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Author(s): S. C. Thomas and J. V. LaFrankie

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SEX, SIZE, AND INTERYEAR VARIATION IN FLOWERING AMONG DIOECIOUS TREES OF THE MALAYAN RAIN FOREST¹

S. C. THOMAS

*Department of Organismic and Evolutionary Biology, Harvard University,
Cambridge, Massachusetts 02138 USA*

J. V. LAFRANKIE

The Arnold Arboretum, Harvard University, Cambridge, Massachusetts 02138 USA

Abstract. In dioecious plants, intersex differences in the frequency and size dependence of flowering may often be important proximate determinants of a population's flowering sex ratio. Such differences have been little investigated among Southeast Asian rain forest trees, where dioecy is perhaps best represented in the world's flora. In this study we recorded flowering activity and sex of reproductive individuals in two separate flowering seasons for ≈ 2600 trees representing three species of *Aporosa* and two species of *Baccaurea* (all Euphorbiaceae) in a primary rain forest in peninsular Malaysia. We found neither sexually mixed trees nor sex switching of trees between years. Flowering sex ratios for the species of smallest stature, *A. microstachya* and *B. parviflora*, consistently exhibited a significant degree of male bias, which was greater in years with lower overall levels of flowering in the population. Two-year cumulative sex ratios were significantly male biased in these two species and in a second relatively small-statured species of *Aporosa*. The size distributions for male trees broadly overlapped those of female trees in all species. In the smaller statured species, male trees displayed a significantly greater degree of relative size variation than did female trees, suggesting that male trees begin flowering at a smaller size, but also grow to a larger size, than do females. Also, males were significantly more likely to flower in both years than were females in the smaller species studied.

Sexual dimorphism in the frequency and size dependence of flowering has previously been explained as a result of higher energy costs of reproduction in females than in males. We suggest that this physiological constraint is most likely to play a strong role in energy-limited environments. We therefore predict that, as found in this study, male-biased sex ratios and associated patterns of sexual dimorphism may generally be most pronounced among diminutive treelets of the rain forest understory.

Key words: dioecy; Euphorbiaceae; flowering; Malaysia; sex ratio; sexual dimorphism; tropical trees.

INTRODUCTION

Dioecious plants, while generally lacking the visually apparent forms of sexual dimorphism found in many animal species, often display pronounced intersex differences in their patterns of growth and reproduction (Lloyd and Webb 1977). Specifically, male plants have often been found to have higher rates of growth, survivorship, and reproductive frequency than females (Lloyd and Webb 1977, Meagher and Antonovics 1982, Jing and Coley 1990). It has been proposed that many of these secondary sex characters are explicable in terms of the higher energy and resource costs on a per-gamete basis of female reproductive function relative to male function (Darwin 1877, Putwain and Harper 1972, Lloyd 1973, Lloyd and Webb 1977, Charnov 1982). Male-biased flowering sex ratios are a predicted result of these intersex differences, even under conditions of

equal or somewhat female-biased primary sex ratios. This is important in a genetic and conservation context because uneven sex ratios operate to reduce effective population sizes (e.g., Lande and Barrowclough 1987, Ackerly et al. 1990).

Previous studies in the New World and Australian tropics (Bawa and Opler 1975, Melampy and Howe 1977, Opler and Bawa 1978, Bullock 1982, House 1985, Armstrong and Irvine 1989, Ackerly et al. 1990) suggest that many patterns in plant secondary sex characters initially described in temperate herbaceous species also often occur in tropical trees. Much of this information is based on a single census of reproductive individuals, however. In the few cases where multiple censuses have been undertaken, flowering sex ratios have been found to vary considerably between reproductive episodes (Bullock and Bawa 1981, Bullock 1982, Bullock et al. 1983, Clark and Clark 1987). Such data are of particular importance in several respects. First, single opportunistic censuses may yield biased results, if, for instance, one sex is more conspicuous or more

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likely to flower in a "good" (and therefore more likely censused) flowering episode. Second, reproductive frequency may only be assessed by examining multiple reproductive episodes. Third, censuses of multiple reproductive bouts may be used to calculate cumulative sex ratios, which may be better estimates of secondary (adult) and possibly of primary (seedling) sex ratios.

