

MATING SYSTEM DYNAMICS OF *OCOTEA TENERA* (LAURACEAE), A GYNODIOECIOUS TROPICAL TREE¹

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Progeny arrays of *Ocotea tenera* (Lauraceae), a gynodioecious tree endemic to Costa Rica, were electrophoretically surveyed for allozyme variation to estimate the outcrossing rate in the overall population and to test for differences in outcrossing rates between hermaphroditic and female trees. Multilocus outcrossing rate estimates across 3 yr indicated *O. tenera* predominantly outcrosses. However, significant heterogeneity in single-locus outcrossing rates was found among loci. Two loci (*Fe1*, *Fe2*) gave high outcrossing estimates, and a third locus (*Gdh*) gave much lower outcrossing estimates. Heterogeneity in *Gdh* pollen allele frequencies, consanguineous matings, and selection against homozygous zygote genotypes at the *Fe1* and *Fe2* loci are factors contributing to the discrepancy in outcrossing rate estimates among loci. There were no differences in the mating systems of hermaphroditic and female trees, which suggests that factors beyond prevention of self-fertilization may have also promoted the evolution of gynodioecy in *O. tenera*.

Key words: Costa Rica; gynodioecy; Lauraceae; mating system; Monteverde; *Ocotea*; outcrossing, tropical tree.

Mating system studies of tree species have furthered our understanding of how population genetic architecture is produced by provided insights on patterns of gamete union, gene flow, and genetic substructuring of plant populations (Hamrick, Linhart, and Mitton, 1979; O'Malley et al., 1988; Hamrick and Godt, 1990; Adams, 1992; Mitton, 1992). However, most studies to date have focused on temperate species, particularly conifers, and tropical species have only recently begun to be studied in detail (Hamrick, Godt, and Sherman-Broyles, 1992).

Many temperate tree species have large population sizes and high densities, which, when combined with wind pollination and high outcrossing rates, promote large neighborhood size and extensive gene flow. This combination of demographic and reproductive traits typically results in high genetic diversity within populations and little genetic differentiation among populations (Hamrick, Mitton, and Linhart, 1981; Brown, Barrett, and Moran, 1985; Hamrick, Godt, and Sherman-Broyles, 1992). Tropical forest trees grow under dramatically different demographic conditions than their temperate counterparts. Tropical trees often have lower population densities than temperate species (Hubbell and Foster, 1986). Population and neighborhood sizes, however, are not easily delimited. For example, tropical trees depend on animals for pollination to a greater extent than temperate species. Thus, neighborhood size and magnitude of gene flow will depend on the specific behaviors and distances traveled by particular pollinators (Bawa et al., 1985; Hamrick, 1987; Renner and Feil, 1993; Bawa, 1994).

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In addition to demographic and ecological differences, the gender systems typically found in tree species also differ between temperate and tropical forests. Hermaphroditism and monoecy, which allow an individual tree to function as both a pollen and a seed parent, tend to be common in temperate forests. In contrast, tropical forests tend to have a greater frequency of dioecious and gynodioecious species in which individual plants specialize gender function as a male or female (Yampolsky and Yampolsky, 1922; Bawa, 1980). Many traits of tropical trees have been hypothesized to be important in promoting gender specialization, but the relative importance and evolutionary relationships among traits are still not completely clear (Muenchow, 1987; Thomson and Brunet, 1990). Prevention of self-fertilization is one factor proposed to be particularly important to evolve and maintain dioecy and gynodioecy (Bawa and Opler, 1975; Charlesworth and Charlesworth, 1978). However, because there are other means of circumventing the costs of selfing without sacrificing the benefits of retaining male and female function within an individual (e.g., monoecy, herkogamy, and self-incompatibility), investigators have speculated that other factors also contribute to the evolution and maintenance of dioecious and subdioecious gender systems (Bawa and Beach, 1981; Gouyon and Couvet, 1987; Delph, 1990).

