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Low Fruit-set from *Hevea* Hand-pollination: Fruit Load and Propensity of Floral Shoots to Fruit-bearing

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Abstract

Low fruit-set in *Hevea* arose primarily from the failure of entire floral shoots to bear fruits. In hand-pollination carried out in the main flowering season, a mean of 83.7% of the floral shoots were barren despite the fact that seven to 9 hand-pollinations were normally carried out on each shoot. Competition between developing fruits on the same floral shoot was not a major cause of low fruit-set. The distribution of fruits among hand-pollinated floral shoots conformed to a negative binomial distribution, indicating that fruit-set was not random but tended to be aggregated to particular shoots that were better disposed to fruit-set.

Changes in this version from the original:
Labels in Figure 6 (p. 152) have been revised to improve clarity.
Error in Reference 9 has been corrected.

Full paper follows

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REPRINT

Low Fruit-set from Hevea *Hand-pollination: Fruit Load and Propensity of Floral Shoots to Fruit-bearing*

H.Y. YEANG* AND S.H. ONG*

Low fruit-set from hand-pollination in Hevea *arose primarily from the failure of entire floral shoots to bear fruits. In hand-pollinations carried out in the main flowering season, a mean of 83.7% of the floral shoots were barren despite the fact that seven to nine hand-pollinations were normally carried out on each shoot. Competition between developing fruits on the same floral shoot was not a major cause of low fruit-set. The distribution of fruits among hand-pollinated floral shoots conformed to a negative binomial distribution, indicating that fruit-set was not random but tended to be aggregated on particular shoots that were better disposed to fruit-set.*

Flowering plants frequently produce flowers far in excess of the fruits that eventually set. This phenomenon is a natural insurance against poor fruit-set of individual flowers. Where the number of fruits that set creates or is liable to create sinks exceeding the carrying capacity of the tree, an adjustment of the sink demand becomes necessary. This adjustment can be achieved through pollinated flowers failing to initiate fruits or, if fruit development is initiated, successive fruit-drop may occur to achieve an optimisation of reproductive sinks compatible to the resources available.

Hevea brasiliensis flowers profusely during the main flowering season from February to April and, depending on clone, less so during the secondary flowering season in August and September. However, fruit-set is generally poor with success from hand-pollination averaging 3% for the main flowering season and 8% for the secondary season[1]. The underlying causes for such low fruit-set have not been fully ascertained. Inefficient pollination[2] and pathogen infection[3,4] appear to be partly responsible while self-incompatibility has also been proposed[5]. Fruit load limitation is yet another possible factor. Exceeding an inherent threshold of fruit-bearing capacity could possibly lead to embryo abortion or fruitlet abscission. Low fruit-set could thus have resulted from competition between developing fruitlets on the same floral shoot as about nine hand-pollinations are made on each shoot. In this connection, Ross[6] has reported a generally linear negative correlation between fruit-set success and the number of pollinations (from four to twenty-three) attempted on a flowering shoot.

This paper examines some aspects of fruit load and the propensity of floral shoots to set fruit in relation to their possible roles as causal factors contributing to low fruit-set following hand-pollination.

MATERIALS AND METHODS

The 'floral shoot' *(Figure 1)* referred to in this paper is synonymous with the 'inflorescence' described by Ross[6]. The floral shoot terminates in a vegetative whorl and several flower panicles are normally developed from the internodal buds but sometimes also from axillary buds of the more basipetal leaves. Occasionally, the vegetative terminal of the floral shoot is delayed in development and expanded leaves are thus absent at the time of flowering. An apical

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Figure 1. A floral shoot of Hevea brasiliensis.

female flower is borne on the primary axis of the panicle, with other female flowers terminating the lateral (secondary) branches of the panicle. Male flowers are borne on the lateral branches. A full description of *Hevea* floral structure has been given by Heusser[7].

Hand-pollination was carried out conventionally as follows. Nine female flowers that were due to open were selected from panicles borne on the floral shoot for pollination though this number was occasionally reduced (usually to eight, seven, or rarely, fewer) when insufficient ripe female flowers were present on the shoot. All excess panicles on the floral shoot and panicle branches bearing male flowers and excess female flowers were cut away. A staminal column from a male flower that was due to open was inserted into the perianth of a female flower. The free edge of the perianth was then kept closed by the shallow insertion of a small wad of cotton wool made sticky with a drop of latex.

Hand-pollination data collected over ten years (1971–80) were analysed in the investigations on the relationship between fruit-set and the proportion of fruit-bearing floral shoots and that between fruit-set and the number of fruits per fruit-bearing shoot. All crosses with hand-pollinations exceeding 1000 made within the ten-year period were included in the study sample, but self-pollinations, inter-specific crosses and crosses where the flowers had been subjected to growth regulator treatments were excluded. On the basis of these criteria, a total of 296 975 hand-pollinations were included in the study, 243 877 of which were carried out during the main flowering season and the remaining 53 098 during the secondary season. The pollinations were carried out on 28 808 and 6666 floral shoots in the main and secondary flowering seasons respectively. There were in all 123 crosses represented in the main flowering season and 35 crosses in the secondary season. The average number of floral shoots per cross was 234 for the main flowering season and 190 for the secondary season while the average number of pollinations carried out for each cross was 1983 and 1517 respectively.