While dioecy is generally well represented among tropical trees (Bawa 1980), available evidence suggests that it is especially prevalent in Southeast Asian forests. Estimates for percent dioecy among tree and shrub species in the New World tropics range from 16 to 24% (mean = 19%: Ruiz and Arroyo 1978, Croat 1979, Flores and Schemske 1984, Bawa et al. 1982, Bullock 1985, Ramirez and Brito 1990). Two comparable values from Southeast Asian forests are 26% at Bukit Raya, Sarawak (Ashton 1969), and 28% at Pasoh Forest Reserve, the site of the present study (recalculated from Whitmore 1972, 1973, Ng 1978, 1989, Manokaran et al. 1990, Kochummen et al. 1991). With one notable exception (Yap 1976, 1982), sex expression in dioecious tree species has been little examined in Southeast Asian forests.

In this study we describe the flowering pattern among five species of dioecious trees in a rain forest in peninsular Malaysia during two successive annual flowering episodes. We make use of a large-scale forest plot in which all trees > 1 cm in diameter were located and identified, thus ensuring a complete enumeration of each species within specified subplots. Our census of 2612 individuals in 2 yr allows us to address the following questions: (1) Is sex expression fixed in these species? (2) Do flowering sex ratios deviate from 1:1? (3) How do flowering sex ratios vary between the two years, and how do these ratios compare with cumulative 2-yr sex ratios? (4) How do the size distributions of male vs. female trees compare? And (5) how does flowering frequency vary as a function of tree size and sex?

STUDY SITE AND METHODS

Pasoh Forest Reserve (PFR) is located on the Malay Peninsula at 2°59' N latitude and 102°18' E longitude, in the interior portion of Negeri Sembilan amidst a broad expanse of flat lands and gently rolling ridges that abut the eastern side of the Main Range. The reserve covers 2650 ha, the study site lying in 650 ha of primary lowland forest surrounded by buffering areas of primary hill forest and regenerating lowland forest. Annual rainfall is \approx 2000 mm with a known range of 1700–3200 mm (Kochummen et al. 1991). Although monthly rainfall means exceed 100 mm, there is generally a 20–25 d rainless period each year in either January–March or July–August (Dale 1959, Soepadmo and Kira 1977).

The primary rain forest is classified as "Meranti-Keruing" and "Red Meranti" of the South-Central subtype (after Wyatt-Smith 1987), based on the identity

of the more conspicuous emergent species in the family Dipterocarpaceae. Typical of Malaysian forest, Euphorbiaceae comprises the greatest number of understory tree and shrub species, and also the most stems over 1 cm dbh (Kochummen et al. 1991). The forest supports an average of 510 trees per hectare over 10 cm dbh; in species it is highly diverse without ecological dominants. The five species included in this study (all Euphorbiaceae, subtribe Antidesminae) are *Aporusa microstachya* (Tul.) M.A. [PFR 3259], *A. sp. ined.* [PFR 1410], *A. symplocoides* (Hk.f.) Gage [PFR 1916], *Baccaurea parviflora* (M.A.) M.A. [PFR 1843], and *B. racemosa* (Reinw.) M.A. [PFR 1847]. Trees identified here as *A. sp. ined.* were named as *A. nigropunctata* in a previous publication (Manokaran et al. 1990), but differ from that taxon in important respects and are currently being described as a new species at present known only from Pasoh Forest Reserve (J. LaFrankie, *unpublished manuscript*). Other species were named in accordance with Whitmore (1972). All are relatively common understory trees at Pasoh. Cited voucher specimens are stored at the Forest Research Institute Malaysia (KEP).

Study plots were located within the 50-ha Large-Scale Permanent Plot at Pasoh Forest Reserve. This plot is a rectangle measuring 1000 by 500 m, divided into 20-m quadrats by theodolite survey. Every free-standing woody stem > 1 cm diameter has been tagged, measured, identified, and mapped (Manokaran et al. 1990). Stem diameter has been measured 1.3 m above the ground with a 99% repeatability of \pm 2 mm. Quality control tests indicated that errors of omission were restricted to trees of the smallest class (1 cm dbh) and amounted to no more than 1 in 500.

