

The effect of the density of flowering individuals on the mating systems of nine tropical tree species

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Mating systems were examined through allozyme analysis for nine tropical tree species that occur on Barro Colorado Island, Republic of Panama. Estimates of outcrossing rates, using a mixed mating model, ranged from 0.35 to 1.08. Most species were highly outcrossed but two species that occurred at low densities had outcrossing rates below 0.7. Heterogeneity among trees in pollen allele frequencies contributing to progeny arrays was significant. The degree of heterogeneity in pollen allele frequencies was measured by Wright's F_{ST} , treating progeny arrays as populations. Mean F_{ST} values were negatively correlated with flowering tree density, which indicates that trees at low density sample pollen from fewer individuals than trees in denser populations. Among-year heterogeneity in pollen allele frequencies for two species was also related to the density of flowering individuals; years with lower flowering tree density had greater heterogeneity and/or more selfing. These results indicate that several population parameters, such as inbreeding, genetic relatedness of progeny arrays, gene flow and effective population size are associated with the density of flowering individuals and thus vary from year to year and among locations.

Keywords: Allozyme analysis, mating systems, Panama, tropical trees, tree density.

Introduction

Plant mating systems can be measured as the proportion of matured seeds that result from outcrossing events. Many tropical tree species possess mechanisms that ensure or encourage outcrossing (e.g. Kalin Arroyo, 1976, 1979; Chan, 1981; Koptur, 1984; Bawa *et al.*, Dayanandan, *et al.*, 1990). Allozyme analyses of progeny arrays have demonstrated that tropical tree mating systems range from mixed outcrossing and selfing, as in *Cavanillesia platanifolia* (Murawski *et al.*, 1990), to predominantly or completely outcrossing as in *Pithecellobium pedicellare* (O'Malley & Bawa, 1987), *Bertholletia excelsa* (O'Malley *et al.*, 1988), and *Quararibea asterolepis* (Murawski *et al.*, 1990).

The degree of outcrossing for hermaphroditic plants depends on factors such as: the presence and intensity of self-incompatibility mechanisms; the degree of protogyny or protandry; foraging behaviour of pollinators within and among plants; and selective abortion of selfed fruit or seed. Flowering plant density should also be a prime determinant of pollinator foraging

behaviour and therefore could have important consequences in terms of the breeding structure of a plant population (Levin & Kerster, 1974). For example, in a low density population of the Bombacaceous tree, *Cavanillesia platanifolia*, there was a positive correlation between flowering tree density and outcrossing rate (Murawski *et al.*, 1990). In that study, isolated trees were highly or completely selfed, which indicates low levels of interplant movement by the pollinators. Other studies have related outcrossing rates to density. Schemske & Lande (1985) list examples of environmentally determined outcrossing rates for three plant species due either to flower density or to pollinator abundance (see also Ellstrand *et al.*, 1978).

Tropical forests show a wide range of tree densities, although most species exist at very low densities (Ashton, 1988; Hubbell & Foster, 1986). Within populations, species may vary greatly in the proportion of adults that reproduce within a season, or even the degree of synchrony in flowering times. Such variation in flowering plant density should affect several aspects of a species' breeding structure. In this paper, we examine how adult or flowering tree density is related to the degree of outcrossing and to the genetic composition of pollen received by individual trees.

We present data on outcrossing rates using allozyme analyses of progeny arrays of nine tropical rain forest tree species. In addition, we address the following questions.

- 1 Are population outcrossing rates related to the density of flowering trees?
- 2 Are maternal trees receiving a random sample of pollen from trees in the study site? Given a negative answer to question (2) then,
- 3 are adult trees at low densities receiving a genetically more heterogeneous sample of pollen than trees with higher densities?

The latter question is addressed by examining the heterogeneity in allele frequencies of pollen received by individuals belonging to populations that differ in adult densities.

Materials and methods

The study site was Barro Colorado Island (BCI), located in Gatun Lake, Republic of Panama. Most collections were made on a 50 ha Forest Dynamics Plot

(FDP) established by S. Hubbell and R. Foster in which all trees and shrubs with a stem diameter greater than 1 cm were tagged and mapped.