Fruit-set data on PB 5/51 (as the female parent) pollinated with RRIM 703 pollen in the main flowering season of 1975 were used in the study on the binomial and negative binomial distributions of fruits on floral shoots. Data on 493 fruits derived from 5859 hand-pollinations on 651 floral shoots were analysed.

The probability distribution of the negative binomial was obtained by expanding $(q - p)^{-k}$ whereby the expected frequency of any class (number of fruits per floral shoot) could be expressed as:

$$\frac{N\,(k + x - 1)!}{x!\,(k - 1)!}\;\frac{p^x}{q^x}\;\frac{1}{q^k}$$

where $p = \dfrac{\bar{x}}{k}$

$q = 1 + p$

x = number of fruits on a floral shoot

$\bar{x}$ = mean number of fruits on a floral shoot

N = total number of floral shoots

The value of k was obtained[8,9] first by estimation using the formula:

$$k = \frac{\bar{x}^2}{(s^2 - x^2)}$$

where s^2 is the variance of the number of fruits on a floral shoot.

This estimate was then refined by iteration to qualify the relationship:

$$k \log\left(\frac{1 + \bar{x}}{k}\right) = \log \frac{N}{f_o}$$

where f_o is the observed frequency of barren floral shoots.

RESULTS

Fruit-bearing and Fruit Load on Hand-pollinated Floral Shoots

The percentage of fruit-bearing floral shoots was calculated for each cross by scoring every hand-pollinated shoot of the cross according to whether it was barren or if it bore (one or more) fruits. The distributions of the percentage values for the 123 crosses carried out in the main flowering seasons are given in *Figure 2*. It is evident that despite the multiple pollinations (mean = 8.5) carried out on each floral shoot, failure rate of the entire shoot to bear any fruit at all was very high. Based on the 123 crosses studied, a cross had, on an average, only 16.3% of the hand-pollinated floral shoots bearing fruits; 83.7% of the floral shoots were barren. The median was 86.0%: half of the crosses attempted had between 86% and 100% of the floral shoots barren *(Figure 2)*.

Floral shoots were more successful in fruit-bearing during the secondary flowering season. Nevertheless, the mean proportion of barren floral shoots in a cross was still high at 62.4%. The median value — 62.7% — was very similar to the mean. Thus, half of the thirty-five crosses carried out had at least 63% of the floral shoots (each bearing a mean of 8.0 hand-pollinated flowers) barren *(Figure 2)*. An unexpected observation in the secondary flowering season was the particularly large number of crosses having between 60% and 65% barren floral shoots *(Figure 2)*; no ready explanation has been found for this observation.

If only the successful floral shoots were considered, it was apparent that large clusters of fruits were rare. In the main flowering season, 98% of the fruiting shoots had an average of fewer than two fruits per shoot while 97% had an average of fewer than three fruits per shoot in the secondary flowering season. The medians for the two seasons were 1.35 and 1.67 respectively *(Figure 3)*.

Average fruit-set success over the ten years, 1971–80, was 3.2% for the main flowering season and 9.2% for the secondary season. As evident from the above results *(Figures 2 and 3)*, better fruit-set in the secondary season was reflected both in the higher percentage fruit-bearing floral shoots (*i.e.* fewer barren shoots) as well as the mean number of fruits per fruiting shoot. Between these two fruit load parameters, the seasonal difference in the proportion of successful floral shoots was far more marked than that in the number of fruits per fruit-bearing shoot.