Prior to reproductive censuses, study areas within the 50-ha plot were chosen to include representative samples of each species. In most cases the species are quite evenly distributed across the 50-ha plot, so arbitrary subplots were chosen. The *Aporusa sp. ined.* population is largely restricted to a small hill in the middle of the plot, and for this species our study population encompasses most of the plot population. We examined all trees of a particular species within a defined region, confirmed identifications, and determined the sex of each flowering individual. In the case of large individuals (> 3 cm) of the cauliflorous species *B. parviflora*, we also noted the location of thickened woody knobs on which flowers are borne. For *Aporusa sp. ined.* the sample area was 4 ha; for *A. microstachya*, and *B. parviflora*, 8 ha (two nonadjacent 4-ha subplots); and for *A. symplocoides*, 25 ha. Two largely nonoverlapping plots were censused for *Baccaurea racemosa*: in 1989 individuals > 4 cm dbh were recorded in 25 ha; in 1990 individuals > 1 cm dbh were recorded in 6.14 ha. Analyses based on repeat observations are therefore not possible for this species.

Available phenological evidence suggests that the species studied here all flower annually and in tight

TABLE 1. Flowering and 2-yr cumulative sex ratios (male/female) for five tree species at Pasoh Forest Reserve, Malaysia. N_{tot} is the total number of trees censused, and N_{rep} the number of trees that flowered during a given year or set of years.†

| Species | N_{tot} | Area (ha) | 1989 | | 1990 | | Cumulative | |
|--------------------------------|------------------|-----------|-----------|------------------|-----------|------------------|------------|------------------|
| | | | Sex ratio | N_{rep} | Sex ratio | N_{rep} | Sex ratio | N_{rep} |
| <i>Aporusa microstachya</i> | 1177 | 8 | 3.225*** | 300 | 2.039*** | 611 | 2.072*** | 636 |
| <i>Aporusa</i> sp. ined. | 192 | 4 | 1.195 | 90 | 1.814** | 121 | 1.464* | 138 |
| <i>Aporusa symplocoides</i> | 186 | 25 | 1.727 | 30 | 1.194 | 79 | 1.216 | 82 |
| <i>Baccaurea parviflora</i> | 731 | 8 | 2.460*** | 519 | 3.182*** | 322 | 2.400*** | 562 |
| <i>Baccaurea racemosa</i> (I) | 181 | 25 | 1.028 | 95 | ... | ... | ... | ... |
| <i>Baccaurea racemosa</i> (II) | 145 | 6 | ... | ... | 1.800 | 28 | ... | ... |

* $P < .05$; ** $P < .01$; *** $P < .001$: (G tests for deviation of flowering sex ratios from 1:1).

† Samples are for all trees > 1 cm dbh, except for *Baccaurea racemosa* where population I is for all trees > 4 cm dbh in 25 ha, and population II is for a largely nonoverlapping sample of trees > 1 cm dbh in 6.14 ha.

synchrony, in conjunction with a variable forest-wide peak in flowering in late March–early April (see Yap and Chan 1990). For the two species of *Baccaurea*, Yap (1976, 1982) documented this pattern through 3 yr of monthly phenological observations. More recent work on both genera, based on monthly censuses with more frequent observations near the time of flowering, also support this conclusion (S. C. Thomas and S. K. Yap, unpublished data). The censuses here were conducted in 1989 between 25 March and 25 April and in 1990 between 20 March and 30 April. A single pass through each species' study plot was made in each year. Individuals in early bud were noted and revisited 1–2 wk later to enable accurate sex determination.

Analysis

Statistical methods employed follow Sokal and Rohlf (1981), except where indicated. Deviations of sex ratios from 1:1 were tested using standard log-likelihood methods (G test for goodness of fit, where expected values are calculated based on the null hypothesis of a sex ratio of 1:1). Differences of sex ratios among species were tested using the G test for homogeneity. Log-likelihood tests were similarly used to examine differences between sexes in the probability of flowering in one vs. two years.