Nine species contribute to the present study (Table 1). Six new species were examined for their mating systems for this study: *Beilschmedia pendula* (S.W.) Hemsl., *Brosimum alicastrum* Sw. subsp. *bolivarense* (Pitt.) C. C. Berg, *Ceiba pentandra* (L.) Gaertn., *Platypodium elegans* J. Vogel, two populations of *Sorocea affinis* Hemsl. with different densities, and *Trichilia tuberculata* C. DC. The other three species previously examined for mating system from the same study site include: *Cavanillesia platanifolia* (H. & B.) H.B.K. and *Quararibea asterolepis* Pitt. (Murawski *et al.*, 1990), and *Tachigali versicolor* Standl. & L.O. Wms (M. D. Loveless and J. L. Hamrick, in preparation). All species typically have single-seeded fruit except *Trichilia*, which usually has one to three seeds per fruit. All species have a seasonal mass-flowering phenology. Species were chosen for mating system analysis opportunistically, because they are hermaphroditic and the mating system is unknown, or because they were shown previously to exhibit sufficient allozyme polymorphism for such an analysis.

Table 1 Study species and their characteristics

Family	Species	Height	Sexual system	Floral visitors
Bombacaceae	<i>Cavanillesia platanifolia</i>	Canopy	H	Hawmoths*, monkeys, bats, bees, birds
	<i>Ceiba pentandra</i>	Canopy	H	Bats†, birds, bees, beetles, Wasps, mammals‡
	<i>Quararibea asterolepis</i>	Canopy	H	Hawkmoths, monkey, bats
Fabaceae	<i>Platypodium elegans</i>	Canopy	H	Bees
	<i>Tachigali versicolor</i>	Canopy	H	Bees
Lauraceae	<i>Beilschmedia pendula</i>	Canopy	H	Not observed Bees?
Meliaceae	<i>Trichilia tuberculata</i>	Canopy	H	Not observed Bees?
Moraceae	<i>Brosimum alicastrum</i>	Canopy	GD§	Bees, wind
	<i>Sorocea affinis</i>	Under-story	D	Small bees, and wind

*From Murawski *et al.*, (1990).

†From Baker & Harris (1959), Carvalho (1960).

‡From Toledo (1977).

§Reportedly gynodioecious, although no bisexual trees have been observed in our study site (R. Foster and Bonifacio de Leon, personal communication).

H = hermaphroditic, GD = gynodioecious, D = dioecious.

Fruit were picked directly from trees (*Sorocea*) or collected from seed shadows beneath maternal trees (all other species). Care was taken to avoid collecting seeds from overlapping seed shadows. Large progeny sample sizes were collected in order to improve estimates of pollen allele frequencies. If fruit were multiple-seeded, one seed was sampled per fruit to avoid biasing the data progeny of correlated mating events.

Seeds were collected from all fruiting trees (*Platypodium*, *Brosimum*) on the FDP or from a representative sample of trees (*Beilschmedia*, *Trichilia* and *Quararibea*). The study area was expanded for the three rarest species, *Cavanillesia*, *Ceiba*, and *Tachigali*, to include all known fruiting trees on BCI. Two 1-ha plots within the FDP, which differed in the density of adult trees, were examined for the understory tree *Sorocea*. *Cavanillesia* was sampled for three consecutive years (1987–1989) and *Platypodium* for two consecutive years (1988–1989). The density of flowering trees was noted for *Cavanillesia*, *Ceiba*, *Platypodium*, *Sorocea*, and *Tachigali*.

Seeds were either lyophilized (*Sorocea*, *Cavanillesia*, *Platypodium*, and *Trichilia*) or germinated in a greenhouse. If germinated in Panama, the seedling leaves were lyophilized (*Cavanillesia*, *Platypodium*, *Quararibea*, *Sorocea*, and *Tachigali*) and shipped to Georgia for ultracold storage prior to enzyme extraction. *Brosimum* and *Beilschmedia* were germinated in the UGA Botany greenhouse and fresh seedling leaves were sampled for analysis.