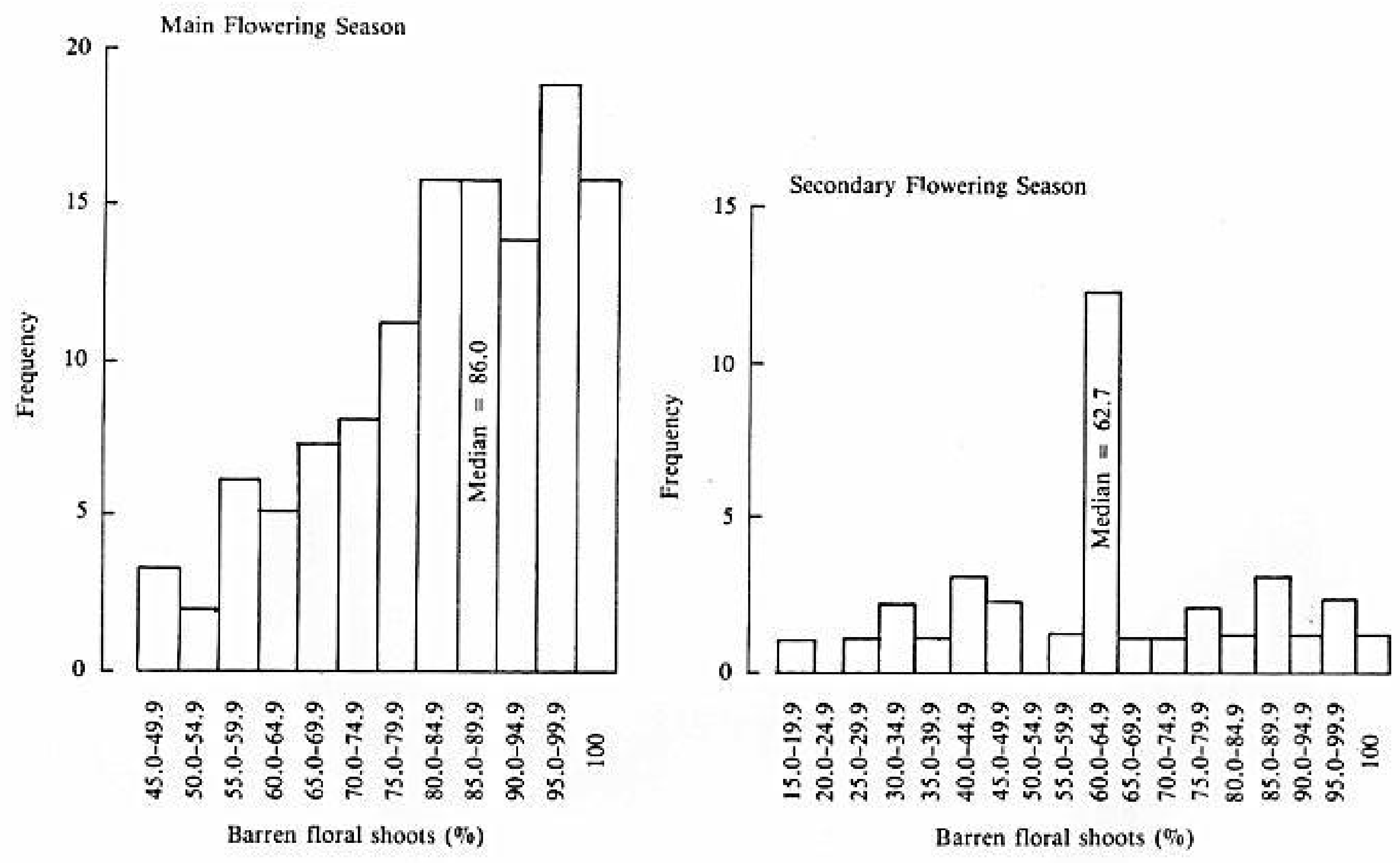


Figure 2. Frequency distributions of crosses by proportion of barren floral shoots.