In previous studies of dioecious trees the size distributions of males have often been found to completely overlap those of females, but include a larger proportion of smaller and sometimes also of larger individuals (e.g., Melampy and Howe 1977, Opler and Bawa 1978, Bullock and Bawa 1981). If size distributions of the sexes generally overlap, then comparisons of the mean sizes of males and females (e.g., Jing and Coley 1990) may not be a useful indicator of sexual size dimorphism. Previous workers have sometimes used tests of distribution identity to address this issue (e.g., the Kolmogorov–Smirnov two-sample test, as used by Opler and Bawa 1978, Bullock and Bawa 1978). However, such tests do not indicate where the distributions differ. Testing of size-category specific differences are called for (as in Clark and Clark 1987). Additionally, we note that if males are over-represented among both small and large size classes, the size fre-

quency distribution of male trees should display a greater degree of relative variation than that for female trees. The coefficient of variation (standard deviation/mean) and the Gini coefficient of inequality (a statistic based on sums of absolute deviations of all observations: for formula see Weiner and Solbrig 1984) were used here to quantify relative size variation of populations of male vs. female trees. Differences between values for these statistics were tested using a bootstrap approach, following Dixon et al. (1987).

RESULTS

Constancy of sex expression

No individuals of any species changed sex between the two years of observation. Although the observation interval in the study is small relative to the likely lifespan of the trees, the relatively large sample sizes involved add weight to our inference that these species do not change sex. In the case of *Baccaurea parviflora* constancy of sex expression is also indicated by a dramatic sexual dimorphism in vegetative morphology. Female trees bear flowers on a swollen woody bulge at the base of the trunk, whereas male trees bear flower stalks from thickened woody ridges all along the trunk to a height of > 2 m (see Whitmore 1973, Yap 1976). All flowering trees > 3 cm dbh could be correctly sexed on the basis of these characteristics, and no trees were found with both types of trunk morphology. Since the remarkable extrusive growths form by nonreversible secondary stem thickening, we infer that sexual expression must be a fixed condition for *B. parviflora*, at least in later stages of development.

Flowering and cumulative sex ratios

The number of flowering male plants exceeded the number of flowering female plants in all five species and in both seasons (Table 1). In the four species for which calculations were possible, cumulative sex ratios ranged from 1.216 to 2.406, and significantly differed from unity in *Aporusa microstachya*, *A. sp. ined.*, and *Baccaurea parviflora*. Among-species differences in cumulative sex ratios were also statistically significant (G test for homogeneity, $P < .05$). In *A. microstachya* and

