

SHORT REVIEW

To self, or not to self... A review of outcrossing and pollen-mediated gene flow in neotropical trees

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Despite the typically low population densities and animal-mediated pollination of tropical forest trees, outcrossing and long-distance pollen dispersal are the norm. We reviewed the genetic literature on mating systems and pollen dispersal for neotropical trees to identify the ecological and phylogenetic correlates. The 36 studies surveyed found > 90% outcrossed mating for 45 hermaphroditic or monoecious species. Self-fertilization rates varied inversely with population density and showed phylogenetic and geographic trends. The few direct measures of pollen flow ($N=11$ studies) suggest that pollen dispersal is widespread among low-density tropical trees,

ranging from a mean of 200 m to over 19 km for species pollinated by small insects or bats. Future research needs to examine (1) the effect of inbreeding depression on observed outcrossing rates, (2) pollen dispersal in a wide range of pollination syndromes and ecological classes, (3) and the range of variation of mating system expression at different hierarchical levels, including individual, seasonal, population, ecological, landscape and range wide.

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Introduction

Mating systems, the genetic relatedness and patterns of pairings between gametes (as distinct from breeding systems, the morphological and physiological characteristics of pairing; Neal and Anderson, 2005), play a central role in evolutionary theories of the origin of tree species richness in the tropics (Bawa, 1992). In species-rich tropical rainforests, the population density of adult trees of a given species is generally low and thus distances between the crowns of flowering conspecifics will be large (Hubbell and Foster, 1983). This observation originally led botanists to predict that most tropical tree species should be highly self-fertilizing or inbred (eg Corner, 1954; Baker, 1959; Fedorov, 1966), under the premise that animal pollinators are unable to move among widely spaced conspecifics. Over the last 30 years, this early view of tropical pollinators and the mating systems of tropical tree species has been completely revised. Community-level studies of breeding systems in tropical trees revealed high levels of dioecy (>20%), and cross-pollination studies provided evidence of self-incompatibility in hermaphroditic or monoecious species (Bawa *et al.*, 1985). Genetic marker-based analyses of mating system have tended to confirm these field studies, revealing high rates of outcrossing and long-distance pollen dispersal for a range of

pollination syndromes (eg Boshier *et al.*, 1995a,b; Stacy *et al.*, 1996; Loveless *et al.*, 1998; Nason *et al.*, 1998).

Genetic marker-based studies have also revealed that outcrossing rate and pollen dispersal distances are sensitive to ecological factors, and show variation over both spatial and temporal scales (Nason and Hamrick, 1997). For example, factors such as population density and pollinator abundance and composition change over the range of a species, have a concomitant impact on outcrossing rate and pollen-mediated dispersal at a landscape scale (Franceschinelli and Bawa, 2000; Dick *et al.*, 2003; Degen *et al.*, 2004). Mating system analyses also indicate the potential for variation in the relative rates of selfing and outcrossing at a micro-scale, where variation occurs among individuals within populations, among populations over years and from one flowering event to another (Murawski and Hamrick, 1991; Nason and Hamrick, 1997). Finally, phylogenetic constraints on floral morphology and self-compatibility system are also expected to influence the observed outcrossing rates and patterns of pollen dispersal (Gribel *et al.*, 1999).

This review examines studies that use molecular genetic techniques to quantify mating systems and pollen-mediated gene dispersal in neotropical tree species. The review is limited to the neotropics, as the authors are familiar with the study species in this region. However, given the pantropical distribution of most tropical tree families and many genera (Pennington and Dick, 2004), our conclusions should have broad geographic application. Our discussion of pollen dispersal is focussed on undisturbed populations, as Lowe *et al.* (2005) reviews studies in fragmented habitats. Our objectives are to (1) examine the relationship between

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the multilocus outcrossing rate (t_m) and phylogenetic and ecological factors, such as population density, pollination syndrome and habitat change, and (2) determine the distances over which pollen is dispersed among low-density, animal-pollinated trees in species-rich lowland neotropical forests.

