

SEX RATIO IN THE TROPICAL TREE *TRIPLARIS*
AMERICANA (POLYGONACEAE)

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Fisher (1958) argued that parental expenditure on each sex should be equal in dioecious species because the genetic contribution of one sex is equivalent to that of the other. This outcome should result in population sex ratios of unity at the termination of parental care unless individuals of one sex are more expensive to rear than those of the other sex. The theory cannot predict sex ratios after the termination of parental care. Numerous attempts have been made to revise or reformulate Fisher's hypothesis (e.g. Shaw, 1958; Kolman, 1960; Bodmer and Edwards, 1960; Leigh, 1970), but the prediction of a sex ratio of unity still holds except in the special cases of gametic drive, extreme inbreeding (Hamilton, 1967) or differential expenditure on individual offspring of different sexes.

Triplaris americana is a dioecious tree that exhibits a female biased sex ratio among flowering individuals. This species occupies riparian habitats in Central America and flowers during the dry season in January and February. It is an early successional species which occupies recently disturbed areas. The tree is insect pollinated, and both sexes produce nectar (Bawa and Opler, 1975). Males produce many more flowers per inflorescence than do females (Opler and Bawa, 1977). The winged seeds are wind-dispersed.

The objective of our study was to determine if sex ratio variation between

habitats and relationships between tree size and inflorescence production could suggest reasons for the female bias in *Triplaris*. Our results lead to an evolutionary rationale for the skewed sex ratio in this species.

METHODS

Measurements and observations of flowering *Triplaris americana* were made in lowland semideciduous forest from 13 to 17 February 1974. The forest, described by Holdridge et al. (1971) and Frankie et al. (1975), is located on Comelco Property, 5 km northwest of Bagaces, Guanacaste Province, Costa Rica.

Four study sites of variable area and tree density were chosen (Table 1). Sites 1 through 3 were located along the Rio Tempisque in areas subject to tidal fluctuations and wet season flooding. Sites 1 and 2 were within 100 m of each other; site 3 was approximately 1 km upstream. Site 4 was situated several km north of the Rio Tempisque along a small stream that was not subject to tidal surges. The forest at site 4 appeared to be more mature than at the other sites as many trees exceeded 30 m in height. Here *Triplaris* was a subcanopy species. At the other sites, *Triplaris* was a dominant member of the canopy. All four study sites were subject to the grazing and trampling of domestic cattle.

The following data were recorded for flowering *Triplaris*: (1) circumference at breast height (CBH); (2) number of inflorescences; and (3) sex. CBH was converted to cross-sectional area (CSA) to allow addition of measurements for multiple trunk individuals. Inflorescences

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TABLE 1. Sex ratios of *Triplaris americana* at individual study sites and cumulated over all study sites. Deviations from unity in the ratios were tested by chi square (1 df).

Site	Area (ha)	Females	Males	χ^2
1	2.6	61	41	3.92*
2	1.6	58	42	2.56
3	1.1	56	44	1.44
4	6.4	47	12	20.76**
Overall	11.7	222	139	19.08**

* $.01 < P < .05$.
 ** $P < .001$.

were counted from the ground with the aid of a hand counter. Sexes are easily distinguished; female inflorescences appear as large clusters of spikes, while male inflorescences consist of distinct spikes. We mapped the positions of individual *Triplaris* at sites 1, 2, and 3. Time did not permit mapping at site 4. The CBH of trees of all species greater than 15 cm CBH and located within circular quadrats of 5 m radius were also measured. The quadrats were spaced at 20 m intervals along transects through each study site.

RESULTS

The sex ratio of *Triplaris* pooled from all study sites is significantly skewed in favor of females. Sex ratios at individual sites show a consistent female bias, but only sites 1 and 4 have significant biases (Table 1).

TABLE 2. Nearest neighbor analysis. Chi square analyses of 2×2 contingency tables comparing the number of male and female nearest neighbors (NN) for male and female base trees indicate no significant segregation of the sexes.