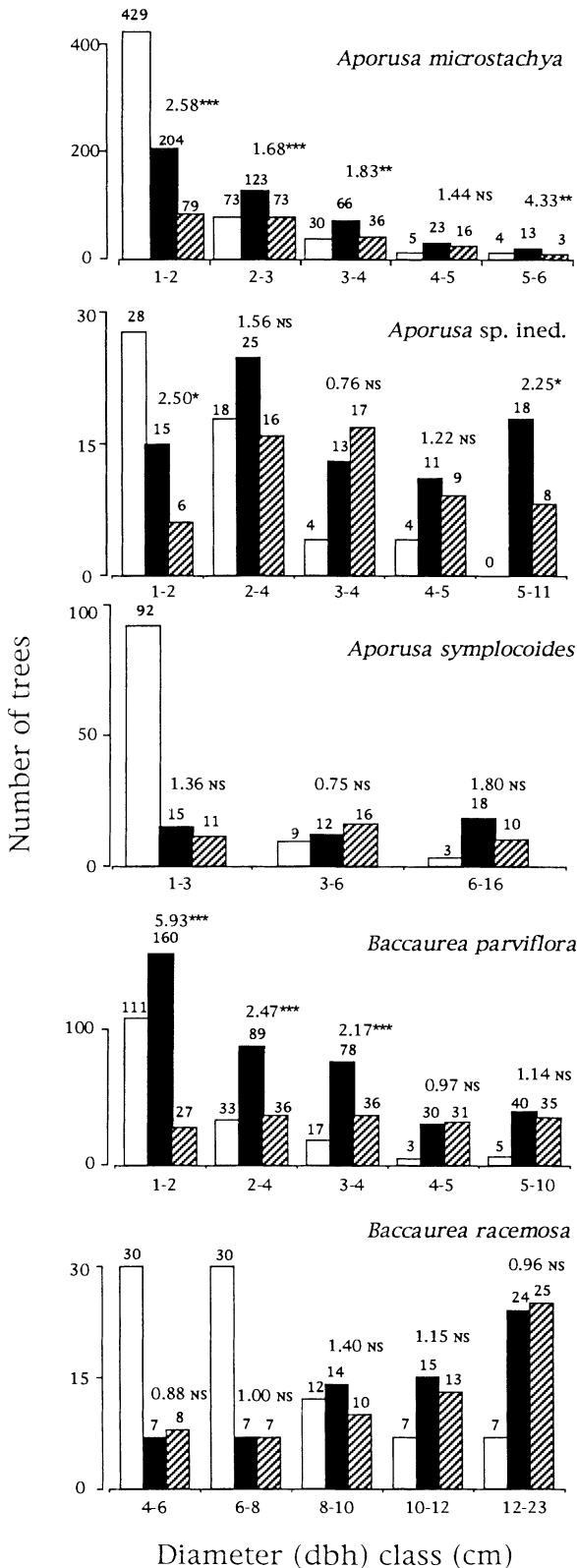


FIG. 1. Frequency distributions of stem diameter (at breast height dbh) by sex in five species of dioecious trees at Pasoh Forest Reserve, Malaysia. □ nonreproductive individuals; ■ males; ▨ females. Note that the scales vary on both axes.

B. parviflora we also noted some males <1 cm dbh flowering, so the degree of male bias may be slightly underestimated for these two species. Cumulative sex ratios were generally intermediate in value between the flowering sex ratios for both years, though closer to the lower (less male biased) value. Flowering sex ratios for each species differed between years by 23–43% (of the larger value). Between-year differences were statistically significant only in *Aporusa microstachya* and *Baccaurea parviflora* (*G* test for homogeneity, *P* < .05). In these two species, a higher degree of male bias occurred in the year with a lower overall rate of reproduction (i.e., smaller total number of trees flowering in that year: see Table 1).

Size distributions of male vs. female trees

Size distributions of male and female trees broadly overlapped in all the species investigated (Fig. 1). In *A. microstachya* and *A. sp. ined.* male trees were proportionately more common among the smallest and largest size classes. The plot of male/female ratio with respect to size is consequently V-shaped in these species. This pattern is present, though much less pronounced (and not statistically significant), in *A. symolocoides*. In *B. parviflora* males were proportionately greatly in excess in the smaller size classes, though not in the largest size class. In *B. racemosa*, the proportions of males and females were nearly equal across all size classes.

Relative size variation was greater among males than among females in *A. microstachya*, *A. sp. ined.*, and *B. parviflora* (Table 2), these being the species in which there is a marked over-representation of males in the tails of the size distribution. Results of the Kolmogorov–Smirnov two-sample test (Table 2) generally confirm the observed patterns. In the case of *A. sp. ined.* the less specific Kolmogorov–Smirnov test failed to detect a difference revealed by comparing relative size variation.

Flowering frequency as related to sex and stem diameter

Only two reproductive events were sampled. We therefore assessed reproductive frequency in terms of the probability of individuals flowering in both years vs. flowering in a single year. Repeat-flowering was highly size dependent in all three species of *Aporusa* (Table 3). Large individuals of both sexes flowered in both years far more commonly than did small individuals. In contrast, small *Baccaurea parviflora* indi-

← Sample sizes are indicated above each column. The values above each set of bars give size category specific flowering sex ratios and significance of associated *G* tests (**P* < .05; ***P* < .01; ****P* < .001). Data are for cumulative (2 yr) sex determinations, except in the case of *Baccaurea racemosa*, where the data are for population I (1989; trees > 4 cm dbh).

TABLE 2. Comparisons of relative size variation by sex, using the coefficient of variation (cv) and Gini coefficient (G). Pairwise tests for intersex differences are based on bootstrapped distributions of 500 iterations (Dixon et al. 1987). Significance of these tests denoted by asterisks: * $P < .05$; ** $P < .01$. Also included for each species are results of the Kolmogorov-Smirnov two-sample test (K-S) of size distribution identity between male and female trees.

