} male parent

Table 1. Analysis of variance for the computation of male parent, female parent and progeny variance components

Source of variation	d.f.	Expectation of mean squares
Between male parents (M)	S - 1	$\sigma_e^2 + k_2 \sigma_F^2 + k_3 \sigma_M^2$
Between female parents/male parents (F/M)	D - M	$\sigma_e^2 + k_1 \sigma_F^2$
Between progenies/female parents/ male parents (P/F/M)	n.. - F	σ_e^2

where

S number of male parents
D total number of female parents
n.. total number of progenies

$$k_1 = \frac{n.. - \frac{\sum_i \sum_j n_{ij}^2}{n_i}}{D - S}$$

$$k_2 = \frac{\frac{\sum_i \sum_j n_{ij}^2}{n_{i.}} - \frac{\sum_i \sum_j n_{ij}^2}{n..}}{S - 1}$$

$$k_3 = \frac{n.. - \frac{\sum_i n_{i.}^2}{n..}}{S - 1}$$

μ the overall mean of the population
M_i the effect of the i^{th} male parent ($i = 1, \ldots, m$)
F_{ij} the effect of the j^{th} female parent mated to the i^{th} male parent ($j = 1, \ldots\ldots, f_i$)
e_{ijk} the environmental plus genetic segregation effect on the k^{th} progeny of the j^{th} female parent mated on the i^{th} male parent ($k = 1, \ldots\ldots n_{ij}$)

The actual analysis of variance of such a model was carried out according to the form given in Table 1. Significant tests for the male parents (M) and the female parents within male parents (F/M) were made by comparing their corresponding mean squares with that of F/M and progeny/female/male (P/F/M), respectively.

The expected mean squares were equated to the corresponding mean squares to obtain the estimation of variance components. From the estimates of the male variance (σ^2_M), the female variance component (σ^2_F) and the environmental plus genetic segregation variance component (σ^2_e), heritabilities based on the male parents (h^2_M), the female parents (h^2_F) and the male plus female parents (h^2_{M+F}) were obtained as described by Cockerham (1963). The standard errors of the estimates of heritability were obtained according to the modified method of Dickerson (1963).

Estimates of Genetic, Environmental and Phenotypic Correlations

The covariance components for male parents ($_{pq}\sigma_M$), female parents ($_{pq}\sigma_F$) and errors ($_{pq}\sigma_e$), between characters p and q for all $p \neq q$ were estimated from covariance analysis similar in form to the variance analysis shown in Table 1.

The error variance σ^2_e contains one half of the genetic variance plus the environmental variance (σ^2_{en}). The value of σ^2_{en} was estimated by $\sigma^2_e - \sigma^2_M - \sigma^2_F$. The male and female components of variance (σ^2_M and σ^2_F) were each assumed to contain one-quarter of the genetic variance under the assumptions of no non-additive genetic variance. Similarly, estimates of environmental covariance ($_{pq}\sigma_{en}$) between pairs of characters were obtained from the following:

$$_{pq}\sigma_{en} = {}_{pq}\sigma_e - {}_{pq}\sigma_M - {}_{pq}\sigma_F \cdot$$

Estimates of correlations were then obtained from the corresponding covariance components and the variance components estimated earlier.

Estimates of Direct Response and Correlated Response

The direct response and correlated response in some of the characters were obtained using the relationships outlined by Falconer (1960). Estimates of heritability, additive genetic variance and genetic correlation used here were the pooled estimates from the male plus female components.

Results and Discussion

Analysis of Variance

Hierarchal analyses of variance for different characters under study have been presented in Table 2a, b. In both Phases III A and B significant differences for all the characters studied were generally not present among male parents. This could be due to the limited degrees of freedom for the appropriate error to test the differences between the male parents. In contrast, variation between female parents within male parents (F/M) was found to be significant for all the characters in both phases, except for girth increment in III A. Moreover, the relative magnitude of the variance for most characters between progenies (P/F/M) was generally much lower in III B compared with III A. The consistent significant differences among female parents within male parents in both the phases would indicate substantial genetic variability for all the characters investigated.

