

Population sex ratios and spatial distribution of *Ocotea tenera* (Lauraceae) trees in a tropical forest

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Summary

1. *Ocotea tenera* (Lauraceae) is a dioecious understorey tree which occurs in the lower montane forests of Monteverde, Costa Rica. In a natural population of *O. tenera* trees whose ages were estimated to range from 14 to 30 years old, staminate trees slightly outnumbered pistillate trees but the sex ratio was not significantly different from 1:1. Staminate and pistillate trees were non-randomly distributed with respect to each other. The probability that a tree's nearest neighbour was of the opposite sex was much higher than expected by chance.

2. Males were also more common in two experimental plots, one established in 1981 and the other in 1984, although only one of the plots showed a significantly male-biased sex ratio. Spatial distributions of staminate and pistillate trees in both experimental plots were indistinguishable from random.

3. Individual trees in both the natural population and experimental plots monitored over a 10-year period occasionally switched in different years from producing almost exclusively staminate to almost exclusively pistillate flowers, and vice versa. Sex ratios within plots changed over time because of variable sexual expression between years rather than differential mortality. Once trees were established, mortality was low.

4. It is suggested that non-random spatial distributions in older *O. tenera* trees in the natural population may be caused by labile sexual expression modified by the presence of neighbouring trees.

Key-words: Costa Rica, dioecy, sex expression, sex change

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Introduction

The spatial distribution of staminate and pistillate trees in certain dioecious plant species is non-random. The most commonly documented non-random spatial distribution is segregation of the sexes, with staminate ('male') and pistillate ('female') plants tending to occur in distinct microhabitats which differ in the availability of resources such as light or water (Bierzychudek & Eckhart 1988; Iglesias & Bell 1989). The existence of such spatial patterns is important to document because they suggest one route by which dioecy itself can evolve or be reinforced (Bawa 1980). Dioecy may be favoured in a spatially heterogeneous environment if plants that allocate more reproductive effort to female function have higher fitness in some microhabitats, while those that allocate more to male function have higher fitness in other microhabitats (Freeman, Harper & Charnov 1980). Sex-specific

differences in dispersal or survival, as well as environmental sex determination or 'sex choice', have been proposed as the mechanisms that cause spatial segregation of the sexes (Bierzychudek & Eckhart 1988).

In rare cases the opposite pattern, negative spatial association of the sexes, has been found, with neighbouring plants tending to be of unlike sex (e.g. *Osyris quadripartita*: Herrera 1988; *Silene alba*: Iglesias & Bell 1989, but see Lovett Doust, O'Brien & Lovett Doust 1987). The mechanisms that produce such patterns have not yet been demonstrated, but one possible selective advantage of having an individual of the opposite sex as a nearest neighbour is that pollination and fruit set may be increased (Iglesias & Bell 1989).

In the few dioecious tropical tree species whose spatial distributions have been determined, population sex ratios are generally 1:1 and individuals seem to be distributed randomly with respect to

sex (Bawa & Opler 1977; Melampy & Howe 1977; Bullock 1982; Ackerly, Rankin-de-Merona & Rodrigues 1990). The majority of such studies are based on a single census. Consequently, little or nothing is known about the ages of trees, their growth rates, reproductive history, variability in sexual expression, or differential mortality of males and females. The shortage of basic biological information has led to disagreements about the mechanisms responsible for observed sex ratios and the spatial distribution of the sexes, even in the same species (e.g. Melampy & Howe 1977; Opler & Bawa 1978). Here we present data on the population sex ratio and spatial relationships of staminate and pistillate individuals of a neotropical tree, *Ocotea tenera* Mez and J.D. Smith ex Mez (Lauraceae), based on a 10-year experimental study in Costa Rica.

