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SPECIAL PAPER

FLOWER, FRUIT AND SEED ABORTION IN TROPICAL FOREST TREES: IMPLICATIONS FOR THE EVOLUTION OF PATERNAL AND MATERNAL REPRODUCTIVE PATTERNS¹

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ABSTRACT

Flower, fruit and immature seed abortion was studied in seven self-incompatible species of trees in a tropical lowland semideciduous forest. The species showed considerable variability in fruit and seed set and the rate at which flowers and fruits were aborted. The amount of flower and fruit abortion also varied over time within species. Small samples of open-pollinated flowers in three species showed adequate amounts of pollen on the stigma, but it could not be determined whether the pollen was compatible or incompatible. In a species with multiseeded fruits, the aborted fruits contained significantly fewer seeds than those retained on the plant. Position of fruit within the inflorescence and of seed within the ovary also had a marked effect on abortion: fruits and seeds at certain positions had a higher probability of abortion than those at other positions. Experiments to test the effect of pollen source on abortion were inconclusive. The factors underlying abortions were evaluated in the context of three mutually non-exclusive hypotheses. It is concluded that selection for increased pollen dispersal and uncertainty in paternity of the zygotes are major factors underlying abortions.

THE LARGE-SCALE abortion of flowers and immature fruits is a common phenomenon. The proportion of flowers that develop into mature fruit varies considerably among species, ranging from less than one percent to one hundred percent (Lloyd, 1980; Lloyd, Webb and Primack, 1980; Stephenson, 1981 and references therein). Darwin (1877a, p. 399) was perhaps the first to note and comment upon the significance of 'excess' flowers produced by plants. Fruit growers have, of course, been generally aware of the problem of flower drop and its effects on eventual fruit set (see Janick and Moore, 1975). Similarly, crop scientists have considered the effect of excess flower and fruit

production on seed and fruit yield (Ojemohn, 1972; Summerfield, Huxley and Steel, 1974; Swaminathan, 1975; Farrington and Pate, 1981). The study of causes and consequences of mortality between fertilization and seed and fruit maturation is also important in understanding the sexual strategies of plants (Lloyd, 1980), particularly the extent of and the manner in which mate competition and mate selection occurs in plants (Janzen, 1977a). But, although selection acting on different stages of life history from seed to adult has received much attention (Harper, 1977), evolutionary biologists have not, until recently, explored the causes and implications of mortality between fertilization and seed maturity (Janzen, 1978; Lloyd, 1980; Lloyd et al., 1980; Stephenson, 1981; Udovic and Aker, 1981; Aker, 1982; Lee and Bazaaz, 1982a, b).

Several workers have implicated lack of successful pollination as a major cause of abortions (Schemske, 1977, 1980a; Schemske et al., 1978; Willson and Schemske, 1980; Bierzychudek, 1981, 1982a, b; Petersen, Brown and Kodric-Brown, 1982; Gross and Werner, 1983; Rathcke, 1983). But the continuous abortion of immature fruits in many species suggests that abortions do not necessarily result from inadequate pollination and that other factors are also involved (Webb, 1979a; Primack, 1979; Lloyd, 1980; Lloyd et al., 1980; Stephenson, 1981; Aker, 1982; Lee and Bazaaz, 1982a, b).

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The most comprehensive treatment of the problem is that by Lloyd (1980), who considered the regulation of flower and fruit numbers to be an adjustment of maternal investment to match available resources. He elaborated upon a number of consequences that such an adjustment entails for paternal and maternal fitness, including the genetic quality of the offspring. Lloyd (1980) emphasized the need for precise data on spatial and temporal patterns of resource allocation to different reproductive functions in order to improve our understanding of the evolutionary implications of flower and fruit abortion.

This paper documents the patterns of flower, fruit, and immature seed abortion in seven species of tropical lowland forest trees. Our work draws heavily upon previous research on flower and fruit abortion in natural populations (e.g., Lloyd et al., 1980; Stephenson, 1980, 1981; Udovic, 1981; Udovic and Aker, 1981; Aker, 1982; Lee and Bazaaz, 1982a, b). The first major departure from prior studies is that we distinguish among flower, fruit, and seed abortions and treat them separately. These distinctions are important because both the timing of abortion and the stage at which abortion occurs can be related to selective forces that have somewhat different origins and effects on the evolution of paternal and maternal reproductive patterns. Second, prior studies based on single species (e.g., Udovic and Aker, 1981; Aker, 1982) view factors responsible for abortions as somewhat unique to that particular species. While recognizing that many plant species have unique reproductive traits, our purpose in examining seven species was to emphasize the widespread occurrence of abortions and to search for its general causes (See also Lloyd, 1980; Lloyd et al., 1980.)

The results are considered in the context of three mutually non-exclusive hypotheses that have been advanced to explain flower, fruit, and seed abortion. The 'pollinator limitation' hypothesis invokes inadequate pollination as the major factor underlying abortions (Schemske, 1977; Waser 1978; Schaal, 1980; Willson and Schemske, 1980; Bierzychudek, 1981, 1982a, b; Petersen et al., 1982; Snow, 1982; Rathcke, 1983). The 'resource limitation' hypothesis traces the abortions to shortage of resources (Willson and Schemske, 1980; Stephenson, 1981; Udovic, 1981; Wyatt, 1981; Lee and Bazaaz, 1982a). The 'sexual selection' hypothesis attributes abortions to conflicts inherent in the optimization of male and female reproductive success. Since male reproductive success may be limited by the quantity of matings and female reproductive success by avail-

able resources for the nourishment of embryos (Bateman, 1948; Williams, 1975), plants may bear many more flowers than can be matured into fruits. Thus many flowers are borne simply to fulfill the male function (Lloyd, 1980; Udovic and Aker, 1981) and fruits are aborted to adjust the number to available resources. We consider the inadequacies of these hypotheses and conclude that uncertainty in the environment, particularly in the paternity of the zygotes (Janzen, 1977a) is a major factor underlying abortions.

METHODS—The study was conducted at Hacienda La Pacifica, 5 km northwest of Cañas, and at the I.T.C.O. (previously 'COMELCO') property, 3–4 km northwest of Bagaces, both in Guanacaste Province, Costa Rica. Both sites are within the tropical dry forest life zone of Holdridge (Tosi, 1969) and in the undisturbed state support a deciduous or semideciduous forest. The climate and vegetation in the study area are described in detail by Holdridge et al. (1971), Daubenmire (1972), and Frankie, Baker and Opler (1974).

Seven species were used to study various aspects of flower, fruit, and seed abortion. *Bauhinia unguolata* (Leguminosae, Caesalpinioideae) is a shrub or small tree, and the remaining species—*Caesalpinia eriostachys* (Leguminosae, Caesalpinioideae), *Dalbergia retusa*, *Myrospermum frutescens*, and *Pterocarpus rohrii* (Leguminosae, Papilionoideae), *Cochlospermum vitifolium* (Cochlospermaeae), and *Tabebuia rosea* (Bignoniaceae)—are small to large trees of the dry deciduous forest.

Except for the bat-pollinated *B. unguolata* (Heithaus, Fleming and Opler, 1975), all investigated species are pollinated by medium to large-sized bees (Frankie et al., 1983).

The seven species differed in several features of their reproductive biology and were therefore subjected to different experiments and observations, all of which were conducted in the dry season of 1981. Time constraints, prevented uniform investigations even when feasible; all seven species flowered within a span of approximately 12 wk.

