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Estimates of General Combining Ability in *Hevea* Breeding at the Rubber Research Institute of Malaysia

I. Phases II and III A

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Summary. Estimates of general combining ability of parents for yield and girth obtained separately from seedlings and their corresponding clonal families in Phases II and IIIA of the RRIM breeding programme are compared. A highly significant positive correlation (r = 0.71***) is found between GCA estimates from seedling and clonal families for yield in Phase IIIA, but not in Phase II ($r = -0.03^{NS}$) nor for girth ($r = -0.27^{NS}$) in Phase IIIA. The correlations for Phase II yield and Phase IIIA girth, however, improve when the GCA estimates based on small sample size or reversed rankings are excluded.

When the best selections (based on present clonal and seedling information) are compared, all five of the parents top-ranking for yield are common in Phase IIIA but only two parents are common for yield and girth in Phases II and IIIA respectively. However, only one parent for yield in Phase II and two parents for girth in Phase IIIA would, if selected on clonal performance, have been omitted from the top ranking selections made by previous workers using seedling information.

These findings, therefore, justify the choice of parents based on GCA estimates for yield obtained from seedling performance. Similar justification cannot be offered for girth, for which analysis is confounded by uninterpretable site and seasonal effects.

Key words: *Hevea* - Rubber - Yield - Selection - Performance - Seasonal Effects

Introduction

In recent years considerable attention has been given to assessing general combining abilities (GCA) of parents to guide the breeding programme of *Hevea brasiliensis* at the Rubber Research Institute of Malaysia (RRIM). This approach is based on the findings of high GCA effects on yield and girth of seedling families (Simmonds 1969; Gilbert et al. 1973; Nga and Subramaniam 1974; Tan and Subramaniam 1975). Of the several investigations on the breeding potential of parental clones (Sharp 1951; Ross and Brookson 1966; Gilbert et al. 1973) the last is the most complete. These workers (Gilbert et al. 1973) successfully fitted the values of GCA for parents involved in an irregular series of earlier crosses (incomplete diallel) by the method of least squares (Gilbert 1967). They suggested that inbreeding depression exists. Consequently, specific crosses or polycrosses between unrelated high-GCA parents were proposed.

So far, seedling data have been used for combining ability studies, but commercial rubber is grown in clonal stands. So, to test the validity of this approach, comparative studies of GCA estimates obtained from seedling and clonal progeny were carried out in this investigation.

Materials and Methods

Seedlings (seedling progeny) and clones derived from them (clonal progeny) were obtained from specific crosses made from 1937 to 1941 (Phase II) and 1947 to 1949 (Phase IIIA) of the RRIM breeding programme. The trial procedure in these phases has been described earlier (Sharp 1951; Ross 1965a, b; Gilbert et al. 1973; Tan et al. 1975).

The seedlings were planted as two-year-old stumps in the field of the RRIM Experiment Station, Sungei Buloh, using a modified randomised block design (Hutchinson and Panse 1937) with replications, except for 1940 and 1941, of hand pollinated materials. Clones were established using budwood from these seedlings on available seedling stocks in adjacent fields. Each clone was represented by 9-11 trees for Phase II and 12 trees for Phase IIIA in a single plot.

The average yield over the first five years of tapping and the girth at opening of the seedlings and clones were studied. Both seedlings and clones were tapped on alternate days on a half-spiral cut (S/2.d/2) when they reached tappable size after about six years from planting. The seedlings from the 1949 crosses, however, were tapped every third day on the half spiral system (S/2.d/3) after two-and-a-half years of tapping on S/2.d/2 (Guest 1940). Yield recording was carried out twice a month by acid-coagulating the latex in the cups, followed by drying and weighing the

Table 1. Analyses of variance for yield and girth of parents in Phases II and IIIA

Source of variation	Degrees of freedom	Mean squares			
		Yield		Girth	
		Seedlings	Clones	Seedlings	Clones
Phase II					
Main parents GCA adjusted for subsidiary parents	8	439.486***	963.590***	-	-
Subsidiary parents GCA adjusted for main parents	17	411.105***	359.282***	-	-
Error	1440	48.467	92.042	-	-
Phase IIIA					
Female parents GCA adjusted for males	12	1814.633***	1290.708***	328.498***	344.639***
Male parents GCA adjusted for females	8	1350.670***	105.268[NS]	39.324[NS]	67.612***
Error	a	500.090 (940)[a]	108.552 (967)	29.052 (951)	10.266 (1012)

Yield data for seedlings in Phase II are in lb/tree/year while others in g/tree/tapping
Girth data are in inches
a : Bracketed figures denote degrees of freedom
NS : Not significant at $P < 0.05$
***: $P < 0.001$

coagula. Girth (circumference) of trees was measured at heights of 127 cm for seedlings and 152 cm for clones before the trees were first tapped. These data are available only for Phase IIIA materials.