Species, study site and methods

Ocotea tenera is common understorey tree of the lower montane forests of Monteverde, Costa Rica (10°18'N, 84°48'W; 1300–1500 m a.s.l.). Endemic to Costa Rica, it occurs on the Atlantic slope of the Cordillera de Tilarán at 900–1200 m a.s.l. (W. Haber, personal communication), and infrequently in the Atlantic lowlands as low as 50 m a.s.l. (Burger van der Werff 1990). On the Pacific slope it ranges down to 1000 m. Trees occur at highest densities under broken canopies and in small light gaps, although they can survive for years as saplings in dense shade. During the middle part of the wet season (August–October), *O. tenera* produces 1–2-mm-diameter flowers which are visited and apparently pollinated by small insects, primarily flies, bees and wasps. Trees mature their 4–8-g, single-seeded fruits between late January and March, with some ripe fruits remaining on the tree until the beginning of the rainy season (May). The major seed dispersers at Monteverde are five species of large fruit-eating birds (Wheelwright *et al.* 1984; Wheelwright 1985, 1992).

About 20% of the species in the genus *Ocotea* in Costa Rica are dioecious (7 of 35 species; Burger & van der Werff 1990). Conflicting reports of dioecy exist for *Ocotea tenera* (Allen 1945; Burger & van der Werff 1990), although in the field pistillate and staminate individuals are easily distinguished. Pistillate flowers are about 30% smaller than staminate flowers. They have nine vestigial stamens which never dehisce and whose thecae lack pollen grains. Stigmas are always exposed in pistillate flowers because the three central stamens are reflexed outwards. The number of flowers on a pistillate tree at any one time is about 17% of that found on a staminate tree of the same size. Staminate flowers have a single pistil, but the style is short and the stigmatic surface reduced and completely blocked by the inwardly reflexed central stamens. At anther

dehiscence, conspicuous thecal flaps remain on the stamen revealing deep thecae. Staminate and pistillate individuals mature at approximately the same age and size (see Results).

Vegetative reproduction by rhizomes, runners or stolons does not occur in *O. tenera*; occasionally one to three sprouts may grow from the base of trees damaged by herbivores or broken by branch falls (7.8% of 64 trees). Therefore, the interpretation of spatial patterns in this species is not confounded by the problem of distinguishing genetic individuals (Lloyd 1973; Iglesias & Bell 1989). The study site and general reproductive biology of *O. tenera* are detailed in Wheelwright (1985, 1986), where it was referred to by the name of a similar congener, *O. bernouliana* (*sic*) (see also Wheelwright 1992). Voucher specimens for this study are deposited at the University of Chicago Field Museum and the Missouri Botanical Garden.

The sex ratio and spatial distribution of male and female *O. tenera* trees were determined in two experimental plots (hereafter referred to as plots 1 and 2) and in a natural population. Trees in the natural population were reproductively mature in 1981, when this study began. At the time they represented all *O. tenera* trees found within a 16-km² study area set up to monitor the phenology of 22 other species of Lauraceae (Wheelwright 1985, 1986). Like most tropical trees, *O. tenera* cannot be aged by annual growth rings, but judging from their sexual maturity, growth rate and size in comparison with trees of known age in the experimental plots, trees in the natural population were estimated to be 14–30 years old in 1990. Plot 1 was established in 1981 as part of a study of the heritability of reproductive traits in *O. tenera* (Wheelwright 1992). Ninety-three seedlings of 11 maternal genotypes, grown from the seeds of mature fruits collected haphazardly from trees, were planted in sibling pairs at 1.5-m intervals around two contiguous sides of a 20-m × 20-m gap surrounded by forest, which, except for the presence of long-neglected and overgrown banana plants in the centre, was not an unusual habitat for the species. Thirty-two of the original plants survived, 28 of which were reproductively mature in 1990. Plot 2 was established in 1984, when seedlings of eight maternal genotypes were planted at 2.5-m intervals in a modified Latin-square design in the middle of a different 20-m × 20-m patch with scattered bananas and overstorey trees several kilometres from plot 1. Of 92 seedlings planted, 32 (as in plot 1) survived and all but three had begun to flower by 1990. One year after planting, 87% of the seedlings in plot 2 were still alive; 6 months later only 39% still survived, after which there was little mortality. Almost all mortality in both plots occurred when the seedlings were 0.1–0.2 m tall, at least 3 years before they began to produce flowers. More than 90% of the mortality was due to branches

falling from overstorey trees, overgrowth by herbaceous competitors, or careless machetes during the attempt to clear herbaceous competitors. Two seedlings were destroyed by leafcutter ants (*Atta* or *Acromyrmex* spp.). The growth rate and fruit production of most plants in the natural population and all experimental plants were monitored every February between 1981 and 1990 (1984–1990 for plot 2).