In *Bauhinia unguolata*, flowers are arranged in terminal or pseudo-lateral racemes and mature seeds are scattered from explosively dehiscent pods. In *Caesalpinia eriostachys*, racemes are terminal or subterminal and seeds are again dispersed from explosively dehiscent pods. Flowers of *Dalbergia retusa*, *Myrospermum frutescens*, and *Pterocarpus rohrii* are arranged in racemes which are in turn clustered toward the branch tips appearing as terminal or axillary panicles; the pod is an indehiscent,

TABLE 1. Percentage of flowers forming mature fruit under open pollination

| Species | No. of individuals | No. of flowers | % Flowers that develop mature fruits |
|--|--------------------|----------------|--------------------------------------|
| <i>Bauhinia unguolata</i> L. | 5 | 2,212 | 10.15 |
| <i>Caesalpinia eriostachys</i> Benth. | 6 | 11,206 | 0.98 |
| <i>Cochlospermum vitifolium</i> (Willd.) Spreng. | 2 | 151 | 26.00 |
| <i>Dalbergia retusa</i> Hemsl. | 5 | 560 | 8 ^a |
| <i>Myrospermum frutescens</i> Jacq. | 4 | 3,022 | 3.40 |
| <i>Pterocarpus rohrii</i> Vahl | 5 | 1,770 | 7 ^a |
| <i>Tabebuia rosea</i> (Bertol.) DC. | 5 | 434 | 1 ^a |

^a Data from Bawa (1974).

winged, mostly one-seeded samara. In *Cochlospermum vitifolium*, flowers are arranged in terminal panicles and the fruit is a five-valved capsule which dehisces to release the wind-dispersed seeds. *Tabebuia rosea* also has flowers in terminal panicles, the fruit is a long, cylindric, dehiscent capsule, and seeds have a membranous wing, which aids dispersal.

In order to determine the extent and rate of flower and fruit abortion for *Caesalpinia eriostachys*, *Cochlospermum vitifolium* and *Myrospermum frutescens*, we marked individual flowers or inflorescences, censused them every 2–4 days and recorded the number of fruits initiated and matured. Fruit set, throughout the paper, refers to the number of mature fruit. The level of fruit set in *Bauhinia unguolata* was scored from pedicel scars on mature infructescences. In *B. unguolata*, samples included inflorescences from all positions on plants and all flowers within an inflorescence; in *C. eriostachys* and *M. frutescens*, samples comprised all flowers of inflorescences selected more or less randomly from lower accessible branches; in *C. vitifolium*, the fate of all flowers was determined for each tree.

Controlled pollinations were carried out for *Caesalpinia eriostachys*, *Dalbergia retusa*, *Myrospermum frutescens*, and *Tabebuia rosea* to test for self-incompatibility in sampled trees. Self-incompatibility in other species could not be investigated for the same trees, but extensive data collected earlier for the same populations (Bawa, 1974; unpubl. observ.) were used to make inferences. Experimental procedures for controlled pollinations were the same as outlined by Bawa (1974).

Aborted fruits found under *Caesalpinia eriostachys* and *Cochlospermum vitifolium* were collected and measured. In *C. vitifolium*, the large size of the seeds and the ease with which the fruit could be opened also allowed scoring of the number of seeds per fruit. Aborted fruits in *C. eriostachys* were collected from selected branches above the ground in which fruit were easier to detect. In *C. vitifolium*, we attempted

to collect all fruits from under the tree. In both cases, care was taken not to miss any aborted fruit but we are not certain about the fraction of the small fruit that might have remained undetected. For both species, three sets of samples were taken on different days. Since the samples did not vary among days, the data were pooled for analysis.

The distribution of fruit among infructescences was investigated in *Caesalpinia eriostachys* by scoring the number of pods for each of 50 infructescences from each of five trees. In two further trees, individual infructescences were tagged and censused to determine the rate of abortion of young fruits at different positions within an infructescence. Samples of nonfruiting inflorescences, infructescences with a single pod set in the lowermost third, and infructescences with a single pod in the uppermost third were collected, dried, and weighed as an estimate of the resources allocated to pedicel and peduncle thickening during fruit development.

Large samples of mature pods were collected, and the number of ovules and the number and position of seeds within pods were recorded for several trees in the five species of the Leguminosae. In *Dalbergia retusa* and *Myrospermum frutescens*, immature pods were sampled from the same trees, and the position of developing seeds within pods were noted.

Pollen loads on the stigmas and pollen tubes in the styles of open-pollinated flowers of *Cochlospermum vitifolium*, *Caesalpinia eriostachys*, and *Dalbergia retusa* were examined following Martin's (1959) technique. Flowers of the first species were collected from the ground under the trees and, of the latter two species from the trees themselves at 3:00 P.M., about 9 hr after anthesis.

As selective flower and fruit abortion may be dependent upon pollen source, we examined two aspects of variation in pollen source and noted resulting levels of fruit set. First, for *Tabebuia rosea*, we compared fruit set resulting from crosses with near (300 m) and far (10–12 km) pollen sources. Second, for *Caesalpinia*

TABLE 2. Percentage of flowers forming mature fruit under controlled pollination^a

| Species | No. of individuals | No. of flowers | Pollination treatment | % Fruit set |
|----------------------|--------------------|----------------|-----------------------|-------------|
| <i>C. eristachys</i> | 2 | 40 | Cross | 40.00 |
| <i>D. retusa</i> | 3 | 239 | Cross | 8.79 |
| <i>M. frutescens</i> | 3 | 239 | Cross | 5.86 |
| | 3 | 344 | Self | 0.58 |
| <i>T. rosea</i> | 3 | 630 | Cross | 40.32 |

^a The number of flowers pollinated on an inflorescence generally did not exceed the average number of fruits initiated per inflorescence.

eristachys and *T. rosea*, we compared fruit set among flowers that received pollen from only one other plant with those that received pollen from a mixture of three sources.

RESULTS—Flower and fruit abortion—We distinguished flower from fruit abortion in *Caesalpinia eristachys*, *Cochlospermum vitifolium*, and *Myrospermum frutescens* on the basis of rate of pollen tube growth, the time it takes for self-pollinated flowers in these self-incompatible species to abscise, and the evident development of the ovary as a fruit. In both *C. vitifolium* and *M. frutescens*, pollen tubes in self-pollinated flowers grow as far as the ovules, and we assume that the time taken until self-pollinated flowers abscise represents the *maximum* time taken for fertilization. If self-incompatibility were to operate via embryo abortion, fertilization would occur sooner, before abscission of selfed flowers is completed, as for example in *M. frutescens* (discussed below). Compatible pollen tubes reach the ovary within 24 hr of pollination in *C. eristachys*; self-pollinated flowers abscise within 72 hr of anthesis and if the flowers are retained the ovary enlarges appreciably after 72 hr. Thus within this species abortions during the first 3 days are termed flower abortions and those after that time, fruit abortions. In *C. vitifolium*, compatible pollen tubes also reach the ovary within 24 hr, but the abscission of self-pollinated flowers may not occur until 120 hr after pollination. We therefore consider all abortions during the first 5 days to be flower abortions and those thereafter to be fruit abortions. The rate of pollen tube growth in *M. frutescens* is comparable to that of *C. eristachys*, and although ovaries, too, increase in size 48 hr after pollination, self-pollinated flowers may not abscise for many days. It is thus difficult to determine the precise time by which the embryos are formed. However, examination of several hundred ovaries revealed

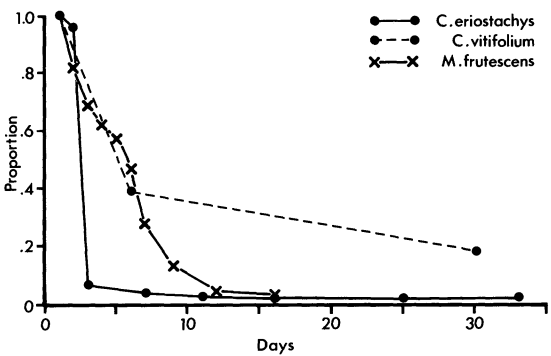


Fig. 1. Timing of abortion in *Caesalpinia eristachys* (mean for three trees), *Cochlospermum vitifolium* (two trees), and *Myrospermum frutescens* (four trees). Points represent proportion of original flowers retained after flowering on Day 1.

that in 4–5-day-old flowers, the ovules are twice their initial diameter; only fertilized ovules are known to enlarge in other legumes (Cooper and Brink, 1940). We therefore consider abortions before and after Day 5 as flower and fruit abortions respectively, though it is likely that many abortions which occur between Day 3 and Day 5 involve young fruits.