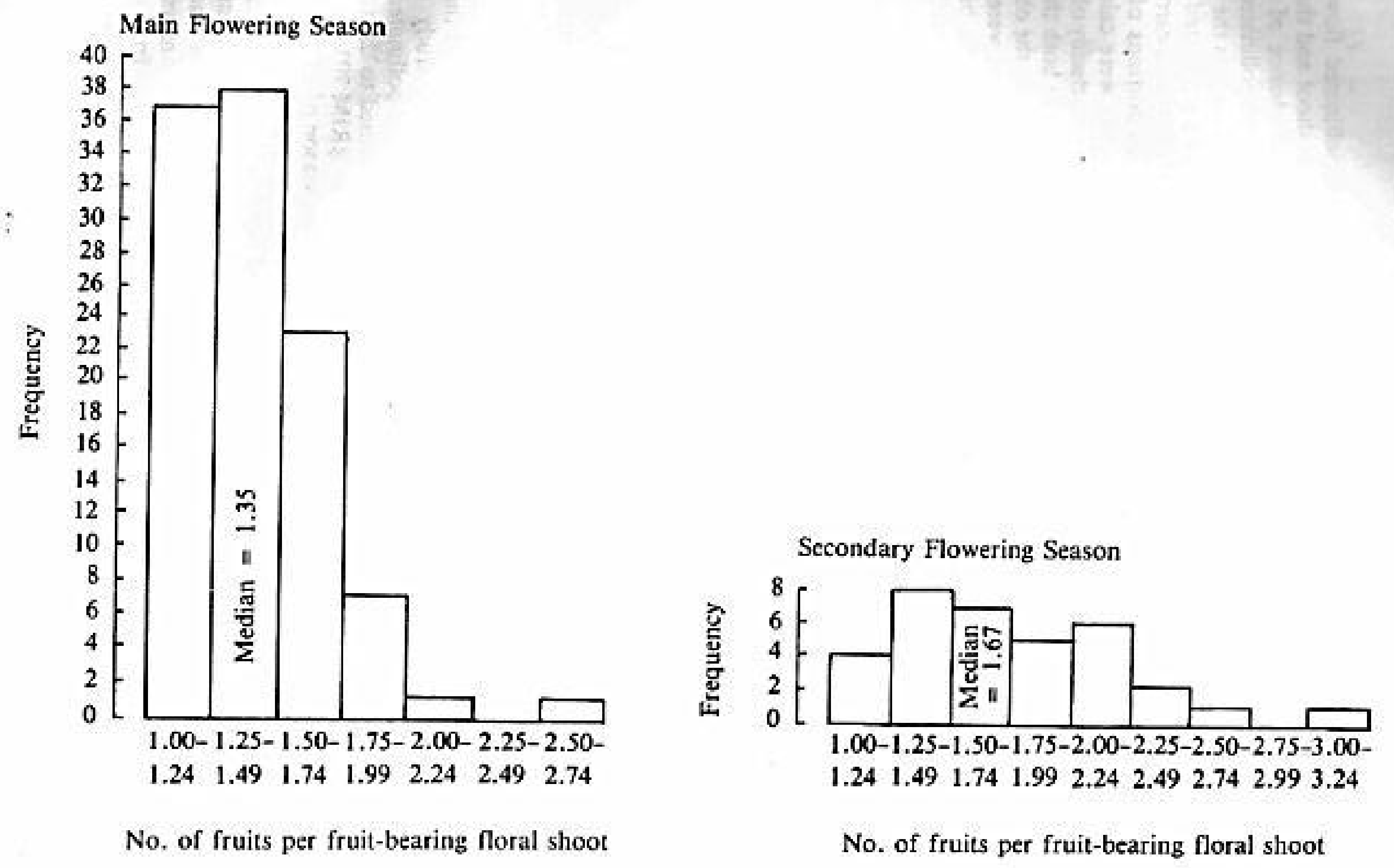


Figure 3. Frequency distributions of crosses by average number of fruits per fruit-bearing shoot.

The relationships between the two fruit load parameters with fruit-set success are shown in the scatter diagrams of the parameters against fruit-set *(Figures 4* and *5)*. Fruit-set success was positively correlated both with the percentage fruit-bearing floral shoots as well as the number of fruits per fruit-bearing floral shoot. Given the low fruit-set and the high incidence of barren floral shoots, it is to be expected that fruit-set would be better correlated with the former parameter. Accordingly, the correlation coefficient, r, between fruit-set and the percentage of fruit-bearing floral shoots for the main flowering season was 0.969 ($P<0.001$) whereas that between fruit-set and the number of fruits per fruiting shoot was 0.546 ($P<0.001$). In the secondary season, the r values were respectively 0.953 and 0.875 ($P<0.001$). The former value could be marginally enhanced to 0.983 by assuming a curvilinear ($y = 0.096x^{1.229}$) rather than a linear relationship.

The relative importance of the two components of fruit load (percentage fruit-bearing shoots and number of fruits per fruit-bearing shoot) in determining fruit-set could be further gauged from the multiple regression between fruit-set (as the dependent variable) and the two fruit load components (as independent variables). The standardised regression coefficient (*i.e.* regression coefficient expressed independently of the units of measurement) for the percentage fruit-bearing shoots was 0.90 whereas that for the number of fruits per fruit-bearing shoot was only 0.16 for the main flowering season. For the secondary flowering season, the standardised regression coefficients were respectively 0.70 and 0.32.

It was evident, therefore, that fruit-set success from hand-pollination was largely determined by the proportion of hand-pollinated floral shoots that were barren. The proportion of hand-pollinated floral shoots that bore fruits was of much greater importance than the number of fruits borne on a successful shoot both in determining the level of fruit-set success attained and in explaining its variation. This was especially the case during the main flowering season when fruit-set was lower.

Distribution of Fruits on Hand-pollinated Floral Shoots

Assuming that hand-pollinated flowers set fruit randomly on a floral shoot and that each floral shoot had an equal chance of setting fruit, the probability of a hand-pollinated floral shoot being barren is q^r, where q is the probability of fruit-set failure of a pollinated flower and r is the number of pollinations carried out on a floral shoot. The proportions of floral shoots expected to be barren were calculated and compared with the values actually observed *(Table 1)*. It was evident that in both the main and secondary flowering seasons, the observed proportions of barren floral shoots were higher than the values estimated on the basis of random fruit-set of the hand-pollinated flowers. Accordingly also, the observed average fruits per fruit-bearing shoot was higher than what was observed. Serving as rough indicators of the trends in fruit-set behaviour, these results pointed to the failure of entire floral shoots to set fruit being more widespread than would be expected if fruit-set were entirely random. It also appeared that the floral shoots were perfectly capable of bearing multiple fruits despite the generally low incidence of fruit clusters.