Review of the literature

A total of 36 case studies encompassing 45 neotropical tree species were surveyed. For 29 of these case studies, a multilocus mixed-mating model (eg Ritland and Jain, 1981; Ritland, 1986) was used to determine the mating system. Henceforth, 'mating system' is used synonymously with the outcrossing rate. Some estimate of pollen dispersal was made in 10 studies. Allozymes were employed in 22 case studies, whereas microsatellites were utilized in 14 case studies. The results of the literature survey are summarized in Table 1.

Correlates of mating system

Phylogeny: As the anatomical and biochemical aspects of self-incompatibility systems may be phylogenetically constrained (Gribel *et al*, 1999), we looked for phylogenetic association with the mating system. The taxonomic breadth encompassed by the relevant literature presently includes 15 plant families (Table 1), with an average of 2.9 species examined per family.

It is noteworthy that species in the Malvaceae (subfamily Bombacoideae; former Bombacaceae) frequently exhibit outcrossing rates lower than 80% (mixed-mating systems). Mixed-mating systems were found in *Pachira quinata* (Fuchs *et al*, 2003), *Cavanillesia platanifolia* (Murawski and Hamrick, 1992b), *Ceiba pentandra* (Murawski *et al*, 1990; Murawski and Hamrick, 1991, 1992a; Gribel *et al*, 1999; Lobo *et al*, 2005) and *Pseudobombax munguba* (Gribel and Gibbs, 2002). This pattern may apply more generally to trees in the order Malvales, which includes the Sterculiaceae, Ebenaceae and Tiliaceae. Self-fertilization rates higher than 50% have been documented in *Shorea* and *Stemonoporus* of the Dipterocarpaceae (Murawski and Bawa, 1994; Murawski *et al*, 1994), which is the dominant family of tropical trees in Asia, also in the Malvales. The dominant tree family of Neotropical forests – the legume family Fabaceae – also exhibits patterns of mixed mating, with outcrossing rates as low as 0.54 in the pioneer legume *Senna multijuga* (Ribeiro and Lovato, 2004), 0.42 in *Dicorynia guianensis* (Latouche-Hallé *et al*, 2004), <0.50 in *Platypodium elegans* (Hufford and Hamrick, 2003) and 0.63 in *Dinizia excelsa* (Dick *et al*, 2003).

Published mating system studies do not encompass the taxonomic richness of tropical forests. We found no mating system studies for some of the most species-rich neotropical tree families, including the Sapotaceae, Annonaceae, Myrtaceae, Chrysobalanaceae and Burseraceae. In controlled-pollination studies, however, Bawa *et al* (1985) report successful self-pollination in the Annonaceae. In the absence of genetic analysis, however, it is not possible to distinguish between self-fertilization and apomixis in such studies. Apomixis, the parthenogenic production of seed, can be induced by pollen, and has been documented in the Malvacean tree genera *Pachira* (Baker, 1960), *Bombacopsis* (Duncan, 1970) and *Eriotheca* (Oliveira *et al*, 1992), and it has also been

documented in the Dipterocarpaceae (Kaur *et al*, 1978). Apomixis may have an important role in the breeding structure of some populations. In a fascinating Malaysian study of a species in the pantropical genus *Garcinia* (*G. scortechinii*), Thomas (1997) found an entirely female population that persisted solely through apomixis.

High outcrossing rates result from self-incompatibility, and may be phylogenetically constrained, but inbreeding depression at the embryo stage can also produce largely outcrossed offspring (Seavey and Bawa, 1986). In order to distinguish between the effects of self-incompatibility and inbreeding depression, Hufford and Hamrick (2003) documented the change in outcrossing rate in *P. elegans* (Fabaceae) at three early life stages: aborted embryos, mature seeds and seedlings. The outcrossing rate increased across each life stage ($t_m=0.79$, 0.82 and 0.91), suggesting that inbreeding depression may explain high outcrossing observed in seedlings, the stage at which many genetic marker studies of mating system are carried out. Several neotropical trees also have late-acting self-incompatibility mechanisms (eg *Tabebuia*; Bittencourt and Semir, 2005), and so a genetic estimation of outcrossing rate would be strongly influenced by the developmental stage at which seeds are assessed.