Horizontal starch gel electrophoresis was used to assay seed or seedling allozymes. Between two and 10 loci were assayed to obtain outcrossing estimates (Table 2). All species exhibited diploid inheritance patterns as interpreted from genotypic frequencies of individual progeny arrays.

We used the multilocus mixed mating model of Ritland & Jain (1981) to obtain: single locus and multilocus outcrossing estimates (t), maternal genotypes, and pollen allele frequencies. Maternal genotypes were assessed directly from leaf material collected from maternal trees of *Platypodium* and *Sorocea*. Standard errors of the outcrossing estimates were calculated using the bootstrap method (as in Ritland, 1990) where the sampling unit is among families if the number of families analysed exceeds 20 or is within families if there are fewer than 20 families per population. Five hundred bootstraps were specified to obtain each variance estimate. The outcrossing rate of *Tachigali* was estimated using the multilocus mixed mating model of Shaw *et al.* (1981).

One of the major assumptions of the Ritland and Jain model, random mating among individuals, was

Table 2 Buffer system and isozyme loci utilized for the study species. Buffer recipes were as in Soltis *et al.* (1983)

Species	Gel and electrode buffer system	Loci
<i>Beilschmedia</i>	2	IDH-1, IDH-2, PGI
<i>Brosimum</i>	6 modified	FE-2, PGI, TO
	4	6P-2, 6P-3, IDH
	8 modified	TPI-1
<i>Cavanillesia</i>	2	IDH, PGI, MDH
	6 modified	PGM, FE, TPI
<i>Ceiba</i>	2	PGI
	6 modified	PGM-1, PGM-2, TPI-3, TPI-4
	8 modified	AAT
<i>Platypodium</i>	6 modified	TPI-2, TPI-3, CE
	8 modified	DIA, GOT, FE-1, FE-2, FE-4, BGAL
	2	PGI
<i>Quararibea</i>	6 modified	PGM-1, PGM-2, PGI
	8 modified	LAP, DIA
<i>Sorocea</i>	6 modified	PGM-1, PGM-2
	11	IDH, AK
	4	DIA-2
<i>Tachigali</i>	4	IDH, DIA-1
<i>Trichilia</i>	11	MDH
	6 modified	TPI
	2	PGI

tested using chi-square tests of heterogeneity of pollen allele frequencies contributing to seed or seedling genotype of different maternal trees. Pollen allele frequencies were obtained assuming normal Mendelian segregation of maternal alleles. Thus, the maternal allele contribution to the progeny was subtracted from the progeny genotypes to obtain pollen allele frequencies. For all hermaphroditic species with outcrossing estimates of less than 100 per cent, maternal trees with the same genotypes at any given locus were compared with each other in order to test for heterogeneity in outcross pollen allele frequencies received by individual trees. Loci were examined for which the frequency of the common allele did not exceed 0.9.

Treating progeny arrays as subpopulations, among tree diversity in pollen allele frequencies contributing to seed/seedlings was examined using Wright's F_{ST} . An F_{ST} value was calculated for each locus based on, $F_{ST} = \sigma^2 / (p_i[1 - p_i])$, where σ^2 is the variance in pollen allele frequencies among seed trees, and p_i is the frequency of the i th pollen allele averaged over all maternal trees. F_{ST} values were calculated on families with a minimum sample size of 25 progeny.

Species and populations were ranked by density of reproductive individuals. The actual or estimated

density of flowering or fruiting trees on the 50-ha plot was used to designate a particular rank. The density estimate was halved for the dioecious gynodioecious species.

Results

Trichilia, *Sorocea*, and *Quararibea* appear to be completely outcrossed (Table 3). Other species have outcrossing rates ranging from 0.213 to 0.937. *Brosimum*, *Cavanillesia*, and *Ceiba*, with outcrossing estimates lower than 0.9 were also tested for an excess frequency of multilocus genotypes identical to the maternal tree in the potentially selfed progeny (as in Murawski *et al.*, 1990), would indicate apomixis by sporophytic agamospermy. No excess was observed, and as a result, apomixis can be ruled out as contributing to the apparent selfing rate for those species.