| Species | Sex | cv | G | K-S result |
|-----------------------------|--------|-------------|-------------|-------------------|
| <i>Aporusa microstachya</i> | Male | 0.533 ** | 0.276 ** | $P < .001$ |
| | Female | 0.441 | 0.240 | |
| <i>Aporusa</i> sp. ined. | Male | 0.547 * | 0.302 * | NS ($P = .101$) |
| | Female | 0.518 | 0.263 | |
| <i>Aporusa symplocoides</i> | Male | 0.650 NS | 0.371 NS | NS ($P = .226$) |
| | Female | 0.482 | 0.268 | |
| <i>Baccaurea parviflora</i> | Male | 0.609 ** | 0.323 ** | $P < .001$ |
| | Female | 0.477 | 0.259 | |
| <i>Baccaurea racemosa</i> | Male | 0.337 NS | 0.196 NS | NS ($P = .441$) |
| | Female | 0.424 | 0.223 | |

viduals were found to flower repeatedly almost as often as did large individuals. Males were significantly more likely to flower repeatedly than were females in *Aporusa microstachya* and *Baccaurea parviflora*. The other two species show a similar, but nonsignificant trend.

DISCUSSION

Flowering sex ratios were significantly male biased during at least one flowering episode in three of the

five species studied. Additionally, all of the species in each season showed an overall tendency toward male bias. For comparative purposes, we have assembled flowering sex ratio data from previous studies of dioecious tropical trees in Central America, Amazonia, Australia, and Malaysia (Fig. 2). It has previously been emphasized that sex ratios among tropical trees vary widely (e.g., Opler and Bawa 1978). While observed sex ratios do span almost the entire logically possible

TABLE 3. Frequency with which trees flowers in both 1989 and 1990, expressed as the proportion of the total number of trees that flowered in either year (N). Significance levels for tests of intersex differences within each size category, and for heterogeneity between sexes and across size classes, are indicated by asterisks (G tests: * $P < .05$; ** $P < .01$; *** $P < .001$; NS $P > .05$).

| Species | Sex | Proportion of trees flowering in both years | | | | | G tests for heterogeneity | |
|-----------------------------|--------|---|-----------------------|---------------------|----------------------|---------------------|---------------------------|---------------------|
| | | 1-2 cm | 2-3 cm | 3-4 cm | 4-5 cm | 5+ cm | | All trees |
| <i>Aporusa microstachya</i> | Male | 0.294 (N) (204) * | 0.610 (123) *** | 0.662 (65) NS | 0.826 (23) * | 1.000 (13) ** | 0.491 (428) NS | Sex:*** Size:*** |
| | Female | 0.177 (N) (79) | 0.342 (73) | 0.472 (36) | 0.500 (16) | 0.333 (3) | 0.314 (207) | |
| <i>Aporusa</i> sp. ined. | Male | 0.067 (N) (15) NS | 0.480 (25) NS | 0.769 (13) NS | 0.700 (10) NS | 0.833 (18) NS | 0.556 (81) NS | Sex: NS Size:*** |
| | Female | 0.167 (N) (6) | 0.500 (16) | 0.471 (17) | 0.500 (8) | 0.875 (8) | 0.509 (55) | |
| <i>Aporusa symplocoides</i> | Male | 0 (N) (14) NS | 0.308 (13) NS | 0.765 (17) NS | | | 0.386 (44) NS | Sex: NS Size:*** |
| | Female | 0 (N) (4) | 0.261 (23) | 0.400 (10) | | | 0.270 (37) | |
| <i>Baccaurea parviflora</i> | Male | 0.500 (N) (158) NS | 0.523 (86) * | 0.641 (78) ** | 0.733 (30) *** | 0.600 (40) NS | 0.561 (392) NS | Sex:*** Size: NS |
| | Female | 0.308 (N) (26) | 0.314 (35) | 0.361 (36) | 0.300 (30) | 0.600 (35) | 0.383 (162) | |

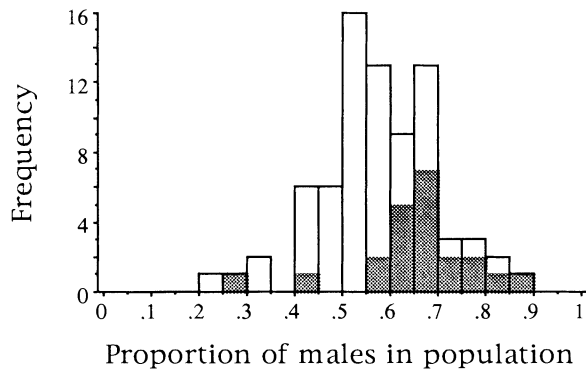


FIG. 2. Distribution of flowering sex ratios observed across studies in 55 species of dioecious tropical trees. For graphical clarity sex ratios are quantified here as the proportion of males in the flowering population. Data are from this study and Yap 1976, Opler and Bawa 1978, Bullock and Bawa 1981, Bullock et al. 1983, House 1985, Armstrong and Irvine 1989, and Ackerly et al. 1990. Multiple determinations are included for 12 species; the distribution based on a single mean value per species is very similar. Shaded bars represent sex ratios significantly different from 1:1 at $P < .05$ (G test).