Individual, population, range and landscape variation: Individual outcrossing rates can vary widely. Murawski and Hamrick (1992a) reported outcrossing rates in *C. pentandra* (Malvaceae) ranging from complete self-fertilization to complete outcrossing. This variation was explained by asynchrony in flowering times and nonrandom foraging behaviour of the bat pollinators. Similar results for *C. pentandra* reported by Gribel (in Wilson *et al*, 2001) showed the percentage of selfed seeds to range from zero to 97.8% for individual trees. Multilocus outcrossing rates for 25 individual trees varied from 0.38 to 1.00 in an Amazonian population of *Swietenia macrophylla* (Meliaceae), although 23 individuals were predominantly or completely outcrossing (Lemes, 2000). Similarly, Latouche-Hallé *et al* (2004) observed marked variation in outcrossing rates among individuals of *D. guianensis* (Fabaceae), likely due to asynchrony in flowering times. Rocha and Aguilar (2001) report spatial and temporal variation in outcrossing rates in *Enterolobium cyclocarpum* over two consecutive years. Despite these multiple sources of individual variation in outcrossing rates, there are some clear ecological correlates of mating system variation.

Murawski and Hamrick (1991) examined the relationship between the density of flowering individuals in a population and its outcrossing rate in nine neotropical tree species, and found that three representatives from the Bombacoideae (Malvaceae) exhibited a correlation between outcrossing rate and flowering tree density. Additionally, Murawski and Hamrick (1992b) reported low outcrossing rates in a low-density population of *C. platanifolia* ($t_m=0.213$) compared to a high-density population ($t_m=0.661$). Murawski and Hamrick (1992b) and Nason and Hamrick (1997) report this pattern for other species.

There can be a geographic or historical component of mating system variation. *C. pentandra* has a neotropical origin, but has become established in Africa via oceanic dispersal at least 14 000 years before present (Dick, unpublished data). While neotropical populations dis-

Table 1 Biological, mating system and pollen-mediated gene flow characteristics of case-study species

Family	Species	Region	Life history	Pollination system	Genetic marker	Sampling design	t_m	Gene flow	Reference
Anacardiaceae	<i>Spondias mombin</i>	Panama	Canopy	Variety of small insects	Allozymes	Leaves and progeny from a 84 ha population	$t_m = 0.989 \pm 0.163$ and 1.304 ± 0.108	<6% pollen movement over 300 m	Stacy <i>et al</i> (1996)
Apocynaceae	<i>Stemmadenia donnell-smithii</i>	Costa Rica	Subcanopy	Euglossine bees, butterflies	Allozymes	Progeny from a single disturbed patch	$t_m = 0.896 \pm 0.107$		James <i>et al</i> (1998)