When outcrossing rates are plotted against flowering tree density for each species an apparent relationship exists (Fig. 1). The rank correlation of t_m (using the mean t_m for species represented by more than 1 year or site) with flowering tree density is significant

(Spearman's $\rho = 0.717$, d.f. = 7, $P < 0.05$). This relationship is largely due to the three representatives of the Bombacaceae (*Canvanillesia*, *Ceiba*, and *Quararibea*). No relationship of flowering tree density and outcrossing rate exists for the other six species.

Significant differences in allele frequencies of pollen received by different maternal trees were observed in all species and for most loci (chi-squared tests of heterogeneity for each locus, $P < 0.05$ for 79 per cent of the cases). These tree species are not mating (or more specifically, not outcrossing) at random, but are sampling pollen from a diverse subset of the available flowering trees.

A grand mean of the F_{ST} values was calculated for species represented by more than 1 year or site (*Cavanillesia*, *Platypodium*, and *Sorocea*). The rank correlation of the mean F_{ST} value for each of the nine species with the density of flowering trees was negative and significant (Spearman's $\rho = -0.738$, d.f. = 7, $P < 0.05$). Significant differences were also seen among F_{ST} values of species analysed in more than one year or site. *Platypodium* had a significantly higher average F_{ST}

Table 3 Multilocus outcrossing rates (t_m) and degree of variation in incoming pollen allele frequencies among maternal trees (F_{SF}) for the nine study tree species in Barro Colorado Island. F_{SF} is averaged over all loci. The densities of flowering trees and adult-size trees in the 50-ha plot are also given

Species	Number of maternal trees sampled	Mean number of progeny per tree	Number of loci	Outcrossing rate (t_m) (\pm SE)	Flowering tree density per ha	Adult* tree density per ha	Mean F_{SF}
<i>Beilschmedea</i>	14	26	3	0.918 (0.058)	2.10†	2.36	0.064
<i>Brosimum</i>	9	44	7	0.875 (0.035)	0.30†	0.44	0.170
<i>Cavanillesia</i>							
VL	3	48	4	0.213 (0.052)	0.10 (32‡)	0.28	0.259
L§	11	45	5	0.347§ (0.025)	0.08 (49‡)	0.28	0.227
H§	20	72	4	0.569§ (0.024)	0.18 (74‡)	0.28	0.151
<i>Ceiba</i> ¶	12	44	6	0.689 (0.032)	0.24	0.50	0.151
<i>Platypodium</i>							
L	5	40	10**	0.924 (0.043)	0.34	0.72	0.163
H	5	31	10**	0.898 (0.043)	0.50	0.72	0.083
<i>Quararibea</i> §	27	34	5	1.008 (0.010)	2.00†	7.28	0.098
<i>Sorocea</i>							
L	8	49	5	1.089 (0.045)	3.56	15.4††	0.104
H	7	71	5	0.969 (0.020)	6.51	15.4††	0.083
<i>Tachigali</i> ‡‡	23	44	2	0.937 (0.044)	0.10	0.16	0.108
<i>Trichilia</i>	17	48	2	1.077 (0.028)	6.00†	10.1	0.082

*Based on dbh of estimated adult size from the FDP.

†Approximation based on density of fruiting trees.

‡Percentage of trees examined on entire island that flowered.

§Outcrossing rates from Murawski *et al.* (1990).

¶Outcrossing rate from D. A. Murawski & J. L. Hamrick (in preparation).

**Ten loci used to determine the outcrossing estimate; 14 loci used to determine F_{ST} .

††Extrapolated for the 50-ha FDP plot. Each plot is only 1 ha in size, imbedded within the FDP plot.

‡‡Outcrossing rate from M. D. Loveless & J. L. Hamrick (in preparation).