This study reports an investigation of the mating system of *Ocotea tenera*, a gynodioecious tropical tree. Gynodioecy is a relatively rare gender syndrome characterized by individual plants producing only hermaphroditic or only pistillate flowers. Population genetic analyses of *O. tenera* have shown that clumped seed dispersal by birds causes relatively high genetic relatedness among individuals within populations ($R = 0.179$) and significant genetic differentiation among subpopulations ($G_{ST} = 0.13$) (Gibson, 1995; Gibson and Wheelwright, 1995). In this study, we measured mating system dynamics of *O. tenera* to (1) measure the frequency of outcross fertilizations, (2) compare genetic attributes of the seed pool and the adult population, and (3) compare the mating

system of female and hermaphroditic trees. Comparison of females and hermaphrodites may shed light on the importance of the prevention of selfing in *O. tenera* gender system evolution.

MATERIALS AND METHODS

Study species and study site—*Ocotea tenera* Mez & J. D. Smith ex Mez (Lauraceae) is an endemic tree species of Costa Rica found on the Pacific slope of the Cordillera de Tilarán between 900 and 1200 m above sea level (asl) (Burger and van der Werff, 1990). The study population grows throughout the lower montane forest surrounding Monteverde, Costa Rica (10°18'N, 84°48'W, 1300–1500 m asl). Trees occur in a natural population of *O. tenera*, which consists of trees identified within Wheelwright's 16-km² survey area, or in two experimental plots established in 1981 and 1984 (see Wheelwright and Bruneau, 1992 and Gibson, 1995 for detailed site descriptions).

O. tenera flowers from July through December (Wheelwright, 1985). Flowers are visited by several insect species, including flies, bees, and wasps, but a majority of pollinators are small bees in the genus *Trigona* (Meliponinae). Bees visit several flowers on a branch or inflorescence in no obvious pattern. Visits last from 5 to 30 s, and then bees fly to another branch on the same tree, to a neighboring *O. tenera* tree, or to other flowering species (Gibson, 1995).

Although previously reported to be dioecious (Burger and van der Werff, 1990), recent investigations of floral development and anatomy showed *O. tenera* is gynodioecious (Gibson, 1995). Female trees produce male-sterile flowers and tend to have high yearly fruit production. Hermaphrodites (labeled "males" in the past) produce flowers containing viable pollen and a functional gynoecium. Hermaphroditic trees produce few or no fruits. While dioecy reflects the functional basis of gender in *O. tenera* (sensu Lloyd, 1980), for the present study, subtle differences in gender expression and mating system behavior of individual trees must be taken into account. For example, female trees contribute gametes only via ovules. Hermaphroditic (as opposed to male) trees are unusual because they contribute gametes predominantly through pollen, but they also make a minor gamete contribution via ovules. Floral dimorphism may cause mating system differences between gender classes such that hermaphroditic trees experience a combination of self and outcross fertilization, while high-fruited trees only outcross.

Tissue collection and electrophoresis—Fruits were collected from hermaphroditic and female trees in February of 1991, 1992, and 1993 and taken to the University of Colorado at Boulder. Since we could not sample the same number of progeny from females and hermaphrodites due to differences in fruit production, we attempted to sample similar proportions of the available seed crops from female and hermaphroditic trees. Seeds were planted in potting soil and germinated on a mist bench until seedling establishment. Leaf tissue was collected, processed, and analyzed according to standard techniques for starch gel electrophoresis (Mitton et al., 1979; Soltis et al., 1983). Samples were surveyed for three loci resolved in previous isozyme surveys of the adult *O. tenera* trees (Gibson and Wheelwright, 1995): fluorescent esterase (*Fe1*, *Fe2*) and glutamate dehydrogenase (*Gdh*). Details of isozyme electrophoresis and allele frequencies for these loci in the Monteverde *O. tenera* population are given in Gibson (1995).

Data analysis—Multilocus (t_m) and single-locus (t_s) outcrossing rates were estimated using Ritland and Jain's (1981) mixed-mating system model (updated by Ritland [1990] as a series of FORTRAN programs). Standard errors of single-locus estimates were calculated by the computer program, but standard errors were not available for all multilocus estimates due to statistical difficulties caused by singularity of the information matrix (Ritland, 1990). Because variance in the multilocus outcrossing estimate is due to variation among the individual loci, the

TABLE 1. Multilocus and single-locus outcrossing rate estimates (t) for 1991, 1992, and 1993. N_f and N_s indicate the sample size of families and seeds, respectively.