Arecaceae	<i>Astrocaryum mexicanum</i>	Mexico	Understory	Small beetles	Allozymes	Progeny from four plots, collections from three different years	$t_m =$ from 0.933 ± 0.174 to 1.050 ± 0.066		Eguiarte <i>et al</i> (1992)
Arecaceae	<i>Euterpe edulis</i>	Brazil	Canopy	Small bees, wind?	Microsatellites	Adults, juveniles and seedlings from two plots	$t_m = 0.90 \pm 0.04$ and 0.98 ± 0.02 , no biparental inbreeding		Gaiotto <i>et al</i> (2003)
Bignoniaceae	<i>Jacaranda copaia</i>	Costa Rica	Canopy, pioneer	Medium to large bees	Allozymes	Progeny from two disturbed patches 1 km apart	$t_m = 0.943 \pm 0.044$		James <i>et al</i> (1998)
Boraginaceae	<i>Cordia alliodora</i>	Costa Rica	Canopy		Allozymes	Progeny from a single stand	$t = 0.904$ to 0.978	Overall extensive gene flow; distances up to 280 m	Boshier <i>et al</i> (1995a, b)
Caryocaraceae	<i>Caryocar brasiliense</i>	Brazil	Canopy	Bats	Microsatellites	Leaves and progeny from four populations	$t_m = 1.00$, high biparental inbreeding		Collevatti <i>et al</i> (2001)
Clusiaceae	<i>Calophyllum longifolium</i>	Panama	Canopy	Variety of small insects	Allozymes	Leaves and progeny from a 84 ha population	$t_m = 1.030 \pm 0.085$ and 1.031 ± 0.035	62% pollen moved more than 210 m	Stacy <i>et al</i> (1996)
Clusiaceae	<i>Symphonia globulifera</i>	Costa Rica	Canopy	Hummingbirds	Microsatellites	Progeny arrays from forest fragments and pastures	$t_m = 0.91$ and 0.89 in continuous forest and forest fragments; $t_m = 0.74$ in pasture trees		Aldrich and Hamrick (1998)
Clusiaceae	<i>Symphonia globulifera</i>	French Guiana	Canopy	Hummingbirds	Microsatellites	Cambium and progeny from three plots within a single site	$t_m = 0.92$; high biparental inbreeding	Mean pollen dispersal between 27 and 53 m	Degen <i>et al</i> (2004)
Lauraceae	<i>Beilschmedia pendula</i>	Panama		Possibly bees	Allozymes	Progeny from a single plot	$t_m = 0.918 \pm 0.058$		Murawski and Hamrick (1991)
Lauraceae	<i>Ocotea tenera</i>	Costa Rica		Small bees, flies and wasps	Allozymes	Leaves and progeny from a 16 km ² population	$t_m = 0.846$ – 0.965		Gibson and Wheelwright (1996)
Lecythidaceae	<i>Bertholletia excelsa</i>	Brazilian Amazon	Canopy	Large bees	Allozymes	Progeny from a single population	$t_m = 0.85 \pm 0.03$		O'Malley <i>et al</i> (1988)
Leguminosae (Caesalpinaceae)	<i>Dinizia excelsa</i>	Amazonas, Brazil	Emergent, fast-growing	Small insects, stingless bees, <i>Apis mellifera</i> in disturbed habitats	Microsatellites	Multiple progeny arrays across fragmented and continuous forest landscape	$t_m = 0.875 \pm 0.049$ for undisturbed forest; $t_m = 0.848 \pm 0.044$ in forest fragments and pasture	Mean pollen dispersal of 1509 m in forest fragments with <i>Apis</i> pollination; 212 m in undisturbed forest	Dick <i>et al</i> (2003)