Sexual expression was determined for most plants by direct inspection of 10 or more flowers from different branches on a single date. To verify that 10 flowers was an adequate sample, 100 flowers per plant were examined in a subset of 10 plants and found to be entirely staminate or pistillate. Both staminate and pistillate flowers were found on the same plant in the same year in only two cases, despite hundreds of censuses. If a tree produced exclusively pistillate flowers, it was designated a pistillate or female tree; a tree with exclusively or predominately staminate flowers was designated a staminate or male tree. Sexual expression for a particular tree within a given year was later checked by looking for evidence of fruit production. Pistillate trees invariably produced fruits, whereas staminate trees rarely did. Staminate trees, which bore as many as 100 000 flowers, sometimes set 1–5 fruits year⁻¹, but always far fewer than a female of the same size (Fig. 1). Fruits on trees designated as staminate presumably developed from a few scattered pistillate (or perfect) flowers. The fruits of staminate trees were similar in size to normal fruits and contained a viable seed. Unlike some other species in the Lauraceae, which reproduce irregularly between years (Wheelwright 1986), all sexually mature individuals of *O. tenera* reproduced each year.

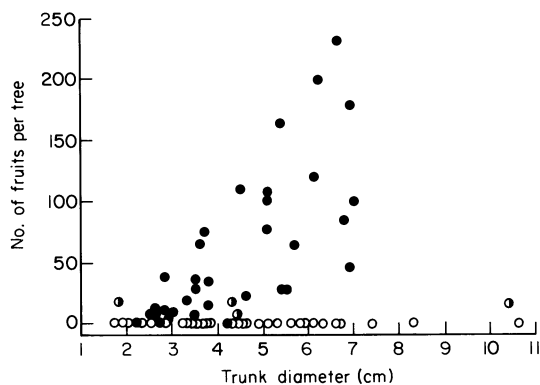


Fig. 1. The relationship between trunk diameter (at 55 cm above ground) and fruit production in *Ocotea tenera* trees from Monteverde, Costa Rica ($n = 79$) whose sex had been determined by inspecting flowers before fruits were counted. Data from 1983, 1986 and 1987 were combined. Presence or absence of fruits is a reliable indicator of sexual expression for most trees: above a diameter of about 2.5 cm, most trees with pistillate flowers (●) set fruit, whereas trees with staminate flowers (○) set few or no fruits. Some trees have both pistillate and staminate flowers (◐).

Thus, abundant fruit production was a reliable indicator that a plant had produced pistillate flowers. The absence or scarcity of fruits was likewise an indicator of staminate flower production, and we used fruit production to designate sexual expression in years when it was not possible to examine flowers (cf. Bullock 1982; see Wheelwright 1992 for further details). Nonetheless, the possibility remains that some plants with pistillate flowers did not set fruits or subsequently aborted developing fruits and thus might have been erroneously scored as staminate individuals. Therefore, we conducted separate analyses for plants sexed by flower and those sexed by the presence or absence of fruits and found similar results to those presented below.

Distances between neighbouring *O. tenera* trees were measured and their relative positions mapped in February 1989 (natural population and plot 1) and February 1990 (plot 2). Distances to the nearest male and female were measured for a randomly selected subset of 23 male and 23 female trees in the natural population and for all trees in the experimental plots. For trees <15 m apart, we used a tape measure; longer distances were estimated by pacing.

To test for spatial segregation of sexes, a coefficient of segregation, S (Pielou 1977) was calculated, where

$$S = \frac{1 - \left(\frac{\text{observed number of unlike nearest-neighbour pairs}}{\text{expected number of unlike nearest-neighbour pairs}} \right)}{\left(\frac{\text{observed number of unlike nearest-neighbour pairs}}{\text{expected number of unlike nearest-neighbour pairs}} \right)}$$

S values can vary between -1 and $+1$, with values greater than 0 indicating positive spatial association of sex (males and females occupying distinct sites) and values less than 0 indicating negative spatial association of sex. Fisher's exact tests were used to test for non-random distribution of sexes in nearest neighbour pairs (contingency-table analysis of the frequency of male–male, male–female and female–female pairs).