Year Locus	N_f	N_s	t	(SE)
	15	45	1.123	(0.12)
	15	45	1.950*	(0.29)
	15	46	0.157*	(0.13)
	15	46	0.926	(0.13)
	15	74	1.151	(0.12)
	15	74	0.832	(0.14)
	15	56	0.588*	(0.14)
	15	74	0.965	(0.11)
	18	173	0.965	(0.09)
	18	213	0.953	(0.10)
	18	189	0.640*	(0.07)
	18	213	0.846*	(0.04)

* Outcrossing rate significantly different from 1.00 based on comparison of 95% confidence intervals.

standard errors of t_m values were calculated via Tukey's jackknife (Sokal and Rohlf, 1981). This method provides a parametric procedure for evaluation of unique statistics, such as t , for which distributional properties have not been resolved (Gibson and Hamrick, 1991). Single and multilocus outcrossing rates were estimated for the entire population and separate groups of individual trees (see below). Outcrossing rates were also separately estimated for pooled groups of females and hermaphrodites. Ninety-five percent confidence intervals were calculated for each outcrossing estimate to compare t values with 1.00 and for pairwise comparisons of t values among different groups of trees.

RESULTS

Most individuals were scored for all three loci. Only individuals scored for at least two loci were included in the analysis. Multilocus outcrossing rates were high in all 3 yr (Table 1). In 1993, the multilocus outcrossing rate was significantly less than 1.00 but still showed greater outcrossing than selfing. Similar to multilocus outcrossing rates, single-locus outcrossing rates for *Fe1* and *Fe2* were consistently high (Table 1). In contrast, t_s values calculated from *Gdh* data were lower than all other estimates and significantly lower than 1.00 (Table 1).

Individual mating events must affect all loci equally (i.e., an individual cannot be outcrossed at some loci and selfed at others). Differences in multilocus and single-locus (*Fe1*, *Fe2*) estimates of t and *Gdh* estimates of t suggested assumptions of the mixed-mating model were violated. We targeted the *Gdh* locus for further analysis since it deviated most from other outcrossing estimates.

We divided seedlings into two groups based upon whether the maternal tree was homozygous (homozygous families) or heterozygous (heterozygous families) at *Gdh*. Single and multilocus outcrossing rates were estimated for pooled groups of homozygous and heterozygous families. If there was strong inbreeding or high selfing within homozygous families, then multilocus outcrossing rates for homozygous families should be lower than outcrossing rates in heterozygous families.

Multilocus outcrossing rates for homozygous (t_{hom}) and

TABLE 2. Multilocus and single-locus outcrossing rate estimates for trees heterozygous (t_{het}) or homozygous (t_{hom}) at the *Gdh* locus. N_f and N_s are sample sizes of families and seeds, respectively.

Year	Locus	t_{het}	(SE)	N_f	N_s	t_{hom}	(SE)	N_f	N_s
1991									
	<i>Fe1</i>	1.131	NA	7	24	1.194	(0.32)	8	21
	<i>Fe2</i>	1.999	(0.72)	7	24	1.417	(0.46)	8	21
	<i>Gdh</i>	0.164	NA	7	25	0.214 ^a	(0.12)	8	21
	Multi.	1.232	(0.14)	7	25	0.949	(0.35)	8	21
1992									
	<i>Fe1</i>	0.924	(0.21)	8	48	1.023	(0.36)	7	26
	<i>Fe2</i>	0.742	(0.16)	8	48	1.231	NA	7	26
	<i>Gdh</i>	0.610 ^a	(0.20)	8	40	0.431 ^a	(0.15)	7	16
	Multi.	0.890 ^a	(0.03)	8	48	1.021	(0.04)	7	26
1993									
	<i>Fe1</i>	0.594 ^{ab}	(0.17)	5	82	1.300 ^b	(0.18)	13	91
	<i>Fe2</i>	0.981	(0.16)	5	99	0.950	(0.12)	13	114
	<i>Gdh</i>	0.729 ^a	(0.13)	5	89	0.590 ^a	(0.08)	13	100
	Multi.	0.793 ^a	(0.02)	5	99	0.875 ^a	(0.03)	13	114

^a Outcrossing rate significantly different from 1.00, $P < 0.05$.