H = High density, M = medium density, and L = Low density.

for the year with few flowering trees (L, Fig. 1) than for the year with a higher density of flowering trees (H, Fig. 1; Mann-Whitney U -test, $P < 0.05$), which reinforces the negative correlation of F_{ST} with flowering tree density observed across all species. *Cavanillesia* shows a similar (although not significant) trend over the three consecutive years of study. It should be noted, however, that the year of very low density (VL, 1989) produced only three trees with fruit. Two of the three trees flowered in isolation and had no obvious outcrossed progeny, whereas the third tree overlapped in flowering time by a few days with a neighbouring tree less than 30 m away and produced some outcrossed fruit [23 per cent (15/66) unambiguous outcrosses]. Therefore the heterogeneity in the mixed mating

Cavanillesia may be due more to variation in the rate of selfing than to outcrossing with few trees. The high and low density plots of *Sorocea affinis* did not differ significantly in F_{ST} values, although the trend was in the expected direction. *Tachigali*, with the lowest adult density, did not fit the pattern seen for the other species. However, flowering trees of *Tachigali* were clustered in the year of analysis (1984). The low average F_{ST} seen for this species might be due to relatively random mating within clusters. In addition, individual *Tachigali* flower for long periods of time and there is evidence that substantial levels of gene flow occur over distances of at least 500 m (M. D. Loveless and J. L. Hamrick, in preparation).

We could have assigned rank order to the species

Fig. 1 Multilocus outcrossing rate (\pm SE) relative to the density ranking of flowering trees for nine tropical tree species on Barro Colorado Island. The species are listed by three letter acronyms: *Tachigali versicolor* TAC, *Cavanillesia platanifolia* CAV (3 years: very low VL, low L and high H density), *Ceiba pentandra* CEI, *Brosimum alicastrum* BRO, *Platypodium elegans* PLA (2 years: low L and high H density), *Quararibea asterolepis* QUA, *Beilschmedia pendula* BEI, *Sorocea affinis* SOR (low and high density sites), and *Trichilia tuberculata* TRI.

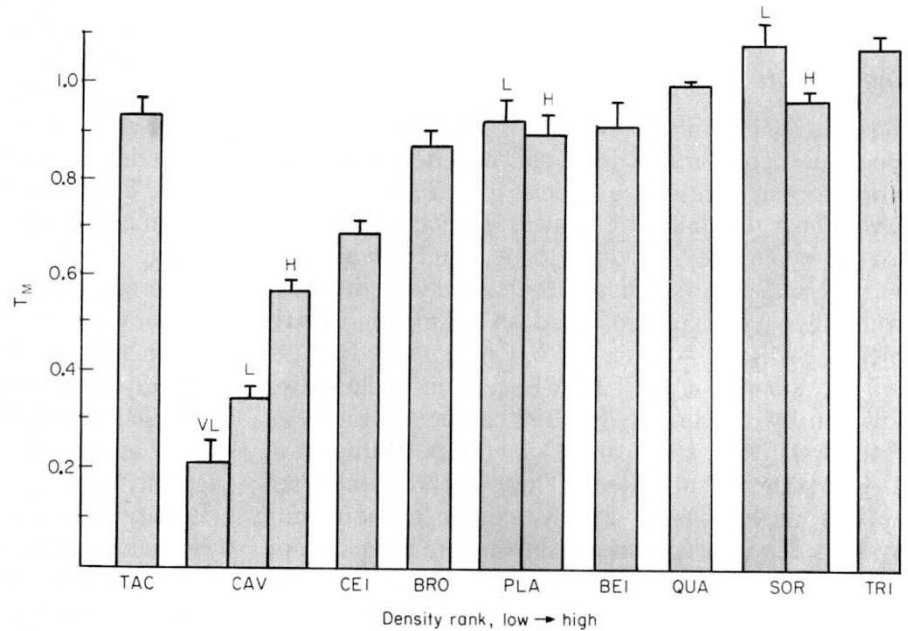
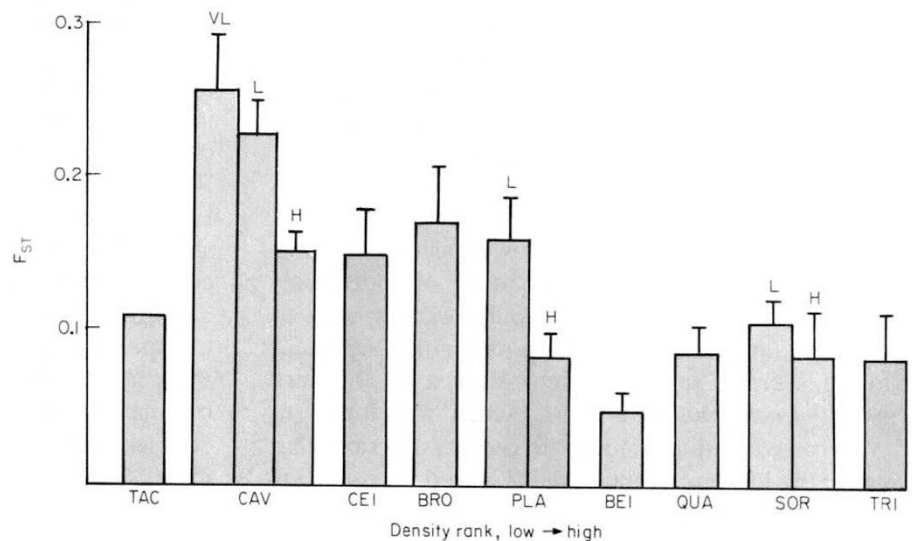