Only a small percentage of flowers eventually matured into fruit in all of the seven species studied (Table 1). The rate of flower abortion varied considerably among species. For example, in *C. eristachys* 93% of the flowers were aborted within 2 days and in *M. frutescens* 53% of flowers were aborted within 5 days (Fig. 1).

About 75% of the open-pollinated flowers in *Caesalpinia eristachys* and *Dalbergia retusa* collected at 3:00 P.M. ($N = 60$; 20 ea. from three trees in each of the two species) had 5 to 15 pollen grains on the stigma. All open-pollinated, aborted flowers ($N = 30$, ten each from three trees) in *Cochlospermum vitifolium* had scores of pollen grains on the stigma and numerous pollen tubes in the style.

As all seven species are self-incompatible (Bawa 1974, and Table 2 for *Myrospermum frutescens*), it might be argued that aborted flowers are those which do not receive pollen from other plants. When flowers were artificially cross-pollinated, the level of fruit set was raised, but even then the level of flower and fruit abortion remained high for all species studied (Table 2).

In addition to flower abortion, a considerable amount of fruit abortion occurs in these seven species. Eighty percent of the young fruits present on day 3 were aborted by *Caesalpinia eristachys*, 45% after Day 6 by *Cochlosper-*

TABLE 3. Number of ovules per pod and number of seeds formed per pod in 5 species of Leguminosae

| Species | No. of individuals | No. of pods | Ovules/pod | Seeds/pod |
|-----------------------|--------------------|-------------|------------------|------------------|
| <i>B. unguolata</i> | 5 | 189 | 18.67 \pm 0.23 | 11.01 \pm 0.40 |
| <i>C. eriostachys</i> | 5 | 342 | 6.17 \pm 0.05 | 2.82 \pm 0.08 |
| <i>D. retusa</i> | 3 | 240 | 4.72 \pm 0.04 | 1.13 \pm 0.02 |
| <i>M. frutescens</i> | 4 | 348 | 5.14 \pm 0.07 | 1.01 \pm 0.001 |
| <i>P. rohrii</i> | 5 | 386 | 6.42 \pm 0.04 | 1.03 \pm 0.01 |

mum vitifolium, and 93% after Day 6 by *Myrospermum frutescens*.

Seed abortion—Seed abortion refers to the rejection of immature seeds between fertilization and seed maturation. Seed abortion was most evident among the five species of the Leguminosae: two patterns of seed set among pods were found (Table 3). In *Bauhinia unguolata* and *Caesalpinia eriostachys*, a variable number of seeds were set per pod and on the average more than half of the ovules developed into good seeds. However, in *Dalbergia retusa*, *Myrospermum frutescens*, and *Pterocarpus rohrii*, almost all pods were one-seeded (88%, 99%, 97%, respectively), and pods with more than two seeds were never observed in either *M. frutescens* or *P. rohrii* and in only three instances for *D. retusa*. In all of these species many immature seeds are aborted as the fruit matures (see below).

The exact number of ovules per flower was not determined for *Cochlospermum vitifolium* and *Tabebuia rosea* as ovaries contain more than 100 ovules. However, we noted that in *T. rosea*, almost all ovules formed good seed, whereas in *C. vitifolium*, the proportion of ovules that matured into seed was extremely variable.

Timing of abortion and quality of aborted fruits—The timing of flower and fruit abortions was documented from flower opening until fruit had reached mature size in three species: *Caesalpinia eriostachys*, *Myrospermum frutescens*, and *Cochlospermum vitifolium*. There was a similar level of fruit set once fruit had reached mature size in *C. eriostachys* and *M. frutescens* (Fig. 1, Day 16), but the patterns of abortion were very different. Most flowers that were open on Day 1 in *C. eriostachys* were retained on Day 2, but most of these were aborted by the end of Day 3. This initial flower abortion was followed by a more gradual abortion of young fruits. Flower and fruit abortion was much more even in *M. frutescens* and occurred from Day 1 onward (Fig. 1).

Abortion of fruit was more frequent when fruits were small than when the tree had already

invested considerable resources toward maturation, as shown by the size distribution of aborted fruits for *Caesalpinia eriostachys* and *Cochlospermum vitifolium* (Fig. 2). Very few fruits of almost mature size were aborted and of those that were, most had been damaged by insects. Most young aborted fruits were undamaged.

The ovary of *Cochlospermum vitifolium* contains several hundred ovules, and a variable number of these develop into seeds. The number of maturing seeds was significantly lower in undamaged but aborted capsules than in capsules retained by the tree in all four trees examined (Table 4). Furthermore, within a tree, there was a strong correlation between the size of the capsule at the time of abortion and the number of good seeds contained in the capsule (capsule length and seed number, $r = 0.87$, $N = 36$, $P < 0.001$; capsule diameter and seed number, $r = 0.80$, $N = 36$, $P < 0.001$).

Variation in fruit quantity and quality during a flowering session—For six trees of *Caesalpinia eriostachys*, fruit set was determined for branches that were flowering early within the tree and the population, and these data were compared with fruit set for branches of the same trees flowering in the middle of the flowering session. Fruit set was consistently and significantly higher among early flowering branches ($\bar{x} = 1.31 \pm 0.26\%$ fruit set) than in midseason branches ($\bar{x} = 0.65 \pm 0.16\%$ fruit set; pairwise t -test on arcsine transformed data = 4.26, $P < 0.01$).

For four trees of *Cochlospermum vitifolium*, fruit formed at different times in the flowering season were examined (Table 5). In two of the trees late capsules had significantly fewer seeds than did early set capsules; in one there was no difference between early and late capsules, and in the remaining tree late capsules had fewer seeds ($P < 0.05$) than those formed in the middle of the flowering season, although they did not differ from those that were formed early. The difference between early and late average fruit quality is a result of the retention, late in the flowering season, of capsules with very low seed numbers (Table 5): capsules with