Further analysis was not attempted on the entire body of data as it comprised data from different crosses carried out in different years. Also, the number of hand-pollinations varied between the different crosses as did the fruit-set success. A more detailed study of the distribution of fruits on hand-pollinated floral shoots was therefore confined to data from a single cross: PB 5/51 × RRIM 703 carried out in the main flowering season of 1975. To allow for the assumption that each hand-pollinated floral shoot had nominally an equal chance of successful fruit-set, only the data from floral shoots on which nine pollinations had been carried out were included for analysis. To minimise day-to-day variation in fruit-set that might otherwise confound fruit distribution on floral shoots, hand-pollination data from pollination days giving similar fruit-set success were grouped together for analysis. Thus, the data were analysed as two separate sets: one

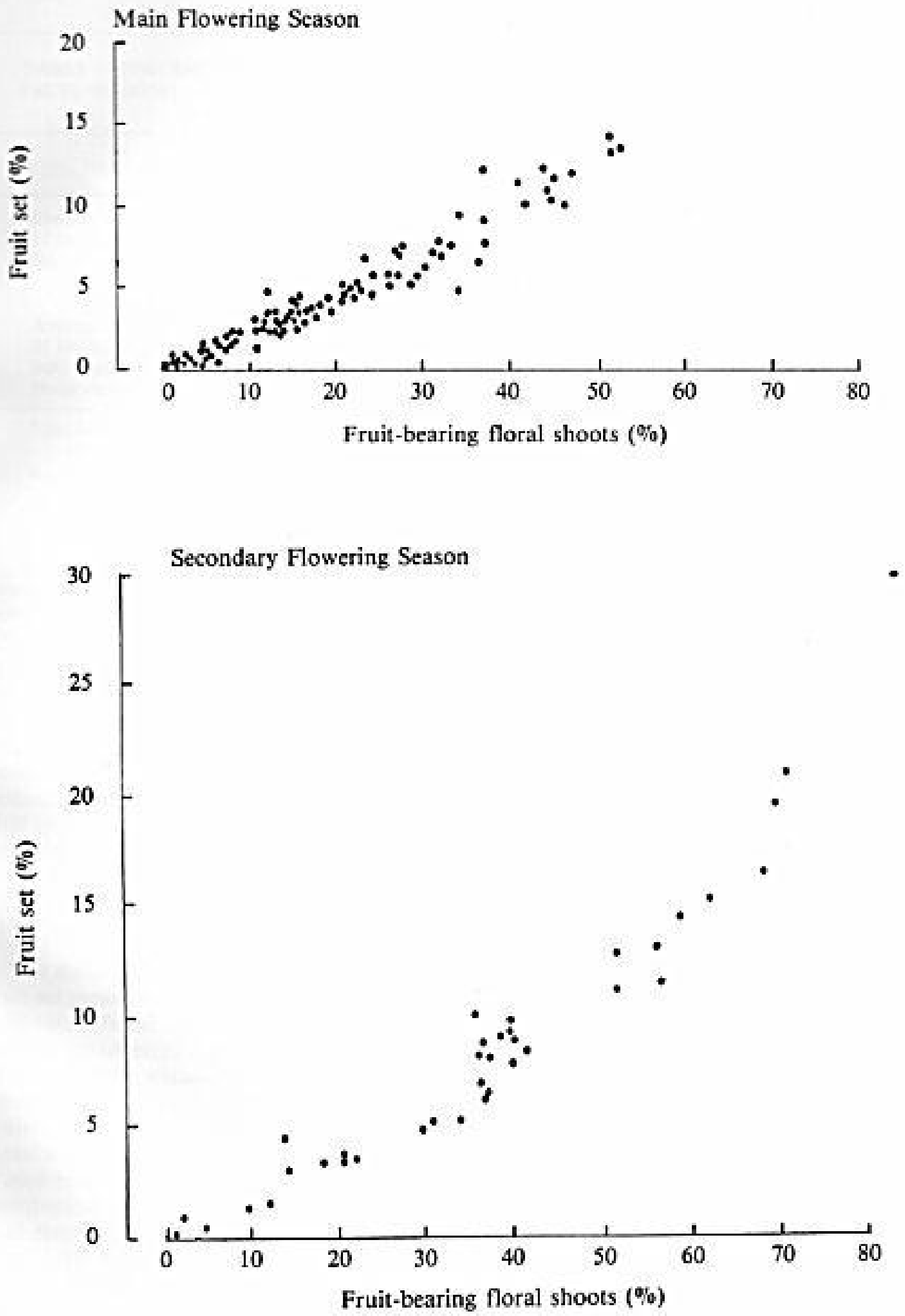


Figure 4. Relationship between fruit-set success of crosses and the proportion of fruit-bearing shoots.