Fig. 2 The relationship between the degree of among-tree heterogeneity in incoming pollen allele frequencies as measured by F_{ST} values (means \pm SE) and the relative density ranking of flowering trees of nine species on BCI. The species ranks and names are as in Fig. 1. Because only two measurements were made on *Tachigali versicolor* (TAC), a value for standard error was not calculated.



because data do not exist on the number of flowering trees for all species, but the number of trees producing fruit was used instead. Estimates of the number of flowering trees based on the number of fruiting trees is a minimum estimate because the fruiting trees may represent a fraction of the total that actually flowered. The upper limit of flowering trees should be somewhat less than the number of 'adult' size trees on the FDP. The given order of *Quararibea* and *Beilschmiedia* could be as given or reversed depending on the number of trees that actually flowered. This is also true of *Brosimum* and *Ceiba*. For these species pairs the most conservative rank was used in the correlation analyses. If these pairs of species were given equal ranks or the ranks were reversed, the correlation between F_{ST} and flowering tree density would be higher.

Discussion

The outcrossing rates observed for most species in this study are comparable to those reported for other tropical rain forest tree species [i.e. *Pithecellobium pedicellare* (O'Malley & Bawa, 1987), *Bertholletia excelsa* (O'Malley *et al.*, 1988), and *Quararibea asterolepis* (Murawski *et al.*, 1990)], and are consistent with the values expected based on pollination experiments (e.g. Kalin Arroyo, 1976; Chan, 1981; Bawa *et al.*, Dayandanan *et al.*, 1990). Exceptions include two low-density species in the Bombaceae: *Cavanillesia* (Murawski *et al.*, 1990) and *Ceiba* (D. A. Murawski & J. L. Hamrick, submitted). These are the only tree species analysed that clearly exhibit mixed-mating systems. Another species not shown here is the canopy tree, *Dipteryx oleifera* (formerly *D. panamensis*), an autotetraploid with a low density of flowering trees ($< 0.5 \text{ ha}^{-1}$), with a relatively low multilocus outcrossing estimate of 0.74 (± 0.07) (D. A. Murawski & J. L. Hamrick, unpublished results). Bawa *et al.* (1985) found that two out of three rare or uncommon hermaphroditic rain forest tree species were self-compatible as compared to the vast majority of the more common species that were self-incompatible. Given these results, one could speculate that outcrossing or underlying incompatibility systems may be relaxed in some species that occur at extremely low densities. Without this concession, the spatial isolation of individuals would constrain the ability of an outcrossing species to reproduce (Ashton, 1984). Support for this argument can be seen in mating system studies of the rare species, *Eucalyptus rhodantha*, which was found to have a mixed mating system with outcrossing rates that were at the low end of the range reported for relatively more common *Eucalyptus* species (Sampson *et al.*,

1989). In cultivated rye, the gametophytic incompatibility system was relaxed and outcrossing estimates were lowered at low-plant density (Vaquero *et al.*, 1989). In that study, the low-plant density corresponded with low-pollen density during fertilization. Alternatively, one could speculate that trees at high densities may have higher outcrossing rates due to self-incompatibility systems, pollen competition (e.g. Bertin, 1982; Snow & Mazer, 1988), and/or the selective abortion of selfed progeny (as in Murneek, 1954; Sarvas, 1962, 1968).