The demonstration of significant spatial association of the sexes using such contingency tests should be interpreted with caution because of the probable non-independence of nearest-neighbour observations (Meagher & Burdick 1980). Therefore, a Monte Carlo simulation was performed to determine the exact probability of finding the observed fraction of nearest-neighbour pairs that were of unlike sex under the null hypothesis of random spatial association of the sexes. The spatial distribution of trees and population sex ratio in the natural population were kept fixed, but in each simulation, the sex of each tree was randomly assigned, and the observed fraction of unlike nearest-neighbour pairs recalculated. This procedure was repeated 1000 times.

Results

Males outnumbered females in the natural population and in both experimental plots although the skew in sex ratio was significant only in the 6-year-old experimental plot, plot 2 (χ^2 test: $P < 0.01$; Table 1). The small shift in sex ratio in plot 1 between the time when trees were 6 and 9 years old was caused by three males reaching reproductive maturity and two plants changing their sexual expression from male to female between 1987 and 1990. Males would significantly outnumber females in plot 2 even if the few remaining pre-reproductive individuals all proved to be females. There was no difference in the mean size of seeds that produced female vs. male plants in the experimental plots (Mann-Whitney U -test: $P > 0.40$).

In neither experimental plot was the skewed sex ratio due to males maturing faster than females (Opler & Bawa 1978). Staminate trees begin to reproduce at an average of 4.6 ± 0.8 years of age (mean \pm SD) and a trunk diameter (measured at a height of 55 cm) of 2.8 ± 0.9 cm ($n = 37$); pistillate trees first begin to flower at 4.7 ± 1.1 years of age and a trunk diameter of 2.3 ± 0.8 cm ($n = 18$; ANOVA: $P > 0.05$). Nor was the predominance of males in plots 1 and 2 apparently due to higher mortality of females, because mortality factors were random (e.g. tree falls) and occurred years before the seedlings would have reached reproductive maturity (see Methods).

In the natural population, where all individuals were at least 14 years old in 1990, the sex ratio did

not differ significantly from 1:1 (Table 1). Annual mortality was quite low in adult trees ($< 2\%$), and, although sample sizes were small, there was no indication that it was sex-specific.

At one scale, 6-year-old trees in Plot 2 appeared to be positively associated with respect to sex, with males predominately clustered on one side of the plot and females on the other (Fig. 2). However, a nearest-neighbour analysis demonstrated that the spatial pattern was indistinguishable from random, and yielded a slightly negative value of S (Table 1). In plot 1, when trees were 9 years old (and also in 1987, when they were 6 years old and comparable in

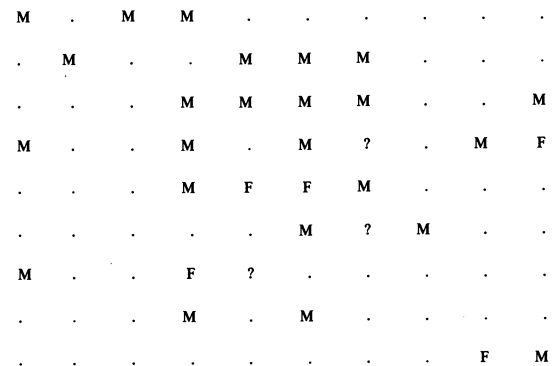


Fig. 2. Map of 6-year-old *Ocotea tenera* trees (plot 2) planted as seedlings in 1984 in an apparently homogeneous habitat in Monteverde, Costa Rica. M = males, F = female, ? = pre-reproductive. Periods indicate plants that did not survive to reproductive maturity. Distance between neighbouring trees is about 2.5 m.