Site	# of base trees	Male NN	Female NN	χ^2
1	♂ 41	20	21	0.43
	♀ 61	24.5	36.5	
2	♂ 42	22.5	20.5	1.07
	♀ 58	22.5	35.5	
3	♂ 44	20	24	0.47
	♀ 56	20.5	35.5	

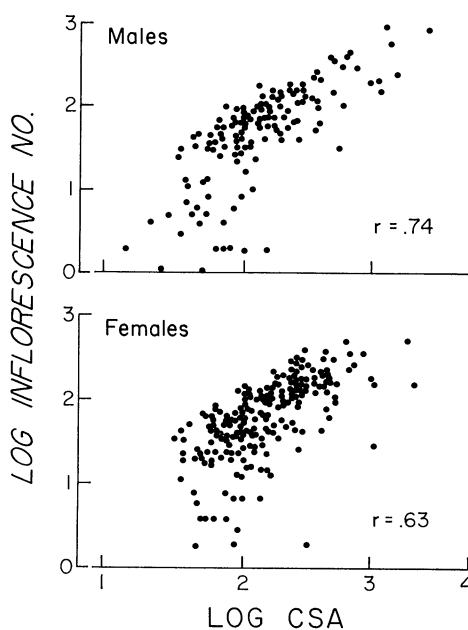


FIG. 1. Inflorescence number plotted against cross-sectional area (CSA) for male and female *Triplaris americana*. Log transformations lessen deviations from normality. r = product-moment correlation coefficient.

We tested for segregation of male and female trees using Pielou's (1961) contingency table technique of comparing nearest neighbor frequencies (Table 2). When determining the frequency of male and female nearest neighbors, we encountered several cases (no more than six per study site) in which a male and female were equidistant from a base tree. In these cases, 0.5 was added to both male and female nearest neighbor totals. Creating a third category for ties does not qualitatively change the chi square values in Table 2. The chi square analyses indicate no significant segregation of the sexes. There is also no significant difference between the distances to nearest neighbors from males ($\bar{x} = 4.45 \text{ m} \pm 0.32$) and from females ($\bar{x} = 4.60 \text{ m} \pm 0.28$).

Plots of inflorescence number versus CSA indicate differences between males and females (Fig. 1). The male plot

TABLE 3. Mean size and inflorescence number for *Triplaris americana* from all study sites. F ratios (male variance/female variance) were computed from log transformed data and are significant at the .05 level. SE = standard error.

	Males	Females	F ratio
Mean cross-sectional area per tree (± 2 SE)	306.9 ± 81.8	301.9 ± 51.2	1.37
Mean # of inflorescences per tree (± 2 SE)	91.0 ± 19.0	91.9 ± 11.7	1.34
<i>n</i>	139	222	

extends over a greater range of CSA and inflorescence number than does the female plot. This is reflected in greater male variance for both these parameters. The means for CSA and inflorescence number do not differ between sexes (Table 3), but at the low end of the CSA range a clear male-female difference arises. Nineteen percent of the males have CSA less than 74 cm²; only 10% of the females fall in this size class. This difference in CSA distribution is significant ($\chi^2 = 5.15$, $P < .025$, 1 *df*). The correlation between CSA and inflorescence number is higher for males than for females ($Z = 1.96$, $P = .05$, where $Z_{.05} = t_{.05, \infty}$ as described by Zar (1974) p. 241). This difference is even more pronounced among trees greater than 400 cm² CSA, with males showing a significant Spearman rank correlation ($r_s = .49$, $P < .02$, $n = 25$) and females showing no significant correlation ($r_s = .21$, $P < .2$, $n = 45$).

In an attempt to assess vegetative reproduction in *Triplaris*, we excavated to a depth of about 30 cm the roots of 6 pairs of adjacent trees, two male pairs and four

female pairs. Only one of the male pairs, separated by about 1 m, was connected.

The mean CSA for trees of all species varied among sites. Site 3 had the smallest mean, which was significantly less than the means for sites 1 and 4 (Table 4).