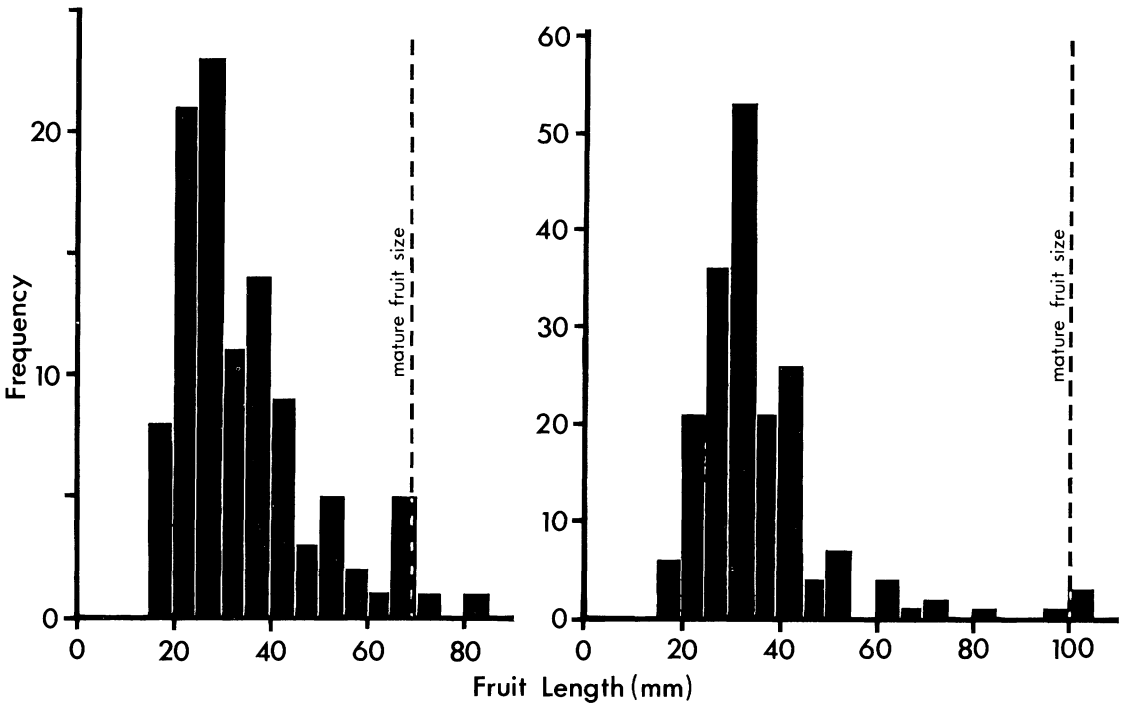


Fig. 2. Frequency distributions of aborted pod sizes for *Cochlospermum vitifolium* (Left: 104 pods from under four trees) and *Caesalpinia eriostachys* (Right: 188 pods from under four trees).

such low seed numbers are usually aborted when set earlier (see Table 4).

Position effects—Flowers and fruits: Although all trees of the species investigated had low fruit set, there was some variation among individuals of a population. In *Bauhinia ungulata*, for instance, fruit set ranged from 7.31–12.76% among five trees, and in *Caesalpinia eriostachys*, 0.50–1.41% among six trees.

Within individual trees mature pods were not distributed at random among infructescences. Inflorescences of *C. eriostachys* had, on average, 15–24 functional flowers and yet most inflorescences matured only a single pod. In a sample of 50 infructescences from each of five trees, 87.2% had only one pod, 12% had two, and 0.8% had three (significantly different from the expected values: $\chi^2 = 8.72$, $P < 0.02$).

Within an inflorescence, pods that were beginning to mature in the upper third were much more likely to be aborted than those in the lower or middle thirds (Table 6). Fifty-three percent of these fruit losses occurred when small pods near the top of the inflorescence were aborted while a larger pod was maturing in the lower or middle third. Another 33% involved the abortion of small solitary pods in the upper third, and all but two of the remaining losses occurred from inflorescences with two or more pods. One possible reason for the loss of all but one pod, and in particular for the loss of upper pods, may be the cost involved in maturing more than one pod per infructescence and the significantly greater investment in pedicel and peduncle thickening which is required to support upper rather than lower pods in

TABLE 4. Number of developing seeds in retained and aborted capsules of *Cochlospermum vitifolium*

| Tree no. | Retained fruits | | | Aborted fruits | | |
|----------|-----------------|------------------|---------|----------------|------------------------------|--------|
| | N | Mean \pm S.E. | Range | N | Mean \pm S.E. ^a | Range |
| 1 | 10 | 210.9 \pm 27.0 | 78–339 | 24 | 123.3 \pm 17.4* | 9–344 |
| 2 | 10 | 126.7 \pm 10.2 | 76–164 | 36 | 59.8 \pm 9.4** | 8–179 |
| 3 | 7 | 210.4 \pm 20.4 | 136–268 | 20 | 110.6 \pm 14.6** | 21–251 |
| 4 | 22 | 187.7 \pm 15.8 | 48–340 | 24 | 72.5 \pm 10.0** | 4–189 |

^a * $P < 0.02$; ** $P < 0.001$, by *t*-test.

TABLE 5. Number of seeds/fruit retained at different times during the flowering of *Cochlospermum vitifolium*

| Tree no. | Stage of flowering | | | | | | | |
|----------|--------------------|--------------|--------|--------|--------------|------|---------------|--------|
| | Early | | | Middle | | Late | | |
| | N | Mean | Range | N | Mean | N | Mean* | Range |
| 1 | 10 | 211.5 ± 22.6 | 81–340 | 12 | 168.0 ± 21.1 | 16 | 94.8 ± 12.1** | 46–199 |
| 2 | 11 | 118.9 ± 19.5 | 52–246 | 17 | 158.3 ± 17.5 | 17 | 108.5 ± 14.7 | 30–236 |
| 3 | 9 | 155.3 ± 18.1 | 56–224 | | No data | 15 | 186.1 ± 23.0 | 37–315 |
| 4 | 9 | 105.7 ± 10.5 | 59–151 | | No data | 21 | 74.7 ± 5.9* | 35–132 |

* $P < 0.02$; ** $P < 0.001$, *t*-test, early cf. late fruits.

Caesalpinia eriostachys (Table 7). Pedicel strength may be important in combating the loss of fruits from high winds late in the dry season (W. Haber, pers. comm.).

In *Myrospermum frutescens* and *Pterocarpus rohrii*, most infructescences had only 1–3 fruits although in these species thickening of the pedicel and peduncle following flowering was much less pronounced.

Seeds: In four of the species of Leguminosae there were striking differences between trees in the number of ovules per pod (Table 8). In spite of this variation in ovule number, there was little difference among trees in the number of seeds formed per pod because most pods were one- or few-seeded (see Table 3). However in *Cochlospermum vitifolium*, many seeds are matured in each capsule and averages varied among trees from 127 to 211 (Table 4).

In all of the Leguminosae studied here, ovules at or near the distal end of the pod were more likely to form seeds than were ovules at or near the proximal end (Fig. 3.1–3.5). This tendency is most clearly seen in the one-seeded pods of *Pterocarpus rohrii* (Fig. 3.3) where the terminal ovule was almost always the one that developed into a seed. In the other two species with one-seeded pods, *Dalbergia retusa* (Fig. 3.4) and *Myrospermum frutescens* (Fig. 3.5), the tendency for distal seed development was not so pronounced and the probability distributions are spread somewhat more, in part as a result of the more frequent occurrence of two-seeded pods. *Caesalpinia eriostachys* (Fig. 3.2) again showed a striking tendency to distal development although pods were, on average,

three-seeded. Even in *Bauhinia ungulata* (Fig. 3.1), which has many-seeded pods, seeds were more likely to be formed in the distal two-thirds than in the proximal third of the pod ($P < 0.001$, *t*-test). In all five species, pods with ovule numbers other than those for which results are presented in Fig. 3 were analysed and the same position effects were noted.

The position at which seeds develop within pods may be a result of either a greater proportion of seed abortion in proximal positions, or the possibility that ovules are seldom initiated to develop in these positions because they do not receive pollen tubes. In two species, immature pods were examined to determine the positions at which seeds were developing. Comparison of these distributions with those of mature pods (*Dalbergia retusa*, Fig. 3.6, cf. 3.4; *Myrospermum frutescens*, Fig. 3.7, cf. 3.5) shows that although many seeds are initiated in proximal positions, few of these mature. Nevertheless, it also appears that fewer seeds are initiated in proximal than distal positions (Fig. 3.6, 3.7), although earlier abortion of proximal seeds could also account for these distributions. In these two species and also in *Pterocarpus rohrii*, two, three or more seeds began to develop, and abortion of usually all but one occurred during pod development.