A few interesting features deserve mention here. The pronounced increase of detectable genetic variation in III B would indicate that tapping systems and agronomic practices could be important in reliable estimates of the genetic parameters. The similarity of variance ratios on renewed bark thickness in all three successive years in III B suggests that first year renewed bark thickness may serve as an adequate index of second and third year renewed bark thickness. The consistency of variance ratios on the average yield over the first three to five years also indicates that the average yield over the first three years offers similar information on the variation of the average yield over the first four and five years. The discrepancy of variance ratios for the average yield over the first one and two years compared with the first three to five years in both the phases, however, may be due to the incomplete expression of genotypes during the early years of tapping.

Heritability Estimates

Table 3 presents the heritability estimates for average yield per tree per tapping for the first one to five years. These estimates were obtained separately from male, female and male plus female variance components. In general, except for the first year yield, estimates obtained from female variance components were greater than the estimates from male variance components. Because of the difference in the estimates from male and female components, combined estimates from male plus female components were computed. The utility of the pooled estimates is reflected in the similarity of heritability estimates in both the III A and B and they are more realistic and closer to the comparable estimates based on the yield over all the five years. These estimates were lower than the estimates earlier presented by other researchers (Simmonds, 1969; Gilbert et al., 1973; Nga and Subramaniam, 1974). A similar situation was found for the pooled estimates of other characters also (Table 4).

Table 2a. Analyses of variance for average yields of the phase III A and B families

Source of variation	d.f.	Mean Squares Average yield over first One year	Two years	Three years	Four years	Five years
Phase III A						
Between male parents	3	4799.21*	1821.85^{NS}	1537.69^{NS}	1771.92^{NS}	1248.96^{NS}
Between female parents/male parents	7	1035.66***	1215.93**	1627.70***	1948.20***	1944.37**
Between progenies/female parents/ male parents	a	299.22 (337)	433.68 (349)	460.87 (354)	549.59 (354)	589.10 (357)
Phase III B						
Between male parents	10	1227.04^{NS}	1329.73^{NS}	838.70^{NS}	1233.85^{NS}	1583.08^{NS}
Between female parents/male parents	15	892.10***	1176.60***	1541.02***	1724.55***	2390.50***
Between progenies/female parents/ male parents	b	164.42 (1168)	251.23 (1284)	305.82 (1337)	378.15 (1348)	455.65 (136)

NS : Not significant at 0.05 level of probability
*, **, *** : Significant at 0.05, 0.01 and 0.001 levels of probabilities respectively. Figures in brackets represent d.f. (a or b) for the respective mean squares

Table 2b. Analyses of variance for certain secondary characters of the phase III A and B families

Source of variation	d.f.	Mean Squares GO	GC	GI	VB	RB 1	RB 2	RB 3
Phase III A								
Between male parents	3	325.08^{NS}	413.44^{NS}	43.18*	26.36^{NS}	20.83^{NS}	11.45^{NS}	27.60^{NS}
Between female parents/male parents	7	78.79**	124.66**	8.63^{NS}	7.18*	9.56***	7.92*	20.03***
Between progenies/female parents/ male parents	a	28.46 (357)	49.65 (356)	6.97 (352)	3.57 (339)	2.70 (329)	3.31 (334)	3.75 (325)
Phase III B								
Between male parents	10	117.61^{NS}	463.40^{NS}	337.34^{NS}	22.62^{NS}	15.06^{NS}	48.76^{NS}	72.42^{NS}
Between female parents/male parents	15	86.75***	287.73***	156.49***	31.02***	12.20***	35.19***	38.56***
Between progenies/female parents/ male parents	b	10.84 (1363)	38.50 (1241)	19.69 (1239)	5.53 (1187)	1.68 (1176)	3.88 (1152)	2.74 (1139)

NS : Not significant at 0.05 level of probability
*, **, *** : Significant at 0.05, 0.01 and 0.001 levels of probabilities respectively. Figures in brackets represent d.f. (a or b) for the respective mean squares
GO : Girth at opening
GC : Girth after five years of tapping
GI : Girth increment over five years
VB : Virgin bark thickness

RB 1, 2 and 3: 1st, 2nd and 3rd year renewed bark thickness respectively

The magnitude and precision of heritability estimates for average yield over the first three years are comparable with those of the average over the first five years. Therefore, the yield data for the first three years should be adequate for predicting the genetic variance of yield over five years in the population, instead of waiting for the testing period of five years suggested by Gilbert et al. (1973) and Nga and Subramaniam (1974). Whether a minimum of five years of observation would be required for effective selection to be carried out among the progenies needs to be examined (Ross and Brookson, 1966) but does not appear to be necessary from the present study.