DISCUSSION

If Fisher's theory is correct, the sex ratios biased in favor of female *Triplaris* could be attributed to either (1) differential sex-related vegetative reproduction, (2) agamospermy or (3) differential mortality by sex. In certain dioecious, perennial herbs, male vegetative reproduction is greater than that of females. In the case of *Rumex acetosella*, Putwain and Harper (1972) showed that females allocate more biomass to sexual reproduction than males, leaving females less for vegetative reproduction. Lloyd (1973) showed that for some dioecious Umbelliferae greater vegetative reproduction by males was correlated with a preponderance of male plants. Presumably female mortality was higher than male mortality due to reduced female size that made females more vulnerable to mortality factors.

Our analysis of nearest neighbors, which corroborates that of Bawa and Opler (1977), shows no significant segregation of the sexes that might suggest cloning. Our excavations of tree roots though limited also revealed no indications of extensive rhizome or root sucker growth.

We did not test for agamospermy in *Triplaris*. However, agamospermy is a relatively rare occurrence among angiosperms (Stebbins, 1941; Fryxell, 1957).

TABLE 4. Mean cross-sectional area for trees of all species at each study site (see text for description of sampling technique). Site 3 has a significantly smaller mean than site 1 ($P < .02$, t-test) and site 4 ($P < .05$, t-test). SE = standard error.

	Site 1	Site 2	Site 3	Site 4
Mean cross-sectional area per tree (± 2 SE)	454.6 ± 176.1	333.4 ± 174.9	228.4 ± 64.1	461.4 ± 196.1
<i>n</i> (trees)	74	75	50	121
<i>n</i> (quadrats)	13	12	7	21

Considering the selective pressures for outcrossing in tropical trees (Bawa, 1974; Levin, 1975), agamospermy is unlikely in *Triplaris*.

Differential mortality is more likely to be responsible for the skewed sex ratio we observed. Energy allocated to reproduction reduces the energy available for growth and maintenance (Gadgil and Solbrig, 1972), and intrinsic differences may lead males and females to follow different strategies in timing and quantity of reproductive effort i.e. total energy expended on reproduction (Trivers, 1972). Seeds individually cost more than pollen grains. Therefore, it is reasonable to suppose that females reproduce only when sufficient reserves provided by a large photosynthetic surface are available to insure that their seeds are adequately provisioned for successful germination and growth. Males, on the other hand, may produce pollen in large quantities even if their reproductive effort is lower than that necessary for females to produce viable seeds. Thus one might predict that intrinsic patterns of parental investment (Trivers, 1972) would lead to male reproduction at an earlier age than would be feasible for effective female reproduction (i.e. production of enough seeds that successful dispersal is likely in a statistical sense).

It is also likely that environmental conditions can produce different selective pressures on males and females. For example, in a wind-dispersed tree such as *Triplaris*, female reproductive effort may be constrained by the necessity to attain a height at which seeds can be caught and carried by the wind. As a species most common in early successional communities, *Triplaris* must also deliver its seeds to sites with sufficient light. Dispersal to heavily shaded sites is unlikely to represent effective dispersal. Older and larger females may be surrounded by shaded habitat due to the effects of succession. These trees may allocate a relatively large amount of energy to maintenance in order to maximize their longevity and chances of

dispersing seeds to nearby areas that will undergo disturbance as a result of fire, floods, storms, etc.

Identical successional conditions could affect male reproduction quite differently. Because males do not incur the costs of provisioning seeds, selection should favor early reproduction among males relative to females. Evidence is available for early male maturation in a variety of dioecious perennials (e.g. Clark and Orton, 1967; Opler and Bawa, 1977). Of course, repeated reproduction is likely to produce higher probabilities of mortality at early ages among males than among females. However, early reproduction can enhance the individual's reproductive value (Cole, 1954). Furthermore, males that escape early mortality are not as reproductively constrained by successional change (e.g. increased shade) because males do not disperse seeds. Large males may produce enormous amounts of pollen and stand a good chance of fertilizing many females, some of which may be adjacent to good seed germination sites.