In *Bauhinia ungulata*, seeds that have been initiated, but aborted during development, can be identified and are found at all positions

TABLE 7. Investment in supporting structures for infructescences of *Caesalpinia eriostachys*

| Nature of peduncle and pedicel sample* | No. of infructescences sampled | Mean dry wt (mg) | % Increase cf. nonfruiting infructescence |
|--|--------------------------------|------------------|---|
| Nonfruiting ^b | 14 | 193.9 ± 21.8 | |
| 1 fruit, in lower 1/3 | 7 | 327.6 ± 23.7 | 69.0 |
| 1 fruit, in upper 1/3 | 8 | 565.5 ± 47.8 | 191.7 ^c |

* Samples included supporting structures only.

^b Sampled after flowering complete, no pods initiated

^c Increase significantly greater than for lower 1/3, *t*-test, $P < 0.01$.

TABLE 6. Abortion of pods within infructescences of *Caesalpinia eriostachys*

| Infructescence position* | No. of pods initiated | % Pods aborted |
|--------------------------|-----------------------|----------------|
| Lower 1/3 | 12 | 16.7 |
| Middle 1/3 | 21 | 23.8 |
| Upper 1/3 | 36 | 91.7 |

* Sample of 41 infructescences on two trees.

within the many-seeded mature pods (Fig. 3.1). There was no significant difference between the proportion of seeds that were aborted in the distal two-thirds and the proximal third of the pod for 21-ovuled pods, but for the next most commonly occurring pod sizes there was a significantly greater proportion of abortion in the distal two-thirds of the pod (19-ovuled pods, $N = 29$, $t = 3.39$, $P < 0.01$; 20-ovuled pods, $N = 34$, $t = 5.10$, $P < 0.001$).

Pollen quality—Distance of pollen source: Within inflorescences of *Tabebuia rosea*, approximately equal numbers of flowers were crossed with pollen from either a near or a far source (Table 9). Although a considerable amount of fruit abortion occurred, there was no significant difference between treatment in the final level of fruit set, nor were there any differences between treatments in mature fruit quality as gauged by length ($t = 0.08$, $P > 0.05$) and mature seed number ($t = 0.92$, $P > 0.05$).

Single and mixed pollen sources: Within inflorescences of *Tabebuia rosea* approximately equal numbers of flowers were crossed with pollen from a single source tree or with a mixture of pollen from three source trees (Table 10). For the two treatments there was no significant difference in the final fruit set, in the mature fruit length ($t = 1.18$, $P > 0.05$) or in the seed number ($t = 1.44$, $P > 0.05$). A similar experiment with *Caesalpinia eriostachys* again showed no differences in abortion levels for mixed and single pollen treatments (Table 10).

DISCUSSION—Abortions can be explained on the basis of both proximate mechanisms and ultimate causes (Stephenson, 1981). To a greater or lesser extent, the factors outlined below are important in both respects. Our emphasis in the discussion, however, is on the ultimate way in which these factors operate to alter flower to fruit and ovule to seed ratios over evolutionary time.

*Pollinator limitation hypothesis—*Pollinator limitation hypothesis in a general sense subsumes two distinct hypotheses. One hypothesis traces low fruit and seed set to the shortage of pollinators and the other to the inadequate transfer of compatible pollen. Only recently attempts have been made to distinguish between the abundance of pollinators and the deposition of compatible pollen (e.g., Roubik et al., 1982). Another hypothesis concerned with the uncertainty of pollination or pollen parentage (Udovic and Aker, 1981; Aker, 1982) is superficially similar to the pollinator limitation hypothesis, but is quite distinct in its

TABLE 8. Differences among selected trees in number of ovules per pod

| Species | Tree no. | % Pods with each ovule no. | | | | | | | | | Sample size |
|-----------------------|----------|----------------------------|---|----|----|----|----|----|----|---|-------------|
| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | |
| <i>C. eriostachys</i> | 1 | — | — | | 4 | 73 | 22 | 1 | | | 80 |
| | 2 | | | | | | 8 | 55 | 34 | 3 | 62 |
| <i>D. retusa</i> | 1 | | | | 59 | 41 | | | | | 80 |
| | 2 | | | | 11 | 69 | 19 | 1 | | | 80 |
| <i>M. frutescens</i> | 1 | 1 | 4 | 37 | 57 | 1 | | | | | 100 |
| | 2 | | | | | | 22 | 73 | 5 | | 41 |
| <i>P. rohrii</i> | 1 | | | | 9 | 43 | 48 | | | | 90 |
| | 2 | | | | | | 24 | 58 | 16 | 2 | 85 |

assumptions as well as its predictions. It is based on the assumption that both the quantity and the quality of pollen arriving on the stigmas is variable because of the dynamics of pollination rather than due to the shortage of pollinators or the insufficient transfer of compatible pollen. Plants therefore have evolved to bear many more flowers than can be matured into fruits. Unlike the pollinator limitation hypothesis, the uncertainty hypothesis does not predict an immediate increase in fruit or seed set with an increase in the abundance of pollinators or compatible pollen.

The stigmas of open-pollinated, aborted flowers of *Cochlospermum vitifolium* and of flowers collected from trees in *Dalbergia retusa* and *Caesalpinia eriostachys* showed pollen grains sufficient in number to fertilize all ovules. Thus, insufficient pollination is not a significant factor in flower abortion. It is virtually impossible to determine whether aborted flowers have received compatible pollen except in those self-incompatible species where the self-pollen shows a characteristic rejection response by stigma or style (de Nettancourt, 1977). The site of the incompatibility barrier in most tropical forest trees is not known; however, it is known that in many species the barrier operates in neither stigma nor style, but somewhere in the ovary either before or after fertilization (Bawa, 1979). Thus, based on our limited sampling of styles in aborted flowers, we cannot eliminate the possibility that the abortion of many 1- and 2-day-old flowers in *C. eriostachys*, *C. vitifolium*, and *D. retusa* resulted from insufficient compatible pollen reaching the stigmas.

Technically, lack of successful pollination cannot be invoked to explain the abortion of fruits. However, pistils may often enlarge to appear as young fruits without the formation of zygotes. Furthermore, fruits may often contain inviable zygotes resulting from self-pol-