Table 1 Continued

Family	Species	Region	Life history	Pollination system	Genetic marker	Sampling design	t_m	Gene flow	Reference
Leguminosae (Caesalpiniaceae)	<i>Vouacapoua americana</i>	French Guiana	Canopy	Small bees and thrips	Microsatellites	Progeny from two stands	5% selfing	Short-distance pollen dispersal up to 100 m	Dutech <i>et al</i> (2002)
Leguminosae (Fabaceae)	<i>Dicorynia guianensis</i>	French Guiana	Canopy	Large bees	Microsatellites	Cambium and progeny from a 40 ha population	$t_m = 0.89 \pm 0.044$	62% of pollen from outside site	Latouche-Hallé <i>et al</i> (2004)
Leguminosae (Fabaceae)	<i>Gliricidia sepium</i>	Guatemala	Pioneer	Large bees	Microsatellites	Adults and progeny from a single plot		6.1% of pollen move more than 75 m, longest dispersal 275 m	Dawson <i>et al</i> (1997)
Leguminosae (Fabaceae)	<i>Platypodium elegans</i>	Panama	Canopy	Bees	Allozymes	Progeny from a single plot	$t_m = 0.924 \pm 0.043$ and 0.898 ± 0.043		Murawski and Hamrick (1991)
Leguminosae (Fabaceae)	<i>Platypodium elegans</i>	Panama	Canopy	Bees	Microsatellites	Aborted fruits, mature fruits and germinated seedlings	$t_m = 0.79$ (aborted fruit), 0.82 (mature seeds) and 0.91 (seedlings)		Hufford and Hamrick (2003)
Leguminosae (Fabaceae)	<i>Senna multijuga</i>	Brazil	Pioneer	Bees	Allozymes	Progeny from two populations	$t_m = 0.540 \pm 0.090$ and 0.838 ± 0.068		Ribeiro and Lovato (2004)
Leguminosae (Fabaceae)	<i>Tachigalia versicolor</i>	Panama	Canopy, monocarpic		Allozymes	Progeny from six populations	$t_m = 0.998$; no biparental inbreeding	Large amounts of pollen migration	Loveless <i>et al</i> (1998)
Leguminosae (Fabaceae)	<i>Tachigalia versicolor</i>	Panama	Canopy, monocarpic	Bees	Allozymes	Progeny from a single plot	$t_m = 0.937 \pm 0.044$		Murawski and Hamrick (1991)
Leguminosae (Mimosaceae)	<i>Enterolobium cyclocarpum</i>	Costa Rica	Canopy	Nocturnal insects, including moths and beetles	Allozymes	Progeny from four populations	$t_m = 0.812$ to 0.913; low biparental inbreeding $t_m - t_s = 0.058$ to 0.079		Rocha and Aguilar (2001)
Leguminosae (Mimosaceae)	<i>Pithecellobium elegans</i>	Costa Rica	Emergent		Allozymes	Progeny from a 150 ha population	$t_m = 0.970$ and 0.986		Hall <i>et al</i> (1996)
Leguminosae (Mimosaceae)	<i>Pithecellobium pedicellare</i>	Costa Rica	Canopy, gap-colonizing		Allozymes	Progeny from a 600 ha population	$t_m = 0.951 \pm 0.021$		O'Malley and Bawa (1987)
Malvaceae (Bombacoideae)	<i>Cavanillesia platanifolia</i>	Panama	Canopy, gap-specialist	Hawk moths, monkeys, bats	Allozymes	Progeny from a single plot	$t_m = 0.213 \pm 0.052$		Murawski and Hamrick (1991)
Malvaceae (Bombacoideae)	<i>Cavanillesia platanifolia</i>	Panama	Canopy, gap-specialist, rare	Hawk moths, humming birds, bees	Allozymes	Progeny from a single population	$t_m = 0.57$ and 0.35		Murawski <i>et al</i> (1990)
Malvaceae (Bombacoideae)	<i>Ceiba pentandra</i>	Central Amazonia	Emergent, fast-growing	Bats	Allozymes	Progeny from two locations	91 and 71% seeds outcrossed		Gribel <i>et al</i> (1999)
Malvaceae (Bombacoideae)	<i>Ceiba pentandra</i>	Central Amazonia	Emergent, fast-growing	Bats	Microsatellites	Leaves and progeny from 400 km ² forest	24.7% selfed seeds at population level	Several matings over > 5 km; longest dispersal 18.6 km	Gribel, reported in Wilson <i>et al</i> (2000)
Malvaceae (Bombacoideae)	<i>Ceiba pentandra</i>	Costa Rica	Emergent, fast-growing	Bats	Microsatellites	Progeny from two populations	$t_m = 0.623$		Lobo <i>et al</i> (2005)
Malvaceae (Bombacoideae)	<i>Ceiba pentandra</i>	Panama	Emergent, fast-growing	Bats, birds, bees, beetles, wasps, beetles	Allozymes	Progeny from a single plot	$t_m = 0.689 \pm 0.032$; no biparental inbreeding		Murawski and Hamrick (1991, 1992a)