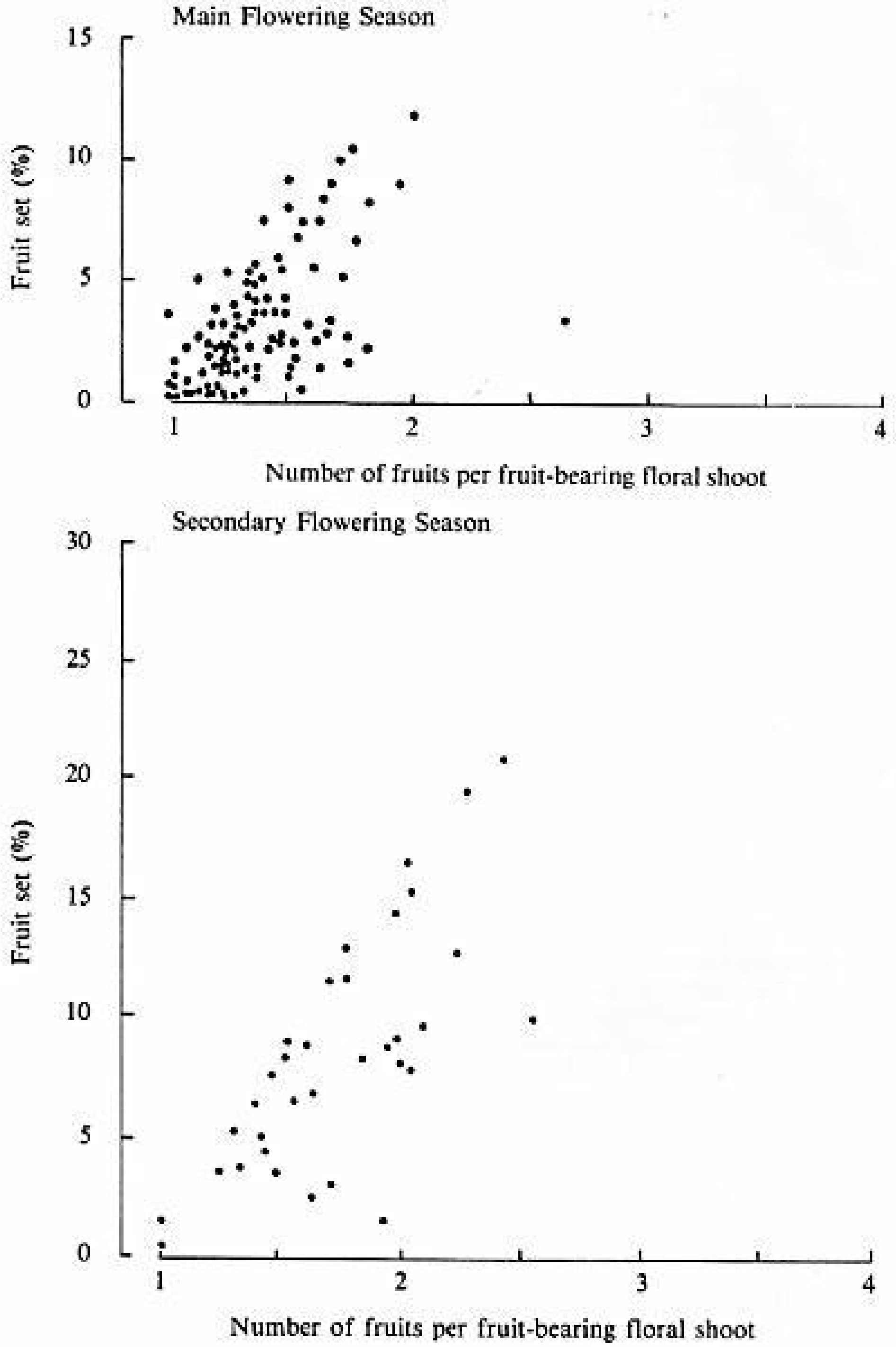


Figure 5. Relationship between fruit-set success of crosses and the average number of fruits per fruit bearing shoot.

TABLE 1. PERCENTAGE OF BARREN FLORAL SHOOTS AND AVERAGE NUMBER OF FRUITS PER FRUIT-BEARING SHOOT: COMPARISON BETWEEN OBSERVED VALUES AND EXPECTED VALUES ASSUMING RANDOM DISTRIBUTION OF THE FRUITS (1971-80)[a]

Item	Flowering season	Expected values[b]	Observed values
Percentage of barren floral shoots	Main	76.1	81.6
	Secondary	46.2	61.5
Average number of fruits per fruit-bearing floral shoot	Main	1.12	1.45
	Secondary	1.37	1.91

[a] Based on all hand-pollinated floral shoots (28 808 for the main flowering season and 6666 for the secondary season), irrespective of cross.

[b] Estimates based on 8.47 pollinations per floral shoot for the main flowering season and 7.97 for the secondary season.