range, a strong interspecific tendency toward male bias is also apparent. Male-biased flowering sex ratios were found in 72% (56/78) of the populations reviewed (or 67% [37/55] of the species). The mean flowering sex ratio for this distribution is 2.04 (median 1.31), which deviates significantly from 1:1 (t test: $P < .05$). The disproportionate representation of male-biased values is even more pronounced when only statistically significant values are considered (shaded bars in Fig. 2). In only two species have significant deviations previously been found in the direction of female bias (*Coccoloba caracasana* and *Triplaris americana*, both Polygonaceae: Opler and Bawa 1978, Melampy and Howe 1977).

Why are male-biased flowering sex ratios disproportionately common among rain forest trees? Our data and previous work suggest the importance of two proximate factors: male trees flower more frequently than do females, and male trees flower at a smaller size than do females. In two of the four repeatedly censused species males were significantly more likely to flower in both years than were females. Although only two flowering episodes were censused, the observed intersex differences were large (Table 3). Previous studies of three neotropical dioecious tree species have also documented higher reproductive frequencies in males than females [Bullock 1982: *Campsonura sprucei* (Myristicaceae), Bullock and Bawa 1981: *Jacaratia dolichaula* (Caricaceae), Bullock et al. 1983: *Guarea rhopalocarpa* (Meliaceae)]. In *A. microstachya* and *B. parviflora* we also found that the year with a higher level of flowering in the population was associated with a lower degree of male bias. This result recalls Meagher's

study of the perennial lily *Chamaelirium luteum* (Meagher 1981, Meagher and Antonovics 1982), in which females were found to flower mostly in years with high overall reproductive activity, while males flowered more regularly. Under the assumption that poor flowering is due in part to unfavorable environmental conditions, this result points to a greater sensitivity of female reproduction to temporal environmental variation. Our observations provide suggestive evidence for such a process in rain forest trees. However, 1989 and 1990 were both years in which a relatively high proportion of species and individual trees flowered at Pasoh ("general flowering" sensu Appanah 1985). It would be of great interest to compare the results here with those from a truly poor year. Yap (1976) presents some limited data from a poor flowering year for *Baccaurea parviflora*. In 1975 only 1 of his 28 monitored trees flowered. It was a male.

In two of the five species studied, males were disproportionately represented among both small and large size classes, supporting the idea that males begin flowering at a smaller size, but also grow to reach a larger size, than do females (Fig. 1). Such a pattern has been noted in several previous studies (e.g., Melampy and Howe 1977, Opler and Bawa 1978, Bullock and Bawa 1981). A common interpretation is that males, in addition to exhibiting higher growth rates, also begin flowering at smaller sizes than do females. Although mechanistic studies are lacking, one likely explanation of this lies in a lower per-gamete cost of male function acting to lower the minimal profitable reproductive investment in males relative to females (e.g., Putwain and Harper 1972, Lloyd and Webb 1977, Charnov 1982). Here we also document a consistent difference between the sexes in terms of relative size variation. Size variability, as quantified by either the coefficient of variation or the Gini coefficient of inequality, was significantly higher among males than among females in three of the five species (Table 2). Such a pattern has previously been found in certain insects (e.g., Alcock 1977, 1984), where it is related to the existence of alternative male sexual strategies. Intersex differences in size variability may also reflect differences in reproductive variability, which figures centrally in the quantification of both sexual selection (Wade and Arnold 1980, Bertin and Stephenson 1983) and effective population size (Lande and Barrowclough 1987). These issues have received little attention in previous studies of dioecious trees (but see Bullock 1982). We are not aware of any previous comparisons of size variability per se between sexual morphs in plants.