Table 1 Continued

Family	Species	Region	Life history	Pollination system	Genetic marker	Sampling design	t_m	Gene flow	Reference
Malvaceae (Bombacoideae)	<i>Pachira quinata</i>	Costa Rica	Canopy	Bats, sphingid moths	Allozymes	Progeny from continuous and fragmented forest plots	$t_m = 0.915 \pm 0.043$ (continuous) and $t_m = 0.777 \pm 0.114$ (isolated trees)		Fuchs <i>et al</i> (2003)
Malvaceae (Bombacoideae)	<i>Quararibea asterolepis</i>	Panama	Canopy, slow-growing, shade-tolerant, common	Hawk moths, monkeys, bats	Allozymes	Progeny from a single plot	$t_m = 1.008 \pm 0.010$		Murawski <i>et al</i> (1990); Murawski and Hamrick (1991)
Meliaceae	<i>Carapa guianensis</i>	Costa Rica	Canopy	Small insects, moths	Allozymes	Progeny from two populations	$t_m = 0.986$ and 0.967		Hall <i>et al</i> (1994)
Meliaceae	<i>Carapa procera</i>	French Guiana	Small tree		Allozymes	Progeny from plots within 300 ha natural forest	$t_m = 0.85$ for unlogged plots and 0.63 for logged plots		Doligez and Joly (1997)
Meliaceae	<i>Cedrela odorata</i>	Costa Rica	Canopy	Small insects, moths	Allozymes	Progeny from a 30 km transect of disturbed forest	$t_m = 0.969 \pm 0.024$		James <i>et al</i> (1998)
Meliaceae	<i>Swietenia humilis</i>	Costa Rica	Canopy	Bees, moths, thrips	Microsatellites	Progeny from three forest fragment plots and one continuous forest plot		Pollen dispersal up to 4.5 km between forest fragments	White <i>et al</i> (2002)
Meliaceae	<i>Swietenia macrophylla</i>	Eastern Amazonia	Canopy	Bees, moths, thrips	Microsatellites	Leaves and progeny from 1 logged population	$t_m = 0.958 \pm 0.025$		Lemes (2000)
Meliaceae	<i>Swietenia macrophylla</i>	Costa Rica	Canopy	Bees, moths, thrips	Microsatellites	Leaves and progeny from three populations	50 and 28.8% progeny outcrossed	Limited pollen movement	Lowe <i>et al</i> (2003)
Meliaceae	<i>Trichilia tunerculata</i>	Panama	Canopy	Possibly bees	Allozymes	Progeny from a single plot	$t_m = 1.077 \pm 0.028$		Murawski and Hamrick (1991)
Moraceae	<i>Brosimum alicastrum</i>	Panama	Canopy	Bees, wind	Allozymes	Progeny from a single plot	$t_m = 0.875 \pm 0.035$		Murawski and Hamrick (1991)
Moraceae	<i>Cecropia obtusifolia</i>	Mexico	Canopy, pioneer	Wind	Allozymes	Leaves and progeny from nine sites	$t_m = 0.974 \pm 0.024$		Alvarez-Buylla and Garay (1994)
Moraceae	<i>Ficus citrifolia</i> , <i>F. dugandii</i> , <i>F. nymphifolia</i> , <i>F. obtusifolia</i> , <i>F. perforate</i> , <i>F. pertusa</i> and <i>F. popenoei</i>	Panama	Canopy	Fig wasps	Allozymes	Leaves and progeny from an area of approximately 15 km ²		Extensive pollen movement over 5.8–14.2 km; breeding units between 106 and 632 km ²	Nason <i>et al</i> (1998)
Moraceae	<i>Sorocea affinis</i>	Panama	Understory	Small bees, wind	Allozymes	Progeny from a single plot	$t_m = 1.089 \pm 0.045$ and 0.969 ± 0.020		Murawski and Hamrick (1991)
Rubiaceae	<i>Psychotria faxlucens</i>	Mexico	Understory	Moths	Allozymes	Progeny from two 25 × 30 m ² plots in 700 ha forest	$t_m = 0.898$ and 0.685		Pérez-Nasser <i>et al</i> (1993)
Staphyleaceae	<i>Turpinia occidentalis</i>	Panama	Subcanopy	Variety of small insects	Allozymes	Leaves and progeny from a 50 ha population	$t_m = 1.006 \pm 0.090$	Small fraction of matings over long distances	Stacy <i>et al</i> (1996)

play predominant outcrossing or mixed mating, African populations are reportedly completely self-compatible (Baker, 1955, 1965), which may have been a requisite for establishing founder populations following oceanic dispersal. At the landscape scale, Ribeiro and Lovato (2004) found two populations of *S. multijuga* (Fabaceae) to have significantly different outcrossing rates ($t_m = 0.838$ and 0.540), thought to be a reflection of genetic and environmental differences among populations. Murawski and Hamrick (1992b) attributed differences in the outcrossing rate of two populations of *C. platanifolia* to differences in flowering-plant densities. Mating system variation at the regional scale may also reflect differences among populations in the genetic load that leads to inbreeding depression.

Changes in the landscape, such as selective logging, deforestation and habitat destruction alter population density, demographic structure, phenology and the abundance, diversity and behaviour of pollinator communities (Dick, 2001; Lowe *et al*, 2005), thereby impinging on the mating system. Doligez and Joly (1997) found significant differences between outcrossing rates of *Carapa procera* in undisturbed plots and logged plots ($t_m = 0.85$ and 0.63 , respectively). A significant increase in self-fertilization rates has been reported for the emergent legume *D. excelsa* in undisturbed and fragmented forests in Brazil ($t_m = 0.897$ and 0.845 , respectively) (Dick *et al*, 2003), and in Costa Rica reduced outcrossing rates were documented for *Symphonia globulifera* ($t_m = 0.902$ and 0.739 ; Aldrich and Hamrick, 1998) and *P. quinata* ($t_m = 0.915$ and 0.777 ; Fuchs *et al*, 2003) in disturbed habitats that contained low population densities of reproductive trees.