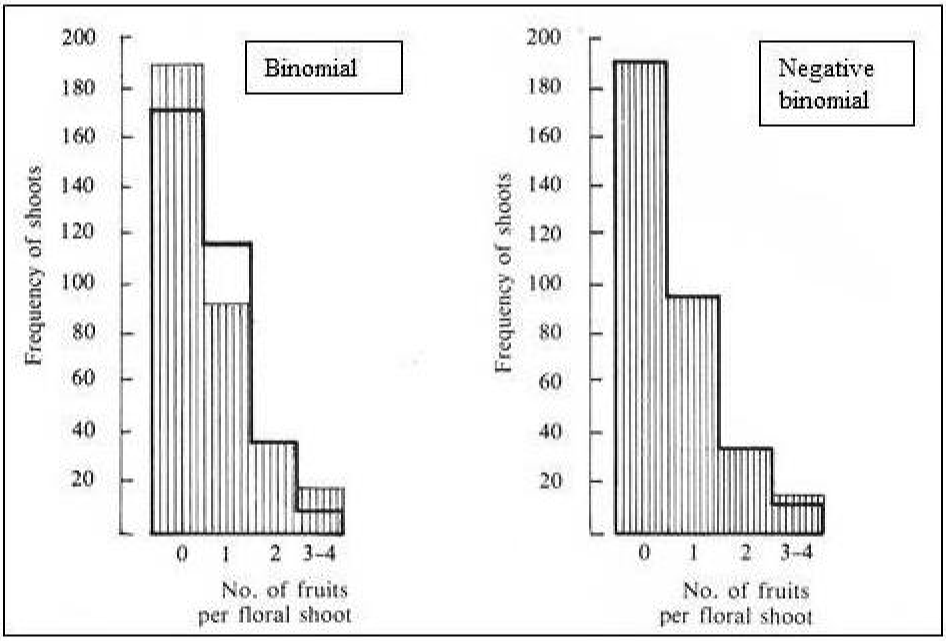
covering fruit-set from 6%-8% and the other covering fruit-set from 9%-11%. For the 6%-8% fruit-set group, 210 fruits were obtained from 2997 hand-pollinations on 333 floral shoots. In the 9%-11% fruit-set group, 2862 hand-pollinations carried out on 318 shoots yielded 283 fruits. Even so, the results were combined from the work of different hand-pollinators. Hence, an analysis of variance was first performed on the success rate of the ten participating hand-pollinators to determine if pollinator differences contributed to fruit-set variation. The results showed no significant differences among the hand-pollinators.

The data were first analysed to determine if fruit-set generally occurred randomly on hand-pollinated floral shoots, *i.e.* with no shoot having any inherent advantage over any other. Floral shoots were classified according to whether they bore 0, 1, 2, 3, 4 or 5 mature fruits. Should fruit-set occur randomly on the floral shoots the number of shoots in each class would be expected to conform to a binomial distribution. When the data were fitted by binomial distributions derived from the expansions of $(0.0701 + 0.9299)^9$ and $(0.0989 + 0.9011)^9$ for the 6%-8% and 9%-11% fruit-set groups respectively (*Figure 6*), significant deviations from the binomial models were observed ($\chi^2 = 16.67$; df = 2; $P<0.001$ for the 6%-8% fruit-set group and $\chi^2 = 31.23$; df = 2; $P<0.001$ for the 9%-11% fruit-set group). Hence the distribution of fruits among the floral shoots did not appear to be a random process.

As can be seen from *Figure 6*, deviation from the binomial distribution took the form of relative excesses both of shoots that were barren as well as shoots that bore multiple fruits. This is in general agreement with the findings of the foregoing analysis (*Table 1*) of all fruit-set data from 1971-80 and suggests that the fruits that were formed had a tendency to group together on certain hand-pollinated floral shoots. As is characteristic of aggregated distributions, the variances in the number of fruits per floral shoot exceeded their respective means ($\bar{x} = 0.63$, $s^2 = 0.74$ for the 6%-8% fruit-set group and $\bar{x} = 0.89$, $s^2 = 1.18$ for the 9%-11% group).

As a further test of aggregation of fruits on hand-pollinated floral shoots, the data were fitted for negative binomial distributions which characterise aggregation[8-10]. The distributions were derived from the expansions of $(1.2574-0.2574)^{-2.450}$ and $(1.4618-0.4618)^{-1.927}$ for the 6%-8% and 9%-11% fruit-set groups respectively. The results showed that the frequencies expected by the negative binomial