^b Outcrossing rates significantly differ between families, $P < 0.05$.

heterozygous (t_{het}) families were also high in all 3 yr, but some were significantly less than 1.00 (Table 2). Multilocus t_{het} values were not significantly different from t_{hom} values calculated in all 3 yr. Single-locus estimates within heterozygous and homozygous families showed no consistent patterns except that outcrossing rates calculated from *Fe* data were high, while estimates from *Gdh* data tended to be lower (Table 2).

Hermaphroditic and female trees were both predominantly outcrossed in most years (Table 3). In 1993, the multilocus t_f was high as in previous years, but the multilocus t_h was significantly lower than t_f and 1.00 (Table 3). As in other analyses, single-locus outcrossing rate estimates were high for both *Fe* loci and low for *Gdh*.

DISCUSSION

The data indicate *O. tenera* has a predominantly outcrossing mating system. These results were consistent with other studies of tropical tree mating systems (Bawa, 1974; Murawski et al., 1990; Loveless, 1992; Murawski, Dayanandan, and Bawa, 1994). A majority of tropical tree mating system analyses have been conducted on species of low elevations in Central America. Our study is the first of which we are aware to investigate the mating system dynamics of a high elevation, Central American tree species. Murawski and Bawa (1994) and Murawski, Dayanandan, and Bawa (1994) studied the mating system of *Stemnocarpus* spp. (Dipterocarpaceae) in high-elevation forests in Sri Lanka, and also detected high outcrossing.

Outcrossing rates were extremely heterogeneous among loci. Multilocus and single-locus (*Fe1* and *Fe2*) outcrossing estimates were high in all groups of individuals, but single-locus estimates from *Gdh* data were considerably lower. The discrepancies among loci indicate mating system "behavior" is different for the *Gdh* locus as compared to other loci. That is, assumptions of the mixed-mating model are clearly violated for the *Gdh* locus. Similar differences in outcrossing estimates among

TABLE 3. Multilocus and single-locus outcrossing rate estimates for maternal trees that were female (t_f) or hermaphroditic (t_h). N_f and N_s indicate the sample size of families and seeds, respectively.

Year	Locus	t_f	(SE)	N_f	N_s	t_h	(SE)	N_f	N_s
		0.909	(0.26)	8	27	1.999	NA	7	18
		1.642	NA	8	27	1.074	NA	7	18
		0.083	NA	8	28	0.144	NA	7	18
		0.918	(0.11)	8	28	1.022	(0.23)	7	18
		1.075	(0.14)	9	52	1.081	NA	5	21
		0.690	(0.16)	9	52	0.792	(0.48)	5	21
		0.482	(0.16)	9	42	0.250	NA	5	13
		0.905	(0.14)	9	52	1.137 ^a	(0.04)	5	21
		0.974	(0.10)	14	167	1.012	NA	4	6
		0.958	(0.10)	14	202	0.501	(0.97)	4	11
		0.650 ^a	(0.07)	14	182	0.122	NA	4	7
		0.924 ^b	(0.10)	14	202	0.541 ^{ab}	(0.06)	4	11

^a Outcrossing rates significantly differ between genders, $P < 0.05$.

^b Outcrossing rates significantly different from 1.00, $P < 0.05$.

loci have been found in other species and suggested to be the result of population substructuring and correlated matings among individuals (Ritland and Ganders, 1985; Yeh and Morgan, 1987; Boshier, Chase, and Bawa, 1995).