Other factors are expected to cause variation in mating system, but have not been covered here due to lack of comparative data. These factors include the influence of pollination syndrome (Barrett, 2003), canopy height (understory, canopy, emergent) and colonization guild. The pollination syndromes of neotropical trees are highly variable, and include small and large insects (eg Bawa *et al*, 1985), hummingbirds (the principal avian pollinator in the neotropics; eg Degen *et al*, 2004), bats (eg Murawski and Hamrick, 1991; Collevatti *et al*, 2001) and, rarely, wind (eg Alvarez-Buylla and Garay, 1994) or wind-directed insect pollination (Nason *et al*, 1998). Insect pollination syndromes are well represented, but important and distinctive groups have been overlooked, such as the small beetle pollination system of the Myristicaceae (Armstrong and Irvine, 1989).

Pollen dispersal

The first allozyme studies of pollen dispersal in tropical trees tracked rare alleles or used fractional paternity analysis, permitting direct inference of pollen dispersal over hundreds of metres in undisturbed forest (Hamrick and Murawski, 1990; Boshier *et al*, 1995b; Loveless *et al*, 1998). Hamrick and Murawski (1990) found that 20% of pollen moved over 750 m in *P. elegans*, and over 25% of pollen moved more than 500 m in *Tachigali versicolor* in undisturbed forest on Barro Colorado Island (BCI) Panama (also see Loveless *et al*, 1998). Both tree species are large, mass-flowering papilionoid legumes found in low densities, and are pollinated by large bees (eg *Centris*, *Xylocopa*). Stacy *et al* (1996) studied pollen

dispersal in three tree species found in low densities (~ 0.3 tree/ha) on BCI, whose small-insect floral visitors include beetles, small bees and moths. The combination of rarity and small-insect pollination leads to an expectation of low outcrossing and nearest-neighbour mating (Levin and Kerster, 1974). Counter to this expectation, all three populations were 100% outcrossed, and pollen dispersal distances exceeded the mean distances to the nearest potential mates. Violation of nearest-neighbour mating may occur in low-density populations because nearest flowering neighbours are in fact not close (> 50 m) and small insects may frequently not fly in the direction of the nearest neighbour. In a study of an almost monospecific stand of moth-pollinated *Cordia alliodora* (Boraginaceae) in Costa Rica, Boshier *et al* (1995b) reported a majority of pollen dispersal at 75 m, with some travelling over 280 m. Though the number of comparable studies is low, these results suggest that trees in low-density populations receive pollen over larger distances than do densely spaced trees.

In addition, or possibly due to an ecological or pollination byproduct of density, the relative canopy position and colonization guild of tropical trees are also expected to influence gene flow and mating system dynamics (Bawa *et al*, 1985; Nason and Hamrick, 1997). However, few mating system studies have been conducted on subcanopy/understory species or slow-growing, shade-tolerant species, making comparisons with the better-studied classes of canopy/emergents and pioneer species, respectively, problematic. Such studies would have to involve a large sample of species with sufficient representation of other key traits (ie inbreeding depression, population density and phylogeny), and may be possible in future, following further work on individual case studies.