6 – 8% fruit-set



9 – 11% fruit-set

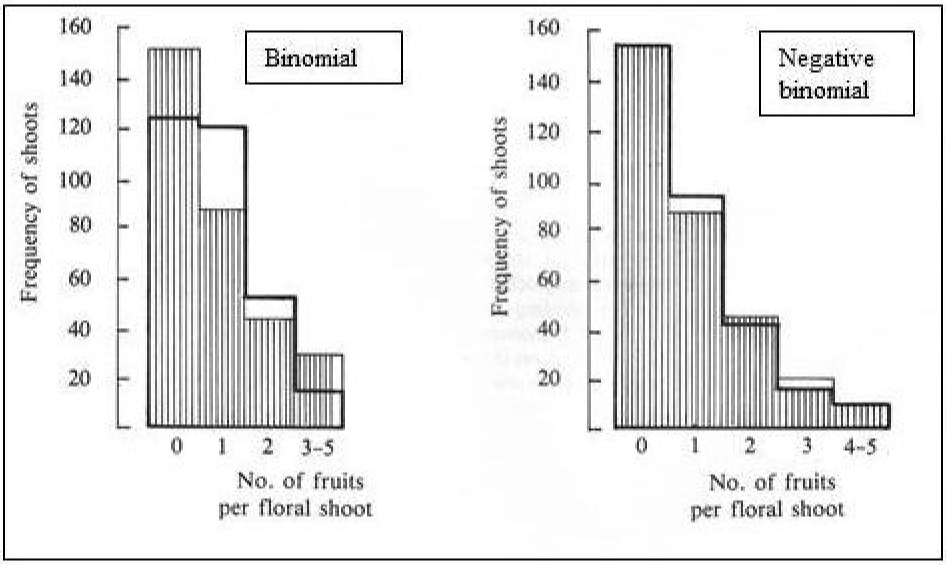


Figure 6. Frequency distributions of floral shoots of the cross PB 5/51 × RRIM 703 by the number of fruits per floral shoot. The observed (shaded) distributions are compared to computed (bold outlines) binomial and negative binomial distributions.

reproduced the observed values closely, with $\chi^2 = 0.58$ (df = 1; $0.25<P<0.50$) for the 6%-8% fruit-set group and $\chi^2 = 0.89$ (df = 2; $0.50<P<0.75$) for the 9%-11% fruit-set group *(Figure 6)*. It would appear, therefore, that *Hevea* fruits did not set randomly on hand-pollinated floral shoots. Some shoots were better disposed to successful fruit-set than others, leading to the aggregation of fruits on the 'favoured' branches.

DISCUSSION

It has been shown in various plants[11,12] that nutrients supplied to developing fruitlets are not transported over long distances but are generally obtained from the immediately adjacent foliage. In the case of *Hevea*, the spatial separation between individual floral shoots might therefore preclude competition for nutrients or other growth factors between them. This assumption requires verification. Nevertheless, insofar as competition *within* the floral shoot (*i.e.* between the approximately nine hand-pollinated female flowers on the shoot) was concerned, it is clear from analyses of the data that this cannot be a substantial cause of fruit-set failure in hand-pollinated flowers. Competition between fruits on the same floral shoot would have resulted in at least one fruit — the most vigorous — being retained on the shoot. As the hand-pollination data revealed, low fruit-set from hand-pollination of *Hevea* arose primarily from the failure of *entire* floral shoots to bear fruits.

Within the range of fruit-set success encountered in the hand-pollination programmes, higher fruit-set was achieved largely from greater numbers of fruit-bearing floral shoots rather than from attaining more fruits per bearing shoot. In the main flowering season when the bulk of hand-pollination activities was carried out, about 85% of the hand-pollinated shoots were barren at fruit harvest. The same situation, albeit less severe, applied to the secondary flowering season. The difference in the proportions of barren floral shoots between the main and secondary flowering seasons reflected the seasonal difference in fruit-set success, some of the reasons for which have been discussed elsewhere[4].

The proposition that competition between developing fruits on the same floral shoot was not the *main* cause of fruit-set failure did not necessarily mean that such competition did not occur at all. Frey-Wyssling[13] noted the abortion of one developing fruit borne adjacent to another (presumably more vigorous) fruit on the same panicle, suggesting the existence of within-panicle competition. To what extent does such putative competition contribute to fruit-set failure? The large proportion of barren floral shoots encountered was not surprising given the low fruit-set characteristic of *Hevea;* this was generally predictable by the law of probability *(Table 1)*. What was notable was the manner in which the observed values deviated from the predicted. If competition between fruits on the same floral shoots were to lead to abortion of the weaker fruits, it might be expected that the average number of fruits per fruiting floral shoot would be less than what would be expected if fruit-set were random and unaffected by competitive influences. Accordingly, for a given fruit-set success, the surviving fruits would be spread over a larger proportion of floral shoots and the proportion of fruit-bearing branches could then be expected to exceed the value estimated on the basis of random fruit-set. However, the results in *Table 1* showed the converse to be true, suggesting that not only were the suspected competitive effects not manifested, but that the successful floral shoots tended in fact to bear multiple fruits more frequently than could be explained by random chance.

Analysis of the fruit-set data from the 1975 cross PB 5/51 × RRIM 703 confirmed that the hand-pollinated floral shoots did not set fruit randomly. Distribution of fruits on the floral shoots conformed to a negative binomial distribution which characterises an aggregated distribution[8-10]. This indicated that certain shoots were better disposed to successful fruit-set than others leading to the aggregation of fruits on the 'favoured' shoots. Propensity to fruit-set has been found to vary between the trees used for hand-pollination (data not presented). As floral shoot data used in this analysis were combined from shoots on different trees, this study does not differentiate between floral shoots on the same tree or on different trees.

Overall, the fruit-set characteristics of *Hevea* give rise to the situation where there are, on the one hand, large numbers of floral shoots that fail entirely (*i.e.* barren) and on the other hand, small numbers of successful floral shoots that often bear multiple fruits. Why some floral shoots should set fruit better than others is not clear. If the reason could be elucidated, the selective pollination of flowers on 'favoured' shoots could lead to significantly improved fruit-set.

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