

# 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

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

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-km<sup>2</sup> 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

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

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

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<sup>-1</sup>, 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.

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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

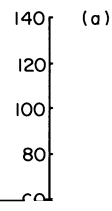
**Results**

Males outnumbered females in the natural population and in both experimental plots although the

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.

**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



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

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

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

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