The analyses of the above families are based on an unbalanced two-way classification model in which the main parents are columns and subsidiary parents are rows. These represent the female and male parents in Phase IIIA respectively. In Phase II, however, reciprocal crosses have been bulked so that female and male parents are not distinguishable. The analyses of variance and GCA estimates of individual parents for the characters studied are obtained by the method basically similar to that of Gilbert (1967), as outlined by Milliken et al. (1970). In the present model interactions are not assumed and GCA estimates are expressed as deviations from the general mean. To conform with an earlier presentation (Gilbert et al. 1973) the GCA estimates have been regarded as deviations plus half of the general mean. The average GCA values of common parents for main and subsidiary groups were calculated and used for subsequent analyses.

In view of the nature of the data, the results should be interpreted with caution. Sharp (1951) reported that the recording, experimental set-up and trial conditions of the Phase II materials were extremely poor because of neglect arising from Japanese occupation (1941-1945) and the Emergency Period (1948-60) in Malaysia. Although, in comparison with Phase II, the general condition of Phase IIIA improved, the clone trials were neither replicated nor completely randomized. The parents used for crosses were sometimes confined to one particular year, resulting in possible confounding effects through site differences, recording periods, and to a lesser extent, tapping system (Gilbert et al. 1973). Since adjustment was impossible, the study could only be made with these limitations.

Results and Discussion

Analysis of variance

Mean squares of yield and girth are presented in Table 1. In seedlings, the GCA for yield of the female and male parents in Phase IIIA (as well as main and subsidiary parents in Phase II) was highly significant, but the GCA for girth was highly significant only for female parents. In clonses, on the other hand, the GCA for yield was highly significant in both the main and subsidiary parents in Phase II but only in female parents in Phase IIIA. The GCA for girth was also highly significant in both male and female parents.

In general, mean squares for the GCA of female parents were greater than those of the males in Phase IIIA, confirming a different analysis carried out on

Table 2. GCA estimates of parents for yield in Phase II

Parents	Parentage	Seedlings	Clones	No. of families
PB 49	Primary clone	29.3(128)[a]	14.8(172)[a]	3
RRIM 514	Pil A 44 × Pil B 58	26.8(160)	10.1(100)	5
AVROS 157	Primary clone	26.6(197)	9.4(262)	8
Tjir 1	Primary clone	26.4(569)	14.7(520)	15
RRIM 509	Pil A 44 × Lun N	26.1(83)	12.5(76)	3
PB 24	Primary clone	20.1(69)	15.0(78)	3
AVROS 33	Primary clone	18.3(38)	10.3(19)	3
Lun N	Primary clone	17.2(132)	11.0(115)	6
RRIM 501	Pil A 44 × Lun N	16.7(161)	17.4(166)	7
PB 186	Primary clone	16.4(38)	18.0(22)	2
RRIM 500	Pil B 84 × Pil A 44	14.9(156)	14.3(150)	7
BD 5	Primary clone	14.6(57)	12.4(64)	3
RRIM 511	Pil A 44 × Pil B 16	14.5(123)	12.1(131)	5
BR 2	Primary clone	14.4(2)	17.0(2)	1
RRIM 506	Pil B 84 × Pil A 44	14.1(86)	9.7(74)	4
Pil B 84	Primary clone	13.0(355)	10.7(378)	14
RRIM 504	Pil A 44 × Lun N	12.2(291)	13.2(276)	6
RRIM 505	Pil A 44 × Lun N	11.7(82)	7.2(63)	3
PB 86	Primary clone	10.8(153)	12.3(192)	3
Gl 1	Primary clone	7.7(52)	15.6(72)	3

Original estimates for seedlings are derived from data in lb/tree/year; but are converted to g/tree/tapping comparable with clonal estimates
a : Bracketed figures refer to numbers of progeny involved in estimation

a larger sample of Phase III seedling families (Tan et al. 1975). Since reciprocal (maternal or paternal) effects were not detected for yield and girth in an earlier study (Tan and Subramaniam 1975), this result may suggest a greater heterogeneity of the females used. It should be pointed out further that the males and females are somewhat arbitrary experimental choices depending on convenience for hand pollination. Highly significant effects of any parental groups should therefore reflect considerable variability for effective selections of potential parents to be used in subsequent breeding.

GCA estimates and their correlations

The GCA estimates of the parental clones for yield and girth are summarised in Tables 2 and 3. These GCA values may have varying degrees of reliability because of differing sample size and the limitations of the data. However, the above estimates should still be useful for practical purposes as meaningful results were obtained for *Hevea* breeding by Gilbert et al. (1973) using similar seedling materials and technique of analysis (Gilbert 1967).