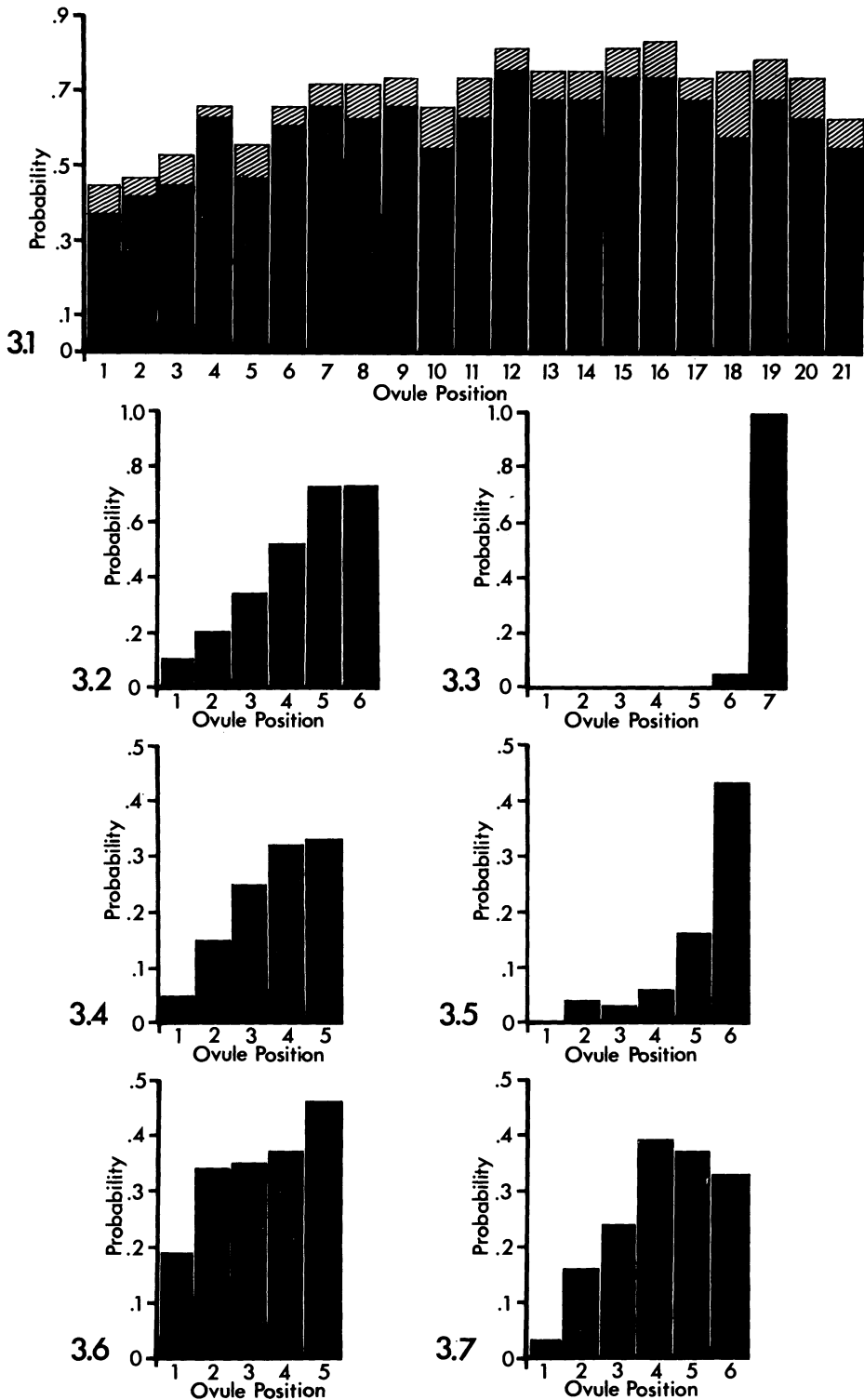


Fig. 3. Probability that a seed has developed for mature pods (3.1–3.5) or that a seed is developing for immature pods (3.6, 3.7) at different ovule positions calculated from pods of equal ovule number for each of five species of Leguminosae. Ovule positions are numbered from base (= 1) to distal end. 3.1 *Bauhinia unguolata*, 38 mature pods from five trees, shaded area represents seeds partly developed but aborted; 3.2 *Caesalpinia eriostachys*, 139 mature pods from five trees; 3.3 *Pterocarpus rohrii*, 161 mature pods from four trees; 3.4 *Dalbergia retusa*, 131 mature pods from 3 trees; 3.5 *Myrospermum frutescens*, 49 mature pods from one tree; 3.6 *D. retusa*, 114 immature pods from three trees as for 3.4; 3.7 *M. frutescens*, 67 immature pods from same tree as in 3.5.

TABLE 9. Effect of distance of pollen source on fruit set in *Tabebuia rosea*

| Distance to pollen source | No. of pollinations | | | % Fruit set |
|---------------------------|---------------------|----------------|---------|--------------------|
| | Trees | Inflorescences | Flowers | |
| <300 m | 2 | 6 | 61 | 26.23 ^a |
| 10–12 km | 2 | 6 | 63 | 39.68 ^a |

^a Pairwise comparison *t*-test for abortion rates within inflorescences, *t* = 0.77, *P* > 0.5.

lination. In *Dalbergia retusa* and *Myrospermum frutescens*, abortion of flowers and young fruits following self-pollination occurs for up to 10 and 20 days, respectively, and is probably indicative of inbreeding depression. But in *Caesalpinia eriostachys*, all self-pollinated flowers abort within 72 hr of pollination. This variation in the speed with which self-pollinated flowers are rejected is, in part, responsible for the difference in the shape of the curves between *C. eriostachys* and *M. frutescens* in Fig. 1.

Aborted fruits in *Cochlospermum vitifolium* on average contained fewer developing seeds than did the fruits retained on the trees; this difference, too, can be explained by an insufficient number of compatible pollen grains reaching the ovary. While fruit abortion resulting from either lack of adequate compatible pollination or inbreeding depression is possible in several of the tested species, we emphasize that in each species a large number of undamaged fruits containing the number of seeds normally found in mature fruits also aborted.

Insufficient pollination in species with many-seeded fruits may result in failure of many ovules to set seeds (Silander and Primack, 1978; Silander, 1978). Two observations suggest that low seed set per flower in the species we investigated was not generally a result of insufficient pollinators or compatible pollen. First, in none of the seven species did all ovules set seed when flowers were artificially cross-pollinated with pollen sufficient to fertilize all ovules. Second, an examination of several hundred open-pollinated developing fruits in *Dalbergia retusa* and *Myrospermum frutescens* revealed that by 5–10 days after fertilization, almost all ovules enlarged to 3–4 times their normal size and thereafter only one ovule continued to increase while others decreased in size and were aborted. In *Medicago sativa*, also of the Leguminosae, it has been shown that only fertilized ovules increase in size (Cooper and Brink, 1940). Cytological evidence for postfertilization ovule abortion exists for *M. sativa* and other legumes (Cooper et al., 1937; Cooper and Brink, 1940; Brink and Cooper, 1947; Sato, 1956; Linck, 1961), although pol-

TABLE 10. Effect on fruit set of mixed and single pollen sources

| Species | Pollen source | No. of pollinations | | | % Fruit set |
|--------------------------------|---------------|---------------------|----------------|---------|-------------------|
| | | Trees | Inflorescences | Flowers | |
| <i>Tabebuia rosea</i> | Single (1) | 3 | 9 | 96 | 32.6 ^a |
| | Mixed (3) | 3 | 9 | 95 | 43.2 ^a |
| <i>Caesalpinia eriostachys</i> | Single (1) | 2 | 11 | 58 | 25.9 |
| | Mixed (3) | 2 | 11 | 58 | 25.9 |

^a Pairwise comparison *t*-test for abortion rates within inflorescences, *t* = 1.01, *P* > 0.05.

len tubes, following artificial cross-pollinations, rarely enter the ovary in sufficient numbers to fertilize all ovules in *M. sativa* (Sayers and Murphy, 1966).

In short, our results show that flowers do receive enough pollen grains to fertilize all ovules, and, at least, in four species of legumes, the abortion of ovules is not due to a lack of compatible pollen.

Interestingly, on the basis of greater fruit or seed set in hand-pollinated as compared to open-pollinated flowers, many workers have argued that fruit and seed set in the species they investigated are pollinator limited (Schemske, 1977; 1980a; Schemske et al., 1978; Willson and Schemske, 1980; Bierzychudek, 1981, 1982a, b; Bertin, 1982a; Peterson et al., 1982; Snow, 1982; Gross and Werner, 1983; Rathcke, 1983; and others). Such arguments, based on the comparisons of hand- and open-pollinated flowers, however, often suffer from one or more of the following short-comings resulting from either inadequacies in experimental design or invalid assumptions.