Table 1. Sex ratios (proportion of males in the population) and nearest-neighbour gender combinations as determined in 1990 at Monteverde, Costa Rica, in three *Ocotea tenera* populations differing in age. Plots 1 and 2 were established as seedlings in 1981 and 1984, respectively. Sex ratios and nearest-neighbour frequencies were determined in Plot 1 in 1990 as well as in 1987, when trees were comparable in age with those of Plot 2 in 1990. n = sample size. S is a segregation ratio (Pielou 1977; see Methods). Deviations from a 1:1 sex ratio were tested with χ^2 tests; non-random association of the sexes were tested with Fisher's exact tests and G -tests

	Nearest neighbours		n	Frequency of males	S	P
	Male	Female				
Plot 1						
9-year-old			28	0.57	-0.09	0.95
males	12	4				
females	10	2				
6-year-old			25	0.60	-0.07	c. 1.0
males	11	4				
females	8	2				
Plot 2						
6-year-old			29	0.83*	-0.07	c. 1.0
males	17	7				
females	4	1				
Natural						
14-30-year-old			84	0.54	-0.38	<0.001
males	20	25				
females	32	7				

* $P < 0.05$

Table 2. Mean (\pm SD) nearest-neighbour distances between *Ocotea tenera* individuals of both sexes established as seedlings in 1981 (plot 1) and 1984 (plot 2) and in a natural population at Monteverde, Costa Rica

	Distance (m) to nearest	
	male	female
Plot 1		
Male ($n = 15$)	0.6 \pm 0.8	1.4 \pm 1.1
Female ($n = 10$)	0.8 \pm 0.6	* 1.6 \pm 1.1
Plot 2		
Male ($n = 24$)	3.5 \pm 2.1	** 7.3 \pm 4.7
Female ($n = 5$)	2.8 \pm 0.4	7.7 \pm 5.8
Natural		
Male ($n = 45$)	8.2 \pm 10.4	* 5.7 \pm 5.6
Female ($n = 39$)	5.7 \pm 6.4	* 9.8 \pm 13.5

* $P < 0.05$, ** $P < 0.01$ (paired t -test).

age to trees in plot 2 in 1990), males tended to have males as their nearest neighbours, but not more often than expected from the male-biased population sex ratio (Table 1). The average distances between males and their nearest male and female neighbours were not significant in plot 1 ($P = 0.07$) but were in plot 2 ($P < 0.01$); the distances between females and their nearest male and female neighbours were significant in plot 1 ($P = 0.02$) but not in plot 2 ($P = 0.12$) (see Table 2). In the natural population both these differences were significant ($P < 0.05$) (Table 2).

In contrast to the random spatial distributions of male and female trees in the two experimental plots, there was a clear negative spatial association of the sexes in the natural population, with trees tending to have an individual of the opposite sex as their nearest neighbour more frequently than expected by chance (Table 1). The Monte Carlo simulation confirmed the improbability of such spatial association of the sexes occurring by chance, with fewer than 4 of 1000 simulations resulting in a frequency of unlike nearest neighbors as high as that observed ($P = 0.003$).

Sexual expression (based on the presence or absence of fruits) varied between years for a few trees. For example, in the relatively young experimental population, 11.5% of 61 reproductively mature trees produced staminate flowers in some years and pistillate flowers in other years (an additional 3.3% are suspected of variable sexual expression). In the natural population, 41.1% of 95 trees are believed, on the basis of the presence or absence of fruits, to have produced staminate and pistillate flowers in different years (N.T. Wheelwright, unpublished data). We excluded these trees and repeated the analysis including only trees observed in 8 or more different years, during which they either produced fruits in at least 7 of 8 years (considered pistillate trees, $n = 24$) or never produced more than one or