The heritability estimates for girth at opening and after five years of tapping, girth increment over five years, virgin bark thickness and renewed bark thickness at first, second and third year are summarized in Table 4. The estimates were low to moderate, but sub-

Table 3. Heritability estimates and their standard errors for average yield over different years in phase III A and B families

Average yield over first		Heritabilities Phase IIIA	Phase IIIB
One year	h^2_M	0.40 ± 0.37	-0.10 ± 0.12
	h^2_F	0.27 ± 0.12	0.53 ± 0.11
	h^2_{M+F}	0.34 ± 0.18	0.21 ± 0.05
Two years	h^2_M	0.02 ± 0.13	-0.11 ± 0.08
	h^2_F	0.25 ± 0.12	0.43 ± 0.10
	h^2_{M+F}	0.13 ± 0.07	0.16 ± 0.04
Three years	h^2_M	-0.07 ± 0.12	-0.18 ± 0.06
	h^2_F	0.35 ± 0.15	0.44 ± 0.10
	h^2_{M+F}	0.14 ± 0.06	0.13 ± 0.03
Four years	h^2_M	-0.07 ± 0.11	-0.13 ± 0.06
	h^2_F	0.35 ± 0.15	0.39 ± 0.09
	h^2_{M+F}	0.14 ± 0.06	0.13 ± 0.03
Five years	h^2_M	-0.10 ± 0.09	-0.17 ± 0.07
	h^2_F	0.32 ± 0.14	0.46 ± 0.11
	h^2_{M+F}	0.11 ± 0.05	0.14 ± 0.03

stantially larger than those for yield. Some of these characters, such as girth at opening and virgin bark thickness, can help the early elimination of several poor genotypes before final yield assessment. It would be useful if a similar study could be made for the clonal and seedling families which have not yet been investigated.

Heritability estimates for all secondary characters based on female variance components were also found to be higher than the male variance components. This observation could have been due to the presence of maternal effect, a fraction of dominance variance, greater heterogeneity of the female parents and a difference in sample size. Another possibility for the above findings is that the sampling variance associated with heritability estimates was not optimal.

The occurrence of negative estimates, particularly h^2_M, in the present study is to be explained. Bogyo (1964) has advocated from theoretical studies that a large number of total observations in an experiment are necessary to obtain precise heritability estimates. Gill and Jensen (1968), in the light of Bogyo's (1964) paper, reported that if true heritability was low, at least 800 observations and five female parents within each male parent were required for a 0.95 chance of obtaining a non-negative estimate from male components of variance. Although in the present analysis there was a greater number of progenies for III B, the number of female parents per male parent averaged three in both the III A and B groups. However, the large number of degrees of freedom for progenies (P/F/M) available in III B and the consistency of the pooled estimates h^2_{M+F} have shown that precision can be maintained by a wide choice of female parents and larger number of progenies sampled, as in this study.

Of the characters studied, only yield and girth have previously been estimated for heritability. Nga and Sub-

Table 4. Heritability estimates and their standard errors for certain secondary characters in phase III A and B families