There are several means by which departures from random mating could occur in *O. tenera*. One possibility is that the *Gdh* marker locus is somehow related to timing of flowering, anthesis, or other aspects of floral phenology, such that individuals with similar *Gdh* genotypes breed simultaneously. Such association between allozyme genotypes and floral phenology has been proposed by Allard (1990). All *O. tenera* trees in the Monteverde population flower during some period in the flowering season, although not all trees bloom synchronously (Wheelwright, 1985). It is therefore possible that, for example, individuals homozygous for *Gdh-1* flower during one time, individuals homozygous for *Gdh-2* flower predominantly at a different time, and individuals heterozygous for *Gdh-1* and *Gdh-2* flower during a period intermediate to and overlapping with the flowering of the homozygotes. Chaisurisri, Mitton, and El-Kassaby (1994) studied Sitka spruce and found a phosphoglucosyltransferase (*Pgm*) locus gave a different outcrossing rate than other single and multilocus estimates. Comparison of pollen and ovule allele frequencies in the seed pool showed that individuals homozygous for different *Pgm* alleles sampled genetically different pollen pools. Genetic variation in the pollen pool was speculated to be due to differences in reproductive phenology among individuals with different *Pgm* genotypes. Our results suggested a similar association between floral phenology and *Gdh* genotype may occur in *O. tenera*, but chi-square tests did not detect significant differences in frequencies of genotypes flowering early in the season and genotype frequencies in the population as a whole (Gibson, 1995).

Another explanation for heterogeneous outcrossing rate estimates is that frequent consanguineous matings may have occurred. Ritland and Ganders (1985) dem-

onstrated that consanguineous matings can give estimates of selfing at some loci and random matings at others. We have previously shown high relatedness among individuals within *O. tenera* subpopulations (Gibson and Wheelwright, 1995). Pollinators tend to move among neighboring trees, so if relatedness among individuals is particularly evident at *Gdh*, then outcross matings among closely spaced trees would give artificially lower outcrossing estimates for that locus. Thus, family structure within the adult subpopulations may promote heterogeneity in pollen allele frequencies over maternal trees among subpopulations and limited pollinator flight distances may generate fine-scale heterogeneity in pollen allele frequencies within subpopulations, thereby causing neighborhood size to be relatively small. Although pollinators tended to move among closely spaced trees, we note that some intrapopulation pollen movement occurred over distances of several metres (2.5–20 m) as determined by the occurrence of the rare *Gdh-4* allele in the seeds of various trees.

A final, potential explanation for dissimilar outcrossing rates is that postpollination selection acted differentially among loci. Selection acting in differing directions and intensities among loci can cause different outcrossing estimates (Schoen, 1982; Linhart et al., 1987). Therefore, high outcrossing estimates for both *Fe* loci could be caused by selection against embryos with homozygous or inbred genotypes at the *Fe* or closely linked loci, while low *t* values for *Gdh* could have resulted from selection acting against heterozygous genotypes (Tables 1–3). Further investigations using larger progeny array sample sizes and controlled pollinations are necessary to detect patterns of differential selection among loci, as well as reduce any ambiguity in outcrossing estimates that may be due to small sample sizes. Although any one of the phenomena described above may be acting alone in this population, it is most likely that consanguineous matings, heterogeneity in pollen allele frequencies, and differential selection among loci are acting simultaneously in producing the observed mating system patterns of *O. tenera*.

Both hermaphroditic and female *O. tenera* trees were predominantly outcrossed. We were unable to test directly for self-compatibility in *O. tenera* via controlled pollination because of the exceptionally small flowers (length < 2.5 mm) and their weak attachment to the pedicel (Gibson, 1995). Mating system analyses, however, suggest *O. tenera* hermaphrodites possess some form of self-incompatibility based upon high outcrossing rates estimated in most instances (Table 3). Therefore, if a self-incompatibility mechanism already exists in *O. tenera*, then evolution of separate sexed plants to prevent selfing would not be necessary. Anatomical studies of hermaphroditic and female *O. tenera* flowers found significantly different patterns of resource allocation in flowers of the two genders. Female flowers make a greater allocation to seed- and fruit-producing structures, and hermaphrodites (functional males) make a greater allocation to attractive and pollen-producing structures (Gibson, 1995). The resource expense of success as a male or female may be such that a plant must specialize as one or the other in order to achieve high fitness. Hence, prevention of self fertilization may be of minor importance relative to ef-

iciency of nutrient allocation in gender system evolution of *O. tenera* and related species.

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