To compare the above GCA estimates for yield and girth between seedlings and clones, correlation studies were carried out. The parental GCAs for yield are positively correlated (r = 0.71***, 16 d.f.) in Phase IIIA but not ($r = -0.03^{NS}$, 18 d.f.) in Phase II. No correlations between parental GCAs were found for girth (-0.27^{NS}, 16 d.f.) in Phase IIIA.

The above findings prompted a more critical appraisal of the original data, experimental procedures used and the manner in which the data were recorded. In Phase II, parents suspected of upsetting the expected positive association were excluded from analysis. These parents include AVROS 33, PB 186 and BR 2, which contributed fewer than 30 progeny or were involved in one cross only; they also include another group (RRIM 514, AVROS 157 and Gl 1) which gave reversed GCA rankings on seedlings and clones. The exclusion of the first group is reasonable because of the small sample size, while the omission of the second group is discussed below. When this is done, a significant positive correlation (r = 0.47*, 12 d.f. in one-tailed test) is obtained.

This result suggests a general correspondence between the GCA estimates except for a few parents. RRIM 514 and AVROS 157 have very high GCAs in

Table 3. GCA estimates of parents for yield and girth in Phase IIIA

Parents	Parentage	Seedlings		Clones		No. of families
		Yield	Girth	Yield	Girth	
33/520	Tjir 1×PB 24	29.7(38)[a]	30.4(38)	17.7(55)	20.4(55)	2
RRIM 600	Tjir 1×PB 86	26.7(111)	33.4(115)	14.8(160)	30.5(160)	6
RRIM 509	Pil A 44×Lun N	26.5(28)	30.6(28)	12.7(23)	27.2(23)	1
44/553	Tjir 1×Pil B 84	24.2(39)	32.9(38)	21.4(44)	22.6(45)	2
RRIM 623	PB 49×Pil B 84	24.1(42)	36.5(39)	15.0(53)	25.4(53)	3
RRIM 632	Tjir 1×Pb 49	21.5(52)	40.8(51)	16.1(62)	23.2(64)	2
RRIM 501	Pil A 44×Lun N	21.5(488)	33.4(491)	12.9(538)	26.2(540)	11
RRIM 610	RRIM 504×Tjir 1	18.7(29)	20.2(30)	8.2(25)	33.6(25)	1
RRIM 507	Pil B 84×Pil A 44	18.4(170)	33.7(172)	9.2(129)	25.7(168)	3
Tjir 1	Primary clone	17.2(284)	31.9(283)	10.2(254)	25.4(256)	6
RRIM 83	Primary clone	14.3(236)	23.8(242)	5.8(166)	36.4(205)	6
RRIM 500	Pil B 84×Pil A 44	14.2(200)	34.9(204)	10.5(229)	25.2(230)	7
Lun N	Primary clone	14.1(48)	28.3(49)	10.0(47)	24.9(48)	6
Pil B 84	Primary clone	13.0(85)	29.3(88)	9.8(86)	21.9(88)	2
34/373	RRIM 504×RRIM 509	11.7(12)	18.7(13)	13.1(16)	20.1(16)	1
BR 2	Primary clone	9.7(4)	34.2(4)	11.0(8)	16.0(8)	1
33/129	PB 49×Pil B 84	8.7(35)	32.1(36)	10.2(55)	18.6(56)	4
44/550	Tjir 1×RRIM 507	3.5(21)	26.8(23)	5.3(26)	20.9(26)	2

Original yield data are in g/tree/tapping
Girth data have been converted from inches to centimetres
a : Bracketed figures refer to numbers of progeny involved in estimation

seedlings but low values in clones, while the reverse is observed in Gl 1. Marked stock-scion interaction, if present, could cause such reversals. Moreover, clone Gl 1 is highly variable in yield performance in different environments (Burkill 1958). If the plastic response trait in this and possibly other parents is heritable, then the observed anomalies could result. Closer examination, however, suggests that the experimental layout of clonal families and site differences are probably responsible for this apparent contradiction. AVROS 157 and Gl 1 were used as parents only in 1937 and RRIM 514 only in 1941. The clones from each family were established as a group in adjacent plots so that families were non-randomly distributed. As a consequence, the observed differences could have resulted from variable soils (Sharp 1951).

In Phase IIIA, the girth data have also been re-examined in the same manner. RRIM 83, which was used as a parent only in 1949, disturbs the correlation considerably because of reversed rankings in its seedling and clonal GCA estimates. When it is removed, along with parents (RRIM 509, 610; 34/373 and 33/129) that had few progeny, the correlation coefficient changes from -0.27^{NS} (16 d.f.) to 0.30^{NS} (11 d.f.) suggesting the presence of confounding influences.