Characters		Heritabilities Phase IIIA	Phase IIIB
Girth at opening	h^2_M	0.31 ± 0.29	-0.08 ± 0.13
	h^2_F	0.22 ± 0.11	0.62 ± 0.13
	h^2_{M+F}	0.27 ± 0.15	0.27 ± 0.06
Girth after five years of tapping	h^2_M	0.21 ± 0.22	-0.01 ± 0.15
	h^2_F	0.20 ± 0.10	0.61 ± 0.14
	h^2_{M+F}	0.20 ± 0.24	0.30 ± 0.07
Girth increment over five years	h^2_M	0.21 ± 0.17	0.10 ± 0.19
	h^2_F	0.03 ± 0.05	0.63 ± 0.14
	h^2_{M+F}	0.12 ± 0.09	0.36 ± 0.10
Virgin bark thickness	h^2_M	0.21 ± 0.21	-0.15 ± 0.08
	h^2_F	0.14 ± 0.09	0.49 ± 0.11
	h^2_{M+F}	0.18 ± 0.11	0.17 ± 0.04
1st year renewed bark thickness	h^2_M	0.12 ± 0.23	-0.10 ± 0.13
	h^2_F	0.36 ± 0.15	0.64 ± 0.14
	h^2_{M+F}	0.24 ± 0.11	0.27 ± 0.06
2nd year renewed bark thickness	h^2_M	0.01 ± 0.11	-0.09 ± 0.16
	h^2_F	0.21 ± 0.11	0.80 ± 0.17
	h^2_{M+F}	0.11 ± 0.06	0.36 ± 0.08
3rd year renewed bark thickness	h^2_M	-0.03 ± 0.23	0.04 ± 0.28
	h^2_F	0.61 ± 0.22	1.13 ± 0.23
	h^2_{M+F}	0.29 ± 0.12	0.58 ± 0.14

ramaniam (1974) reported the heritability estimates for yield, girth at opening and after five years of tapping to be around 0.50. These values are obviously higher than the present estimates of h^2_{M+F} but they do not differ much from h^2_F for most characters in the present analysis. The lower values of h^2_M have reduced the estimates for h^2_{M+F}. This could probably be overcome by introducing male parents of more diverse origin into the breeding programme. The high heritability estimates for various characters on using female variance components suggest that higher selection pressure could be applied in a large seedling population to obtain greater selection response. Thus, considerable genetic progress could be achieved by selecting suitable parents for breeding purposes.

It is noteworthy that the estimates from III B in the present study are slightly higher than the estimates from III A. The range of total number of progenies used in III A and B was from 355 to 367 and 1139 to 1389 respectively. In view of the larger sample size in III B, the estimates obtained from this study are perhaps more reliable than the estimates from III A.

Table 5. Genetic (r_G), environmental (r_E) and phenotypic (r_{Ph}) correlation coefficients of yield and certain secondary characters in phase III A and B families

Characters	Correlation	Average yield over first five years	
		Phase IIIA	Phase IIIB
Girth at opening	r_G	0.38	0.33
	r_E	0.65	0.46
	r_{Ph}	0.65	0.46
Girth after five years of tapping	r_G	0.62	0.41
	r_E	0.57	0.43
	r_{Ph}	0.55	0.43
Girth increment over five years	r_G	1.00	0.26
	r_E	0.25	0.24
	r_{Ph}	0.22	0.23
Virgin bark thickness	r_G	0.29	0.60
	r_E	0.20	0.60
	r_{Ph}	0.55	0.38

Genetic, Environmental and Phenotypic Correlations

Estimates of genetic, environmental and phenotypic correlations of average yield over five years with certain secondary characters in III A and B families are presented in Table 5. The data indicate a considerable influence of environment, with genetic correlations accounting for only about 0.07 to 0.36 of the variation in the characters studied.

Yield and girths (at opening and after five years of tapping) are highly subjected to similar environmental influence (r_E = 0.41 - 0.65). Seedling families should therefore be raised under favourable conditions for the maximum expression of their potential yield and girths. Under such conditions the yield and growth (i.e. girths) performance of seedlings would tend to be better, thus giving a more effective assessment of individual seedlings or seedling families.

The magnitude of genetic, environmental and phenotypic correlations between yield and girth increment over five years was lower than for similar estimates between other pairs of variables. However, there was high genetic correlation (r_G = 1) between yield and girth increment over five years in III A families. This may be a spurious correlation arising out of the estimation procedure with large environmental variances and inadequate sample size. Yield and virgin bark thickness had a moderately high genetic correlation in both the phases.