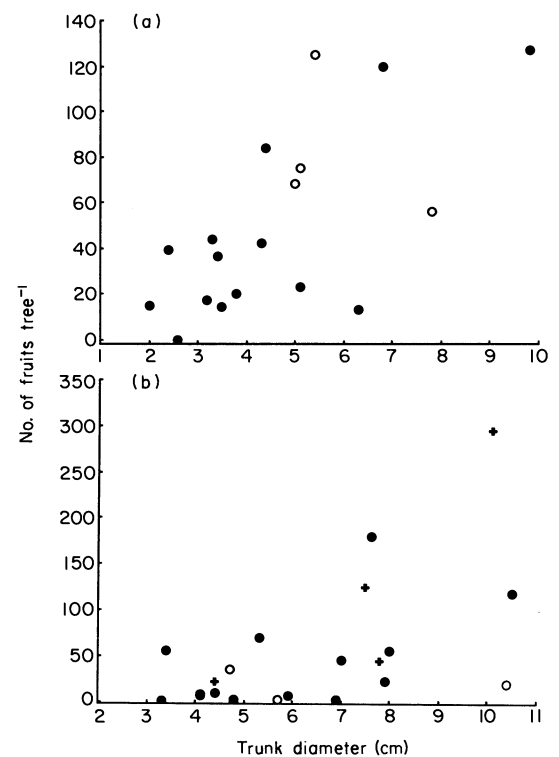


Fig. 3. The relationship between trunk diameter (at 55 cm above ground) and fruit production in *Ocotea tenera* trees in Monteverde, Costa Rica, in 1990 as a function of distance to the nearest male: $< 1\text{ m}$ (\circ), $1\text{--}10\text{ m}$ (\bullet), $> 10\text{ m}$ ($+$). (a) 6- and 9-year-old trees in experimental plots 1 and 2; (b) 14–30-year-old trees in a more widely spaced natural population.

two fruits (staminate trees, $n = 43$). A nearest-neighbour analysis showed the same negative spatial association of the sexes as that reported in Table 1 (Fisher's exact test, $P = 0.004$).

In neither the experimental plots nor the natural population was there an obvious effect of distance from the nearest male on a female's fecundity (Fig. 3).

Discussion

The sex ratio of mature *Ocotea tenera* trees in a natural population was about 1:1, as reported for several other dioecious neotropical tree species (Opler & Bawa 1978; Bullock & Bawa 1981; Bullock 1982; Bullock, Beach & Bawa 1982). The one temperate-zone member of the Lauraceae previously studied, *Lindera benzoin*, also has a 1:1 sex ratio (Primack 1985). Balanced sex ratios seem typical of other temperate-zone trees (e.g. Herrera 1988). To the extent that sex ratios in tropical trees deviate from 1:1, they are most commonly male-biased (Opler & Bawa 1978; Ackerly, Rankin-de-Merona & Rodrigues 1990). In this study, the sex ratio was decidedly male-biased in one experimental plot of young *O. tenera* trees. The male-biased sex ratio in 6-year-old trees is difficult to reconcile with

theoretical expectations of a 1:1 sex ratio, assuming the per-offspring parental investment in males and females is equivalent at the time of independence (e.g. Trivers 1972). Seeds that produced female plants were no different in mass, length or diameter (presumed indicators of investment) than those that produced males in the experimental plots. Higher mortality of female seedlings is unlikely to have produced the skew in sex ratio because of the stochastic sources of mortality and the early age at which mortality occurred (cf. Freeman & MacArthur 1984). Moreover, male and female trees are evidently equally susceptible to herbivory (N.T. Wheelwright *et al.*, unpublished data; see Methods).

If population sex ratios become increasingly less skewed as a cohort ages — as indicated by the significantly male-biased sex ratio in the youngest experimental cohort, plot 2, the trend towards equal sex ratio with age in plot 1, and the 1:1 sex ratio in the natural population — the most probable explanations are age- or size-specific sexual expression or sex-switching. Evidence comes from documented cases of young trees switching from male to female with age. Primack (1985) found that sex-switching occurred but was uncommon in *Lindera benzoin* (<2% of plants changed sex over a 4-year period), and that gynodioecy occurred at a low level in the population. However, he was unable to follow a young cohort as it aged; his focal trees were well-established reproductively mature plants by the time he began his observations. Moreover, the distinct sexual dimorphism of *L. benzoin* flowers suggests that changes in sex expression in that species may require rather large morphological adjustments. In contrast, morphological differences between staminate and pistillate flowers are relatively subtle in *O. tenera*, as illustrated by Burger and van der Werff's (1990) classification of the species as hermaphroditic, which they based partly on specimens from Monteverde. Given the morphological similarity of staminate and pistillate flowers in *O. tenera*, sex-switching may also not involve major physiological adjustments, predisposing individuals to be able to switch sex. We intend to continue to monitor sexual expression in the natural population and experimental plots, and we predict that the male-biased sex ratio in the 6-year-old experimental plot will gradually approach 1:1 as the trees age.