A possible explanation for the closer correspondence between seedlings and clones for yield than for girth is the nature of the measurements. Girth was taken at a particular time, in contrast to yield which was sampled over five years. The varying periods taken to open the trials for tapping would have also increased the variability in the girth records. This may have resulted in more pronounced confounding effects for girth than for yield.

Ranking of parents

The ultimate objective in the estimation of GCA values of parental clones is to select the top ranking parents for future breeding. The five best parents assessed from seedling and clonal data in the present study are compared in Table 4. Based on yield, the best five parents are identical in Phase IIIA. Only two out of the five parents, however, are common to Phase II. The latter proportion is also obtained for the ranking on girth in Phase IIIA. These results can be expected from the foregoing correlation study and the probable confounding factors detailed above.

These results are compared with those reported by earlier workers in Table 4. In Phase II, the top ranking parents for yield correspond closely with

Table 4. Top ranking parents for Phases II and IIIA

	Seedlings				Clones
	Sharp (1951)	Ross and Brookson (1966)	Gilbert et al. (1973)	Present[+] study	Present[+] study
Phase II					
Yield	Tjir 1 AVROS 157 PB 49 RRIM 501 RRIM 509	AVROS 157 Tjir 1 PB 49 RRIM 501 RRIM 509	PB 49 RRIM 514 PB 24 AVROS 157 RRIM 509	PB 49 RRIM 514 AVROS 157 Tjir 1 RRIM 509	RRIM 501 Gl 1 Tjir 1 PB 24 PB 49
Phase IIIA					
Yield			33/520 44/553 RRIM 623 RRIM 632 RRIM 600	33/520 RRIM 600 44/553 RRIM 623 RRIM 632	44/553 33/520 RRIM 632 RRIM 623 RRIM 600
Girth			RRIM 632 33/129 Tjir 1 RRIM 623 Pil B 84	RRIM 632 RRIM 623 RRIM 500 RRIM 507 RRIM 501	RRIM 83 RRIM 600 RRIM 501 RRIM 507 Tjir 1

+: Parents with fewer than 30 progeny and those involved in one cross only were excluded

Table 5. Ranking of parents common to both Phases II and IIIA for yield

Phase II				Phase IIIA			
Seedlings		Clones		Seedlings		Clones	
Tjir 1	(26.4)	RRIM 501	(17.4)	RRIM 501	(21.5)	RRIM 501	(12.9)
RRIM 501	(16.7)	Tjir 1	(14.7)	Tjir 1	(17.2)	RRIM 500	(10.5)
RRIM 500	(14.9)	RRIM 500	(14.3)	RRIM 500	(14.2)	Tjir 1	(10.2)
Pil B 84	(13.0)	Pil B 84	(10.7)	Pil B 84	(13.0)	Pil B 84	(9.8)

Bracketed figures denote GCA estimates
Parents with fewer than 30 progenies and those involved in one cross only were excluded

those reported by Gilbert et al. (1973) and to a lesser extent with those given by Sharp (1951) and Ross and Brookson (1966) when seedling data are used. The correspondence is poorer when information from clonal families are used instead. Even so, only one of the five best parents from the clonal families was not selected when the top ranking parents, based on seedling families in the present and earlier studies, are considered as a group. In Phase IIIA the five best parents for yield are identical to those of Gilbert et al. (1973) for both clonal and seedling data. For the ranking of parents on girth in Phase IIIA, the correspondence between the present study and that of Gilbert et al. (1973) is poor, more so when clonal data are used.

Ranking of parents common to Phases II and IIIA based on their GCA estimates for yield are compared in Table 5. Good correspondence is seen in relative rankings in the two phases. RRIM 501 and Tjir 1 generally rank higher as parents than RRIM 500 and Pil B 84. This agrees with the findings of Gilbert et al. (1973).

Conclusion

The close association observed between GCA estimates for yield in Phase IIIA using clonal and seedling data justifies the use of seedling information for the choice of parents in the breeding programmes. Anomalies in Phase II arise probably because of limitations in the data used.

For girth performance, parallel information is not provided by the clonal and seedling data. Adjustments to the data using a common control may reduce confounding site and seasonal effects and thereby improve the association between the clonal and seedling GCA estimates. However, since clones are preferred for commercial planting, greater reliance should perhaps be placed on clonal than on seedling information.

Among the two characters studied, yield is the main objective in *Hevea* improvement. Choice of parents should therefore be based primarily on yield information. However, girth, bark thickness and renewal, latex vessel number, plugging index and resistance to diseases, wind damage and dryness are important in determining yield of a clone (Ho 1975; Rubber Research Institute of Malaysia 1975). *Hevea* breeders perhaps need to incorporate these accessory variates, after yield has been considered, in making breeding decisions.

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