Direct and Correlated Response to Selection in Yield

The genetic correlation estimates of certain secondary characters with yield as found in this study suggest that simple measurements, such as girth at opening and virgin bark thickness, can be important in predicting the average yield of five years' tapping. To test this, the expected direct response of average yield over the first five years to selection for yield itself, and the expected correlated response in five years' average yield to selection for girth at opening and virgin bark thickness, were estimated using different arbitrary selection intensities of 1.40, 0.97 and 0.64 (Table 6), corresponding to the proportions of 20%, 40% and 60% respectively selected from the population.

The response to direct selection for yield based on 20%, 40% and 60% plants selected are expected to have

Table 6. Direct response and correlated response in yield to selection of certain secondary characters in phase III A and B families

Characters	Proportion Selected		Response Phase IIIA	Response Phase IIIB	CR_{MY}/R_{MY} Phase IIIA	CR_{MY}/R_{MY} Phase IIIB
Average yield over first five years	0.20	R_{MY}	2.41	2.86	-	-
	0.40		1.67	1.98	-	-
	0.60		1.10	1.31	-	-
Girth at opening	0.20	$CR_{MY.GO}$	1.47	1.46	0.61	0.51
	0.40		1.02	1.01	0.61	0.51
	0.60		0.67	0.67	0.61	0.51
Virgin bark thickness	0.20	$CR_{MY.VB}$	0.90	1.96	0.37	0.69
	0.40		0.63	1.36	0.37	0.69
	0.60		0.41	0.90	0.37	0.69

R_{MY} : Direct response in yield to selection
$CR_{MY.GO}$: Correlated response in yield to selection of girth at opening
$CR_{MY.VB}$: Correlated response in yield to selection of virgin bark thickness

maximum genetic advances over the parental population by approximately 2.9, 2.0 and 1.3 times, respectively, in one generation (Table 6). On the other hand, the correlated response to selection for girth at opening and virgin bark thickness will show maximum genetic advances ranging from 0.7 to 1.5, and from 0.4 to 2.0 times, respectively, in one generation. The correlated response in yield is approximately half that for direct response. These values do not normally encourage selection based on correlated characters. However, considering that it is much cheaper to obtain measurements of correlated characters than the five years' tapping record, and allowing for the amount of time saved for selection, indirect selection for yield would seem worthwhile.

Simple correlation estimates of yield with some secondary characters such as girth at opening and bark thickness have been reported by various workers (Whitby, 1919; Heusser, 1921; La Rue, 1921; Bryce and Gadd, 1922; Belgrave, 1925; Sanderson and Sutcliffe, 1929a and b; Narayanan and Ho, 1970; Gilbert et al., 1973). In general, the correlation estimates of yield and girth at opening range from 0.26 to 0.60, while those of yield and bark thickness range from 0.12 to 0.82. Because of the low repeatability of these estimates, which do not take genetic correlation into account, no recommendation for using girth at opening or bark thickness as sole selection criterion has been made. However, these correlation estimates are the same as phenotypic correlations, which in certain cases differ widely from the genetic correlations between two characters. Based on the data from III B, one could conclude that virgin bark thickness is probably better than girth at opening as a correlated character for yield. Greater emphasis, therefore, may be laid on this character in future experiments on selection.

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Literature

Belgrave, W.N.C.: Some observations on tapping of *Hevea*. Malay. Agric. J. 13 (8), 257-270 (1925)

Bogyo, T.P.: Coefficients of variation of heritability estimates obtained from variance analysis. Biometrics 20, 122-129 (1964)

Bryce, G.; Gadd, C.H.: Improvement in *Hevea* by the selection of seed bearers. Dep. Agric. Ceylon, Bull. 55, 1-42 (1922)

Cockerham, C.C.: Estimation of genetic variances. Statistical Genetics and Plant Breeding, pp. 53-94. In: NAS-NRC Publication 982 (1963)

Comstock, F.E.; Robinson, H.F.: Estimation of average dominance of genes. In: Heterosis (ed. Gowen, J.W.), pp. 494-516. Ames.: Iowa State College Press 1952