First, unless whole plants or large flowering branches are the units of experimental pollinations the elevated fruit set in hand-pollinated flowers merely suggests that seed or fruit set is pollinator limited at the flower rather than the individual level. Open-pollinated flowers may not set as many seeds or fruits because many flowers may fail to receive an adequate amount of compatible pollen (Mirick and Quinn, 1981; Heithaus, Stasko and Anderson, 1982). Because plants may bear excess flowers to meet the vagaries of pollination, as discussed below, eventual seed and fruit set at the individual level may closely match the available resources. Indeed, embryological studies in some species have shown that although many flowers may remain unfertilized, more seeds and fruits are initiated to develop than can be eventually matured (Sweet, 1973; Morgensen, 1975; Sedgley, 1980). Our own results show continued abortion of seeds and fruits much beyond the fertilization stage.

Second, increased seed and fruit set follow-

ing hand-pollinations could also result from reallocation of resources from other parts of the plant (Janzen et al., 1980). Such increases, as Janzen et al. cautioned, could also lead to decreases in survival and future fecundity, or influence other components of fitness. Since flowers and young fruits may compete for resources (Stephenson, 1981), increased fruit set may interfere with flower production (Bawa, unpubl. observ.; T. D. Lee, pers. comm.). Thus, increased fruit set following hand-pollinations may reduce the number of flowers borne by an inflorescence, thereby decreasing the dispersal of pollen or the male component of fitness. Willson and Schemske (1980), found that increased seed set in hand-pollinated flowers also resulted in a decrease in pulp: seed dry weight ratio. Lee and Bazzaz (1982b) showed that more intensively pollinated flowers were selectively matured. This raises the possibility that flowers in the immediate neighborhood of hand-pollinated treatments may show lower fruit set than those close to open-pollinated flowers.

Third, in experiments purporting to show pollinator limitation of fruit set, the data for hand-pollinated treatments are generally derived from the pollination of a few flowers per inflorescence, but that for open-pollinated flowers are based on all flowers in an inflorescence (see e.g., Schemske, 1980b; Gross and Werner, 1982; and several studies cited by Rathcke, 1983). Such a bias in the selection of the two types of flowers makes greater fruit set in hand-pollinated flowers almost inevitable. That is why our data in Table 2, and those cited by Rathcke (1983) from our earlier papers (Bawa, 1974; Frankie, Opler and Bawa, 1976) cannot be used to support the notion of pollinator limitation of fruit set. Similarly, Bierzychudek's (1981) use of Schemske's (1980b) data in support of pollinator limitation hypothesis is questionable. Note that even if the flowers for hand- and open-pollinated treatments were randomly assigned, fruit set in open-pollinated flowers usually will not equal, much less exceed, that of hand-pollinated flowers.

Fourth, in a few cases evidence in support of pollinator limitation hypothesis has been diluted by the absence of pollinators with which the plant might have coevolved (Petersen et al., 1982) or the rarity of coevolved pollinators due to unusual circumstances (see Bertin, 1982a for populations of *Campsis radicans* at disturbed sites; Bierzychudek, 1982b).

The foregoing arguments do not imply the absence or the rarity of cases where pollinators may limit seed or fruit-set. Schemske's (1980a) evidence for pollinator limitation of fruit set

in the orchid (*Brassavola nodosa*) is largely free of the shortcomings mentioned above. The evolution of autogamy in plants is sometimes attributed to competition for, or the rarity of, pollinators (Levin, 1972; Jain, 1976). Pollinators may also limit seed or fruit set in the temperate-zone plants that flower in the early spring as pointed out by Schemske et al. (1978) and Bierzychudek (1982b), though in several such cases the difficulties inherent in the test of the pollinator limitation hypothesis, on the basis of experimental pollinations alone, remain.

As far as the pollinator uncertainty hypothesis (Udovic and Aker, 1981; Aker, 1982; see our p. 743) is concerned, we do not know what fraction of the excess flowers in each of the species we investigated are borne to counter this uncertainty. We have no data on the fluctuations in the availability of bees on an intra-seasonal or annual basis. Variability in the flower abundance of conspecifics and potential competitors can also introduce spatial and temporal heterogeneity in the receipt of compatible pollen. Many flowers may be borne to counter this heterogeneity. However we believe that a large fraction of excess flowers is produced to increase the male component of fitness and to optimize selection among pollen genotypes, as discussed below.

Resource limitation hypothesis—Resource limitation is considered to be a major factor in the abortion of fruits (Lloyd, 1980; Stephenson, 1981; Lee and Bazzaz, 1982a). Variation in fruit crop size between plants and years may be caused by spatial and temporal heterogeneity in total available resources (Janzen, 1978), and variation in seed and fruit set of flowers, inflorescences or floral branches may result from competition for limited resources on a local basis within the plant (Wyatt, 1982). Our results do show some variation between plants in fruit or seed set and our data also indicate that a certain fraction of fruits abort as a result of competition for resources within the plant. In both *Caesalpinia eriostachys* and *Myrospermum frutescens* fruits set by flowers that open first in an inflorescence have a higher probability of retention than those set by flowers that open subsequently. Additionally, in *C. eriostachys*, early blooming flowers set proportionately more fruits than late blooming ones, suggesting interference by older fruits in supply of resources to the younger ones (see also Aker, 1982). It is, however, also possible that once an optimal number of fruits has been set, more and more flowers are destined to fulfill only male function.

The importance of resource limitation as a factor in seed abortions is less clear than in fruit abortion. Competition for resources within and among ovaries of the same inflorescence may be responsible for abortion of some seeds in the multi-seeded fruits of *Bauhinia unguolata* and *Cochlospermum vitifolium*. The slight trend for early fruits to contain more seeds than late fruits (Table 5) is also consistent with the hypothesis that more resources are available early than later in the season; other interpretations based on differences in the quality and quantity of the pollen are also possible. However, in the single-seeded fruits of *Dalbergia retusa*, *Myrospermum frutescens*, and *Pterocarpus rohrii*, the pattern and frequency of abortions are so regular that they appear to be under the influence of factors other than resource limitation.

Increases in seed and fruit yield are commonly observed following the application of resources in the form of fertilizers. There is, however, no evidence that such applications also alter flower to fruit or ovule to seed ratio. Furthermore, although it is obvious that the available resources should limit fruit and seed production, it is not clear how natural selection would favor genotypes that bear excess flowers, fruits and seeds unless there is uncertainty in the availability of resources (Lee and Bazzaz, 1982a). While some uncertainty in resource availability cannot be ruled out, it is unlikely that much of the variation in fruit or seed set among species is due to differences in the certainty of available resources.

Sexual selection—According to Bateman's principle (Charnov, 1979) developed in the context of sexual selection, male reproductive success is likely to be limited by the ability of male gametes to gain access to female gametes, whereas female success is more likely to be limited by their ability to provide resources for eggs and embryos (Bateman, 1948; Williams, 1975; Janzen, 1977a). In the light of sexual selection, abortions are presumed to reflect differences in paternal and maternal reproductive strategies (Udovic, 1981). A large fraction of abscised flowers are assumed to serve only male function.

Many workers have pointed out that a substantial number of flowers in hermaphroditic species may be borne mainly to increase male reproductive success in the face of competition for males (Willson and Rathcke, 1974; Willson and Price, 1977; Janzen, 1977a; Primack, 1979; Webb, 1979a; Willson, 1979; Lloyd, 1980; Primack and Lloyd, 1980; Stephenson, 1981; Udovic, 1981; Aker, 1982; Lee and Bazzaz, 1982a; Wyatt, 1982). Such flowers are expected

to abscise soon after anthesis. Reasons for the lack of morphological differentiation between flowers that function via only pollen and those that function via both pollen and ovules have been reviewed by Lloyd (1980) and Bawa and Beach (1981). In the species examined here, the significant factor may be unpredictability in the sexual role of flowers. Whether a flower performs only male or both male and female functions may depend upon its position in time and space. In *Caesalpinia eriostachys* for example, the late-blooming flowers in the upper one-third of the inflorescence generally function only as pollen donors, but if no fruits have been set in the lower part of the inflorescence then these flowers are more likely to set fruits. Recently, detailed studies of the floral biology in some species have also revealed subtle morphological differences between flowers that set no fruits, or do so with a low probability, and flowers that set fruits with high probability (Ishihata, 1981; Bawa and Webb, 1983; Snow, 1982). Conceivably, then, a large fraction of flowers abscise after the male reproductive function is fulfilled. A larger number of flowers in male as compared to female plants (Opler and Bawa, 1978) also indicates that the number of flowers needed to disperse pollen is greater than those required for the adequate receipt of pollen.