In several previous studies examining intersex differences in reproductive frequency in dioecious tropical trees, flowering sex ratios were found to be highly variable, though most often male biased, while cumulative sex ratios did not deviate significantly from 1:1 (Bullock and Bawa 1981, Bullock 1982, Bullock et

al. 1983). However, a significant male bias in a (6-yr) cumulative sex ratio was found in a primary forest population of the cycad *Zamia skinneri* (Clark and Clark 1987). In this case male bias was thought to be related to the small proportion of adult-sized plants reproducing: a secondary forest population in which a larger proportion of adult-sized individuals were sexed was not male biased. In the present study a significant degree of male bias in 2-yr cumulative sex ratios was found in three of four species examined (Table 1). In at least one species this apparently represents a true bias in the adult (secondary) sex ratio. In *Baccaurea parviflora*, 54% (397/731) of the total population was male. Even if all nonflowering individuals are assumed to be female, the secondary sex ratio still deviates significantly from 1:1 ($P < .05$; G test).

While secondary sex ratios are of interest in some respects, the genetic and demographic consequences of skewed sex ratios are a function of the population that actually reproduces. In the simplest case of nonoverlapping generations, Lande and Barrowclough (1987) present a formula for effective population size in which the "effective number of males" and "effective number of females" are calculated as a function of the mean and variance in lifetime reproductive output within each sex. If most reproduction takes place infrequently in good flowering years, then the flowering sex ratios observed in these years may be of greatest relevance in such calculations. The general problem of effective population size in populations with overlapping generations and temporally varying sex ratios has not been treated (R. Lande, *personal communication*). Beyond inbreeding effects, skewed sex ratios may have important consequences that are strictly demographic. Chance mortality of a male tree will affect the probability of local population extinction only to the extent that female reproduction is pollen limited. In contrast, mortality of a female tree has a more direct and inevitable effect on the population's future demographic potential. Male-biased sex ratios in dioecious tropical trees are of particular concern in this regard. From a conservation perspective such demographic effects may be of greater relevance than genetic effects, and have received much less attention, theoretically or empirically.

Although overall flowering sex ratios were numerically male biased in every case, there were also significant differences among the species studied here. Part of this variation may be accounted for as a function of tree species stature. Intersex differences in the energy costs of reproduction have often been held responsible for sexual dimorphism in reproductive frequency and size dependence, and these differences appear to generally result in male-biased sex ratios. If so, we should expect male-biased sex ratios and associated patterns of sexual dimorphism to be more pronounced among species that inhabit strongly energy-limited environ-

ments. Tropical rainforests, like all closed-canopy systems, are characterized by a strong vertical gradient in light availability (see Aoki et al. 1975 for Pasoh Forest). In the present study, the two smallest species in each genus are *Aporosa microstachya* and *Baccaurea parviflora*. These species showed the largest degree of sexual dimorphism in flowering frequency (Table 3), and both also exhibited a strong prevalence of male trees in small size categories. Concomitantly, these species were those for which larger intersex differences in size variability were found. Overall, these species also exhibited the greatest degree of male bias in both flowering and cumulative sex ratios (Table 1). A similar pattern is apparent in a previous comparative study in Costa Rica by Opler and Bawa (1978). Of the seven species for which size data are presented, the two smallest statured species (*Randia spinosa* and *R. subcordata*) have the greatest degree of male bias, and also show the most pronounced intersex differences in population size structure. Thus there is suggestive evidence for a general trend between species' stature and flowering sex ratios among rain forest trees. Data from additional species are required and problems resolved in the quantification of species "size" (e.g., given skewed diameter at breast height distributions of unequal sample size) in order to more rigorously test this hypothesis.

While species stature may explain some of the variation observed in sex ratios of tropical trees, other factors are clearly also important. Proximate determinants of secondary sex ratios in dioecious plants may include genetic effects of primary sex determination, gametic selection, and apomixis, as well as ecologically determined differences between the sexes in mortality, growth, maturation, and reproductive periodicity (e.g., Opler and Bawa 1978). The observed variability of sex ratios in tropical trees is a product of changes in these factors resulting from population genetic forces (selection, drift, etc.), with constraints imposed by physiology and phylogeny. Further comparative studies of dioecious species might be usefully aimed at teasing apart those population attributes that are general to all dioecious plants from those that are characteristic of higher taxa such as families and genera, and those that reflect habitat- or species-specific traits.

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