Our results bear out expectations derived from the above theory rather well. The significantly greater proportion of male than female *Triplaris* under 74 cm² CSA shows that males breed at smaller sizes than females. Greater constraint on reproduction in large females relative to large males is illustrated by the lack of correlation between CSA and inflorescence number in females greater than 400 cm² CSA and the presence of a significant correlation in males of the same size class. It appears that low parental investment in pollen may be associated with opportunistic male breeding strategies.

Gamete selection is another possible explanation for the skewed sex ratio in *Triplaris*. The type of gamete selection normally associated with plants is not encompassed by Fisher's theory of sex ratio (Lloyd, 1974; but see Hamilton, 1967). It occurs when males are the heterogametic sex, and female-determining pollen outcompetes male-determining pol-

len for unfertilized ovules. Correns (1928) and Mulcahy (1967) suggested on the basis of progeny sex ratios that female-determining pollen in *Silene alba* grows faster and reaches ovules before male pollen. However, Mulcahy's data are not convincing (Lloyd, 1974). Correns (1928) also claimed that gamete selection occurs in *Rumex acetosa*, but Putwain and Harper (1972) found that the sex ratios of progeny from female biased *R. acetosa* populations in Wales did not deviate significantly from unity. Smith (1963) was able to sex *Rumex hastatulus* seedlings grown from seeds collected in natural populations. He found a predominance of females among the seedlings and suggested that gamete selection may be occurring because of the male Y chromosome's "genetic inefficiency." However, Zarzycki and Rychlewski (1972), who were able to sex the seedlings of *Rumex acetosa* and *R. thyrsiflorus*, found no predominance of females among seedlings although females were predominant among mature plants in natural populations. They concluded that differential mortality is important in determining the sex ratios of these *Rumex* species. Production of males under the gamete selection system requires that very small amounts of pollen be deposited on stigmas. If the flower has many ovules per ovary, there may not be enough female pollen to fertilize all the ovules, leaving some to be fertilized by male pollen. However, in insect pollinated species that have few ovules per ovary, such as those of the Polygonaceae, the amount of pollen deposited on a stigma by even a single pollinator visit could be large enough to allow female pollen to fertilize all the ovules (Lloyd, 1974). Under these circumstances, it would be difficult for males to attain a frequency of 40% or better, which is what we observed for *Triplaris* at 3 of our 4 study sites. Another serious problem with gamete selection, as it is applied to plants, is that it does not allow for the production of predominantly male progeny in the event that pollen should become a limiting

factor in seed production. The selective advantage of such an inflexible system is obscure.

If reproduction produces a risk of mortality (e.g. Trivers, 1972), early reproduction among males may lead to differential mortality in favor of females. The risk of mortality should be highest where resources are most limited. Thus one might expect to find the greatest preponderance of females in habitats where resources are least available to *Triplaris*. It is noteworthy that the most pronounced female bias occurs at site 4, where *Triplaris* is a subcanopy tree. Due to its subcanopy status, *Triplaris* may be subject to considerable interspecific competition for light. Small reproductive males succumb to such competitive stress sooner than females which postpone reproduction and consequently have more energy available for growth and maintenance under competitive conditions. It is also noteworthy that the sex ratio which most closely approximates unity occurs at site 3, where the mean CSA for all tree species is smallest. The small tree size suggests recent colonization of the area by trees. Colonizers should experience a minimum of competition and, in the case of a dioecious tree, the sex ratio should be unity. We suggest that intermediate biases in favor of females at sites 1 and 2 reflect the intermediate successional status of those stands.

SUMMARY

The sex ratio of *Triplaris americana*, a tropical dioecious tree, is skewed in favor of females. Site to site variation in the sex ratio suggests that the basis for this female bias is sex-dependent mortality, which reflects different strategies used by males and females to maximize their reproductive success.

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