How can sexual selection account for the abortion of fruits and seeds? Outcrossing plants have a promiscuous mating system and there is always a considerable amount of uncertainty about pollen parentage. On the other hand, maturation of seeds and fruits involves considerable expenditure in resources for the maternal parent (Darwin, 1877b). Abortion of fruits and seeds may allow the maternal parent to selectively abort genetically inferior progeny (Janzen, 1977b; Stephenson, 1981; Lee and Bazzaz, 1982a), as the maternal investment is adjusted to match available resources (Lloyd, 1980). Extra fruits, and extra ovules within flowers, permit selection among ovules that might have been fertilized at different times with pollen grains from different sources, thereby optimizing gamete competition and its attendant benefits (see Mulcahy, 1979).

Our experiments to test the effects of pollen parentage on the abortion of fruits were inconclusive (but see, Bertin, 1982b). However, non-random abortion of seeds in the species of the Leguminosae we examined (Fig. 3.1–3.5) suggests the role of paternity in the retention of the embryos. As we noted earlier, the frequency of abortion decreases from the proximal to the distal end of the ovary (see also Godley, 1979). It has been shown that the fast-

est-growing pollen tubes are the first to reach the ovules located towards the stigma (Correns, 1928; Jones, 1928; Cooper and Brink, 1940; Harding and Tucker, 1969). Embryological studies seem to indicate that embryos located towards the distal end have the highest number of cells in early developmental stages (Gableman and Williams, 1962). The fact that the speed of pollen tube growth reflects genotypic superiority of the paternal genome is indicated by superior sporophytes that result from gametes delivered from fast-growing pollen tubes (Mulcahy, 1971, 1979). In some legumes, it is the basal (proximal) ovules that have the highest probability of setting seed (Horovitz et al., 1976). In such cases pollen tubes may first reach ovules in the basal position (Jaranowski, 1962). Mulcahy (1974) has shown that the positive correlation between rate of pollen tube growth and seedling weight holds even when the influence of differences in the time of fertilization is neutralized. Thus, the competitive advantage that the embryos resulting from fastest pollen tubes might have is not entirely due to the head-start in development. If uncertainty in pollen parentage were an important factor, then one would predict that the proportion of abortions should decline with increasing certainty of pollen source. Three observations suggest that plants may indeed show such a response. First, fruit set in obligate or frequent selfers is generally close to unity (Knuth, 1906; Arroyo, 1973; Garnock-Jones, 1976). Second, proportionately fewer flowers and fruits are aborted in self-compatible than in self-incompatible species (Lloyd, 1968; Bawa, 1974; Webb, 1979b; Bawa, Webb and Tuttle, 1983; Webb and Bawa, 1983). Third, the frequency of ovule abortion is greater in outcrossing than in selfing species of *Lotus* (Bubar, 1958).

Fruit and seed abortion may thus be regarded as a mechanism to regulate the genetic quality of the offspring (Lloyd, 1980). Of course, the likelihood of an abortion may depend not only on the quality of the pollen genotype, but also the compatibility of paternal and maternal genomes (Bertin, 1982b). In addition, whether or not a particular embryo would complete development may also be contingent upon available resources so that when resources are plentiful or there are no competing embryos in the neighborhood, fruits or seeds that would have been otherwise aborted might be retained (Janzen, 1978).

Other explanations—Selection exercised by seed dispersal agents may also regulate the number of seeds per fruit (McKey, 1975; Cas-

per and Wiens, 1981; Herrera, 1981) and, thereby, the abortion of seeds. Casper and Wiens (1981) noted regular but random abortion of ovules in *Cryptantha flava*, and suggested that the abortions increase the buoyancy of the wind-dispersal nutlets. Seeds with intact fruits are dispersed by wind in *Dalbergia retusa*, *Myrospermum frutescens*, and *Pterocarpus rohrii*. In all these species the aborted immature seeds occur in that portion of the fruit which is flattened to aid in dispersal. In *Lonchocarpus pentaphyllus*, one seeded fruits have been shown to disperse over longer distances than the two to four seeded fruits (Augspurger and Hogan, 1983). Note that the hypotheses relating abortions to seed dispersal do not explain why particular seeds are aborted.

Mortality due to florivores and predispersal seed predators (Janzen, 1977b; Stephenson, 1981; Lee and Bazzaz, 1982a, b) may also select for the production of excess flowers and seeds. However, in the species we examined, florivores damaged as many as 5% of the flower buds in only *Caesalpinia eriostachys* and during the first few days when most of the fruits and seeds abort, virtually no damage from predispersal seed predators was observed in any species.

Conclusions—Our work, like that of Lloyd (1980), Lloyd et al. (1980) and Stephenson (1981), shows that the abortion of flowers, fruits and seeds is a general phenomenon in plants. We believe that much of the variation in flower to fruit and ovule to seed ratios among species is inherent and due to differences in the intensity of sexual selection rather than due to the availability of pollinators or resources as implied by many previous studies. In particular, selection for increased pollen dispersal in the face of competition for mates appears to be the major factor in the production of excess flowers, and uncertainty about the paternity of the zygotes seems to select for extra fruits and ovules. In addition, excess flowers might be selected for by the uncertainty created by florivores (Bawa and Webb, unpubl. observ.; W. A. Haber, pers. comm.) and vagaries of pollination (see also Aker, 1982) and excess fruits by uncertain survival due to pre-dispersal seed predation (see also Janzen, 1977b; Stephenson, 1981; Lee and Bazzaz, 1982a). Note that uncertainty is the prominent element of all the hypotheses, and that the concept of uncertain survival as applied to abortions of flowers, fruits and seeds has parallels in the brood reduction in birds (Lack, 1954; Ricklefs, 1965; Howe, 1976) and the adjustment of survivability to

fecundity in insects (Price, 1973) and fish (Svardson, 1949; Ware, 1975; Shine, 1978; D. Polincansky, pers. comm.).

Despite the importance of abortions in regulating the quality and quantity of the seed crop, little research has been done in this area from an evolutionary perspective. The neglect is particularly surprising because many other reproductive traits such as flowering patterns (Bawa, 1983), the design of inflorescences (Wyatt, 1982), resource allocation to male and female functions (Janzen, 1977a; Lloyd, 1979; Charlesworth and Charlesworth, 1981), pollen to ovule ratios (Cruden, 1977), the relationship between pollen units and ovule number (Kress, 1981), pollen-pistil interactions (Mulcahy, 1979 and references therein), incompatibility reactions in the ovary (Bawa, unpubl. observ.), fruiting and seeding patterns (Janzen, 1978) and infructescence and fruit architecture (Casper and Wiens, 1981) is directly linked with selection for the genetic quality of the offspring. With an increased understanding of the possible causes and consequences of abortions, studies on populations of a single species or related species that differ in the intensity of selection acting between flower anthesis and fruit maturity should be valuable in understanding the manner in which the above-mentioned reproductive traits interact and evolve as components of an integrated reproductive system to regulate the number and the genetic endowment of the offspring.

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