Fig trees (*Ficus*) on BCI are the lowest density populations yet studied with respect to pollen dispersal (Nason *et al*, 1996, 1998). Figs are generally obligately outcrossing and are pollinated by miniscule (~ 2 mm) wasps (Agaonidae), which live only for 2–3 days. Figs usually have species-specific relationships with wasp pollinators (for counterexamples, see Molbo *et al*, 2003). Several species of *Ficus* on BCI occur at very low population densities; for example, there are only 20 known adults of *Ficus dugandii* in 16 km² of forest of BCI. Often, a single pollinating wasp visits the inverted fig inflorescence, in which case the seeds from that fruit are full siblings. Nason *et al* (1998) reconstructed paternal diploid genotypes of singly pollinated fruits through exclusion analysis, and found that fruits on maternal trees had numerous pollen donors. In all, 15 fruits from a *F. dugandii*, for example, yielded a minimum estimate of 11 pollen donors. The authors suggest that the number of pollen donors would have continued to rise if more single-sired fruits had been genotyped. Based on the population density, the authors estimated that pollen is routinely dispersed over distances of 5.8–14.2 km, and that the breeding areas of these figs range from 106 to 632 km². How do tiny, ephemeral wasps orient themselves and travel such long distances between conspecific trees? The authors suggest that the fig wasps become windborne, then hone in on scents produced by the receptive flowering tree. Further research is needed to precisely characterize mating patterns in this

fascinating system, and to test the hypothesis of directed pollen dispersal.

Vertebrate pollinators are also capable of maintaining tree reproductive populations over large spatial scales. For example, bats have been noted to carry *C. pentandra* pollen over distances greater than 5 km in many instances, and a maximum dispersal distance of 18.6 km observed (Gribel, reported in Wilson *et al*, 2001), the greatest single pollen dispersal distance so far recorded in the literature.

The development of analytical techniques such as Two-Gener (Austerlitz *et al*, 2004; Smouse and Sork, 2004) has made it possible to infer the shape of the pollen dispersal curve using genotyped seed arrays, mapped maternal trees and an estimate of population density. The method treats the pollen pool of a progeny array as a population, then estimates genetic differentiation with an F_{st} -based statistic. Using this approach, Dick *et al* (2003) estimated the mean pollen dispersal distance of *Dinizia excelsa* of 212 m in undisturbed forest. Degen *et al* (2004) estimate the mean pollen dispersal distances for *S. globulifera* of between 27 and 53 m, depending on the model used. The shorter pollen dispersal distance may be explained by the pollination system of *S. globulifera* (hummingbird) compared to *D. excelsa* (small bee), or by the difference in population density: the effective density of *S. globulifera* is more than 10 times greater than *D. excelsa*.

Conclusions and future recommendations

Neotropical tree species exhibit characteristics in the reproductive system that allow demographic persistence and heterozygosity even at low population densities. Selection pressures against inbreeding in low-density populations of tropical trees has presumably been the main driving force responsible for the evolution of these characters, which include (1) the constellation of attraction mechanisms for animal pollination and pollinator constancy (see Endress, 1998), and (2) the widespread occurrence of self-incompatibility mechanisms (eg Bawa *et al*, 1985). Genetic studies show that tropical animals can be very efficient vectors of pollen flow, capable of promoting outcrossing and successfully moving pollen between distantly spaced individuals in heterogeneous habitats.

Despite these advances in our understanding of reproduction and gene flow in neotropical trees, the available research barely touches the surface of the taxonomic and ecological diversity represented in these plants. Several areas for future research can be highlighted based on the findings of this review:

- (1) Further work is required to examine the fitness consequences of mating system variation. This requires focus on the effects of inbreeding depression, and measurement of the relative fitness of selfed *vs* outcrossed progeny at various life-history stages.
- (2) Researchers need to be aware of the possibility of apomixes in the seed production. This will be evident with microsatellites when maternal trees and seeds share identical multilocus genotypes.
- (3) There is a need to understand how particular classes of pollinators serve as pollen vectors. These include

the small-beetle pollination system found in the nutmeg family (Myristicaceae), euglossine bee and hummingbird pollination.

- (4) Genetic studies of pollen dispersal often fail to document the putative pollinators. While many neotropical trees are visited by generalist pollinators, there is often a narrower range of effective pollinators (Bawa, 1992) and pollinator communities may shift across habitats (Dick, 2001). The effective pollinators need to be identified so that generalizations can be applied to other plant taxa sharing those pollinators.
- (5) More studies should document the range of mating system variation across multiple seasons, as significant seasonal variation has been noted where investigated (eg Rocha and Aguilar, 2001).
- (6) More work is required to examine the relationship between mating system and key ecosystem class (canopy *vs* understory, pioneers *vs* shade tolerant). Several theoretical predictions have been made connected with population density and pollinator motility, but lack of comparative data sets has so far not allowed rigorous empirical assessment.

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