Appendix A. Relationships of parental clones used in the RRIM breeding programme

Phase	Years	Clones used as parents	Designation of clones selected and tested on large scale clone trials
I	1928-1931	18 Primary Malayan clones	RRIM 500 series (30)[b]
II	1937-1941	9 Primary Malayan clones (5)[a] 17 RRIM 500 series 6 Foreign clones	RRIM 600 series (39)
III	1947-1958	6 Primary Malayan clones (4) 7 RRIM 500 series (6) 18 RRIM 600 series 6 Clones of other selection 9 Foreign clones (2) 3 Dothidella resistant clones	RRIM 700 series (35)
IV	1959-1965	2 Primary Malayan clones (2) 4 RRIM 500 series (4) 8 RRIM 600 series (5) 1 RRIM 700 series 7 Clones of other selection (2) 9 Foreign clones (3) 4 Clones from Peruvian *H.brasiliensis*	RRIM 800 series
V	1966-1973	2 Primary Malayan clones (2) 3 RRIM 500 series (3) 5 RRIM 600 series (5) 5 RRIM 700 series (4) 10 Clones of other selection (3) 19 Foreign clones (4) 2 Clones from *H.pauciflora* and *H.Spruceana* 1 Clone from Peruvian hybrid	RRIM 900 series

Clones of other selection are secondary or tertiary clones selected in Malaya
Figures in ( )[a] denote number of clones used in previous phases
Figures in ( )[b] denote the number of clones in the RRIM series

Dickerson, G.E.: Biological interpretation of the genetic parameters of populations. In: Statistical Genetics and Plant Breeding, pp. 95-107. NAS-NRC Publication 982 (1963)

Dudley, J.W.; Moll, R.H.: Interpretation and use of estimates of heritability and genetic variances in plant breeding. Crop Science 9, 257-261 (1969)

Falconer, D.S.: Introduction to Quantitative Genetics. Edinburgh: Oliver and Boyd 1960

Fyfe, J.L.; Gilbert, N.: Partial diallel crosses. Biometrics 19, 278-286 (1963)

Gilbert, N.E.; Dodds, K.S.; Subramaniam, S.: Progress of breeding investigations with *Hevea brasiliensis*. V. Analysis of data from earlier crosses. J. Rubb. Res. Inst. Malaya 23 (5) 365-380 (1973)

Gill, J.L.; Jensen, E.L.: Probability of obtaining negative estimates of heritability. Biometrics 24, 517-526 (1968)

Guest, E.: Amendments and addition to the international tapping notation. J. Rubb. Res. Inst. Malaya 10, 16-25 (1940)

Heusser, C.: Tapping test and bast examination of *Hevea* plants from selected seed. Arch. Rubbercult 5, 303-333 (1921)

Hutchinson, J.B.; Panse, V.G.: Studies in plant breeding technique II. The design of field tests of plant breeding material. Indian J. Agric. Science 7, 531-564 (1937)

La Rue, C.D.: Structure and yield in *Hevea brasiliensis*. Arch. Rubbercult. 5, 574-588 (1921)

Narayanan, R.; Ho, C.Y.: Yield-Girth relationship studies on *Hevea*. J. Rubb. Res. Inst. Malaya 23 (1), 23-31 (1970)

Nga, B.H.; Subramaniam, S.: Variation in *Hevea brasiliensis*. I. Yield and girth data of the 1937 hand pollinated seedlings. J. Rubb. Res. Inst. Malaysia 24 (2), 69-74 (1974)

Ross, J.M.: Progress of breeding investigations with *Hevea brasiliensis*. IV. The crosses made in the years 1947-1958. Rubb. Res. Inst. Malaya, Res. Archs. Docum., No. 28 (1965)

Ross, J.M.; Brookson, G.W.: Progress of breeding investigations with *Hevea brasiliensis*. III. Further data on the crosses made in the years 1937-1941. J. Rubb. Res. Inst. Malaya 9 (3), 158-172 (1966)

Sanderson, A.R.; Sutcliffe, H.: Vegetative characters and yield of *Hevea*. Q.J. Rubb. Res. Inst. Malaya 1, 75-90 (1929a)