Heterogeneity of pollen allele frequencies received by maternal trees can be caused by factors such as family structure, different flowering schedules of individual trees, or any factor that leads to variation in pollinator behaviour at different trees, such as shifting schedules of nectar production (e.g. Frankie & Haber, 1983). Given the spatial scale and tree densities (Table 3) of this study, it seems unlikely that family structure is an important source of heterogeneity in pollen allele frequencies among maternal trees. Information on flowering schedules of a few of the study species (e.g. for *Platypodium*, *Sorocea*, *Cavanillesia*; Murawski, unpublished data) would indicate that differences in timing of flowering of individual trees may be an important factor, as would the degree of isolation of individuals (e.g. *Cavanillesia*; Murawski *et al.*, 1990).

An allozyme analysis of mating systems, such as that employed for these species, provides a basis for a more detailed examination of the species' mating behaviour. The association of pollen allele frequency heterogeneity experienced by maternal trees with population density indicates that trees at low adult population densities tend to mate with fewer pollen donors (correlated matings) than trees at high adult densities. The usual conclusion, that most non-random mating is among near neighbours, reduces effective population sizes. However, as Hamrick & Murawski (1990) have noted, heterogeneity in pollen allele frequencies can occur without a predominance of near-neighbour matings. Asynchronous flowering and interplant incompatibilities can greatly modify the breeding structure of the population and the effective population size. Furthermore, Hamrick & Murawski (1990) and M. D. Loveless and J. L. Hamrick (in preparation) have shown that long distance pollen movement is relatively common for two of our study species (*Platypodium* and *Tachigali*) increasing apparent population sizes. Thus, it appears that the breeding structure of low density tropical trees may consist of a large proportion of correlated matings (either due to time or space) coupled with substantial long distance pollen movement (Hamrick & Murawski, 1990). Moreover, to measure effective population size adequately and its

effect in genetic structure, one would need to know the life-time mating patterns of individual trees. This need is obvious in view of the among-year variation in pollen composition found among maternal trees of *Cavanillesia* and *Platypodium* (Murawski *et al.*, 1990).

Earlier authors differed in respect to their view of the levels of gene flow and the importance of drift in tropical tree evolution (e.g. Baker, 1959; Federov, 1966; Ashton, 1969; Bawa, 1974). If gene flow is limited and if most matings occur among relatively few individuals, most tropical tree populations should lose genetic variation due to random genetic drift. A comparison of allozyme diversity of common and uncommon tree species on Barro Colorado Island showed that uncommon species were less polymorphic on a per capita basis than the common species (Hamrick *et al.*, 1991; Hamrick & Murawski, 1991). Thus, it is possible that the lower polymorphism of the uncommon species is the result of genetic drift brought on by reduced numbers of pollen donors. On the other hand, the uncommon species analysed by Hamrick & Murawski (1991), maintained higher levels of genetic diversity than would be predicted based on the number of adults on the FDP. Once again, breeding systems that combine significant levels of correlated mating with long distance gene flow could explain these apparent inconsistencies.

The breeding systems of these tropical trees may represent a complex and variable mixture of correlated matings and long distance pollen movement. Our results indicate that the density of flowering individuals plays a significant role in shaping the breeding structure with low-density species apparently having fewer pollen donors. Among-tree pollen dispersal distances may, on the other hand, be much greater for these species (Hamrick & Murawski, 1990) partially compensating for the higher rates of correlated matings. Conversely, higher density species seem to have more random mating but pollen dispersal distances may be less. These speculations are consistent with what little is known of pollen movement in tropical plant populations (Hamrick & Murawski, 1990; Webb & Bawa, 1983; Murawski, 1987).

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