In one of the few studies demonstrating skewed sex ratios in tropical trees, Melampy & Howe (1977) and Opler & Bawa (1978) demonstrated a female-biased sex ratio in flowering individuals of *Triplaris americana* (Polygonaceae). However, they were unable to determine the age at which females began to outnumber males or identify the mechanism responsible for the observed sex ratio (differential mortality or differential reproductive maturity). Facultative sexual expression (sex choice) was not considered and the ages of trees were unknown.

In this study, *Ocotea tenera* exhibited an unusual pattern of spatial association of the sexes (Primack 1985; Bierzychudek & Eckhart 1988; Iglesias & Bell 1989). Male and female trees in a natural population were non-randomly distributed with respect to each other. The frequency of nearest-neighbour pairs of unlike sex was much higher than expected by chance. Such a spatial distribution could be adaptive if female fecundity were pollen-limited and/or if male fertilization success were limited by distance to the nearest female (Levin 1974; Bawa & Opler 1978). We found little evidence for a negative effect of distance on fruit set, however. In the experimental plots, where trees were randomly distributed with respect to the sex of their nearest neighbour, distance-dependent fecundity should not have been expected because no female was located more than 3.3 m from the nearest male, and no male more than 17.7 m from the nearest female. Moreover, the small, generalist insects that pollinate *O. tenera* may be effective pollinators over relatively long distances. Yet even in the natural population, where distances between individuals were much greater, there was little support for the notion that relatively isolated females show disproportionately low fruit set.

There are several admittedly controversial mechanisms that could produce negative spatial association of the sexes. Such non-random patterns could arise through sex choice in a spatially heterogeneous environment as shown in other species (Freeman, Harper & Charnov 1980). The 'environment' should include not only the physical habitat but also an individual plant's social environment, i.e. the sexual expression and proximity of other members of the population. There are two requirements for adaptive sex choice under such circumstances: first, the ability of a tree to determine the sex of its neighbours, and secondly the ability to alter its own (or its neighbour's) sexual expression. With regard to the second requirement, variable sexual expression within individuals has been documented in this study and in numerous other species (Freeman, Harper & Charnov 1980), although manipulating the sexual expression of neighbouring plants has not. As for the first requirement, little is known about the reproductive physiology of non-commercial tropical trees, so we can only guess about possible mechanisms for determining the sex of one's nearest neighbour. Potentially, the density of sex-specific volatile chemicals, produced by sexually dimorphic flowers or by fruits, could give information about the sex of a plant's nearest neighbour, assuming the plant could detect them. Such chemical communication and adaptive responses have been proposed for plants under attack by herbivores (e.g. Rhoades 1983; Baldwin, Sims & Kean 1990, but see Fowler & Lawton 1985) and for sexual expression influenced by antheridogen production in fern gametophytes (Voeller 1971; D. Lloyd, personal communication).

An indirect but more likely possibility is that the sexual identity of nearest neighbours or the relative isolation from trees of the opposite sex could possibly be determined through monitoring pollen deposition, pollen removal, or fruit set. For example, heavy conspecific, but genetically non-identical, pollen loads deposited on a male's flowers, if detectable, could serve as a cue to change to producing female flowers. So, conceivably, could low pollen removal rates. In the case of females, natural selection might favour trees with a heritable tendency to switch to producing staminate flowers after failing to set fruits despite producing pistillate flowers; low fruit set could be gauged by a surplus of stored reserves at the end of the reproductive season. Granted, such scenarios are highly speculative and we advance them with the intent of stimulating future research in the area. They also assume that being located near a tree of the opposite sex improves reproductive success, a plausible notion but one not demonstrated by this study.

Although the diminutive flowers of *O. tenera* do not lend themselves easily to manipulative study, experimental approaches will be required to reveal the mechanisms that cause a male-biased primary sex ratio in *O. tenera* and to explain the negative spatial association of the sexes in older trees. In 1991 one of us (NTW) initiated such experiments by planting *O. tenera* seedlings near established, isolated male and female trees in an effort to determine whether or not a sapling's social environment can influence its sexual expression as an adult, either through adaptive sex choice or manipulation by its larger neighbour. The results of the experiment, which will take 5–10 years, should shed light on the observations presented in this study.

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