Sanderson, A.R.; Sutcliffe, H.: Vegetative characters and yield of *Hevea*. Q.J. Rubb. Res. Inst. Malaya 1, 151-200 (1929b)

Sharp, C.C.T.: Progress of breeding investigations with *Hevea brasiliensis*. The Pilmoor crosses 1928-1931 series. J. Rubb. Res. Inst. Malaya 10, 34-66 (1940)

Sharp, C.C.T.: Progress of breeding investigations with *Hevea brasiliensis*. II. The crosses made in the years 1937-1941. J. Rubb. Res. Inst. Malaya 13, 73-99 (1951)

Simmonds, N.W.: Genetical bases of plant breeding. J. Rubb. Res. Inst. Malaya 21 (1), 1-10 (1969)

Subramaniam, S.; Ong, S.H.; Sultan, M.O.: *Hevea* breeding and selection in the Rubber Research Institute of Malaya. I. An outline of the methods. Sabrao Newsletter 4, 59-65 (1972)

Whitby, S.: Variation in *Hevea brasiliensis*. Ann. Botany 33, 313-321 (1919)

Appendix B. Crosses and progenies involved in the N.C.M.I. families of phase III A and III B

Male Parents	Crosses ×	Female Parents	No. of Progenies
Phase III A			
RRIM 500 (Pi1 B84 × Pi1 A44)+		33/520 (Tjir 1 × PB 24)	25
		34/373 (RRIM 504 × RRIM 509)	14
RRIM 501 (Pi1 A44 × Lun B)		RRIM 623 (PB 49 × Pi1 B84)	25
		RRIM 632 (Tjir 1 × PB 49)	20
		33/129 (PB 49 × Pi1 B84)	24
		44/550 (Tjir 1 × RRIM 507)	17
		44/553 (Tjir 1 × Pil B84)	32
Pi1 B84 (Primary Clone)		RRIM 501 (Pi1 A44 × Lun B)	71
		RRIM 600 (Tjir 1 × PB 86)	17
Tjir 1 (Primary Clone)		RRIM 500 (Pi1 B84 × Pi1 A44)	53
		RRIM 507 (Pi1 B84 × Pi1 A44)	88
Phase III B			
RRIM 501 (Pi1 A44 × Lun N)+		RRIM 618 (Lun N × RRIM 501)	35
		PB 5/60 (PB 56 × PB 24)	156
RRIM 504 (Pi1 A44 × Lun N)		RRIM 610 (RRIM 504 × Tjir 1)	17
		RRIM 611 (RRIM 504 × Tjir 1)	32
RRIM 527 (Pi1 B50 × Pil B84)		AVROS 157 (Primary Clone)	35
RRIM 612 (AVROS 157 × PB 49)		GT 1 (Primary Clone)	167
		PR 107 (Primary Clone)	100
RRIM 623 (PB 49 × Pi1 B84)		LCB 1320 (Primary Clone)	31
		PB 86 (Primary Clone)	113
AVROS 157 (Primary Clone)		RRIM 513 (Pi1 B16 × Pil A44)	32
		War 4 (Primary Clone)	21
FX 25 (Primary Clone)		RRIM 600 (Tjir 1 × PB 86)	41
		RRIM 623 (PB 49 × Pil B84)	38
LCB 1320 (Primary Clone)		RRIM 501 (Pi1 A44 × Lun N)	57
		Tjir 1 (Primary Clone)	159
PB 49 (Primary Clone)		RRIM 605 (Tjir 1 × PB 49)	19
		RRIM 612 (AVROS 157 × PB 49)	15
		War 1 (Primary Clone)	13
PR 107 (Primary Clone)		PB 49 (Primary Clone)	152
Tjir 1 (Primary Clone)		RRIM 527 (Pi1 B50 × Pi1 B84)	53
		RRIM 606 (Tjir 1 × PB 49)	39
		RRIM 608 (Pi1 B50 × Pi1 B84)	40
		RRIM 616 (Tjir 1 × PRIM 507)	78
		34/373 (RRIM 504 × RRIM 509)	18
		Djas 1 (Primary Clone)	

+ Parentage or origin of parents involved in the crosses

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