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BREEDING SYSTEMS OF EPIPHYTES IN A TROPICAL MONTANE WET FOREST

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ABSTRACT. We determined the breeding systems, in this case the physiological acceptance or rejection of self-produced pollen, of epiphytic species in a tropical montane wet forest in Monteverde, Costa Rica. Controlled pollinations were performed in the field and self-compatibility was determined on the basis of fruit set. All fifteen species, distributed among five families, were found to be self-compatible. This represents the highest incidence of self-compatibility among any life form at any tropical site. It is suggested that aspects of epiphytic existence may favor self-compatibility. Thus, some inbreeding may occur in the epiphytic community, despite the prevalence of highly specialized pollination systems which promote outcrossing.

Predominantly outcrossed plant species maintain higher levels of genetic diversity than do predominantly selfing species (Hamrick & Godt 1990). Compatibility systems are correlated with outcrossing levels by either permitting or preventing self-fertilization, therefore the sampling of compatibility systems has provided an estimate of outcrossing in tropical communities. Self-compatibility was proposed for the majority of tropical trees due to the spatial isolation of conspecifics (Fedorov 1966). However, studies indicate that tropical lowland rainforest trees are overwhelmingly outcrossed due to self-incompatibility or dioecism (Bawa 1990, Kress & Beach 1994). Although self-incompatibility and diocey are less frequent among tropical understory plants, reproductive characters which enhance outcrossing are prevalent (Kress 1983; Kress & Beach 1994).

The reproductive biology of epiphytes, particularly outcrossing mechanisms, is not as well documented as in other tropical forest life forms (Ackerman 1986, Kress & Beach 1994). Dioecy is less common among epiphytes than trees at a lowland site in Panama (Croat 1979). However, epiphytes tend to have more highly specialized pollination systems than do other life forms in tropical forests, particularly in the Orchidaceae (Ackerman 1986, Gentry & Dodson 1987). Here we present the results of a breeding system survey in Monteverde, Costa Rica which is, to our knowledge, the first of an epiphytic community. We sampled species primarily from the Bromeliaceae, Gesnereaceae, and the Orchidaceae. The neotropical angiosperm families with the most epiphytic species are, in decreasing order, the Orchidaceae, Bromeliaceae, Araceae, Piperaceae, Melastomataceae, and Gesnereaceae (Gentry & Dodson 1987). In Monteverde, a similar species composition was found in a survey of epiphytes upon *Ocotea tonduzii,* a common dominant tree species (Ingram & Nadkarni 1993). In addition to a previous study of epiphytic Melstomataceae (Lumer 1980), our survey completes a representative sampling of the epiphytic community of Monteverde.

STUDY SITE

The study was conducted in the montane forest of Monteverde, Costa Rica (10°18′N, 84°48′W), between 1500 and 1800 m in elevation. Forest types included Leeward Cloud Forest, Windward Cloud Forest, Swamp Forest and Elfin Forest (Lawton & Dryer 1980). The plants studied were growing in the canopies of host trees in forests and cleared fields, as well as upon fallen limbs and trees. Pollinators were not observed for all species studied. Eight species tested are known to be pollinated by hummingbirds (see Linhart *et al.* 1987), which are common pollinators in tropical montane forests (Linhart *et al.* 1987). *Epidendrum obesum* is pollinated by hawkmoths, and *Utricularia praetermissa* is likely pollinated by large bees (B. Haber pers. comm.). Bat pollination is widespread in the Vriesea genus (Benzing 1990). Although pollinators were not observed for the three species of Vriesea studied, bat pollination is likely. Each species produced flowers which opened at dusk and displayed floral morphologies which were consistent with bat pollination.

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TABLE 1. Results of pollinations documenting self-compatibility.

Family and species	P	Proportion of flowers setting fruit: Selfed (n)	P	Crossed (n)
Bromeliaceae				
Guzmania nicaraguensis	6	*0.62 (52)		
Pitcairnia brittoniana	5	1.00 (44)	5	1.00 (12)
Vriesea bracteosa	5	0.78 (28)	5	0.41 (22)
Vriesea hygrometrica	6	0.89 (10)	6	0.46 (13)
Vriesea sp.	1	1.00 (9)		
Gesnereaceae				
Campanea grandiflora	3	0.75 (4)		
Columnea microcalyx	15	0.45 (82)	14	0.67 (83)
Columnea magnifica	9	0.73 (34)	6	0.64 (22)
Drymonia conchocalyx	4	0.77 (17)	2	0.67 (3)
Drymonia rubra	12	0.68 (19)	3	1.00 (6)
Lentibulariaceae				
Utricularia praetermissa	3	0.83 (12)	3	0.67 (9)
Lobeliaceae				
Burmeistera tenuifolia	5	0.77 (17)		
Orchidaceae				
Epidendrum obesum	3	0.33 (18)	3	0.41 (12)
Pleurothallis cardiothallis	4	0.75 (20)	4	0.67 (21)
Sobralia amabilis	5	0.43 (32)	5	0.41 (22)

P = number of plants tested.
n = number of flowers pollinated.
* Flowers were bagged without experimental pollen transfer.

METHODS

Controlled pollinations were conducted in the field to determine breeding systems. Flowers from 15 species were isolated prior to opening in either paper pollination bags or cloth mesh bags. Pollinations were performed on the first day of flower opening by placing a visible quantity of pollen upon the stigma. For eleven species, on each plant one or more flowers were pollinated with pollen from the same flower, and one or more flowers were cross pollinated. Equivalent amounts of pollen were used for self and cross pollinations. In four species only self-pollinations were performed. Plants were then checked periodically for the production of fruit. Four hummingbird pollinated species were tested for autogamy, in this case self-fertilization achieved in the absence of pollinators, as flowers were isolated in bags and no experimental pollen transfer was performed.

RESULTS

Successful pollinations were those which resulted in the production of fruits which contained seeds. Following the criteria of Bawa (1974) self-compatible species were those in which fruit set in self-pollinations was at least 33% of that observed in cross pollinations. In the four species in which no cross pollinations were performed, self-compatibility was determined on the basis of extensive fruit set resulting from self-pollinations. All 15 species studied were found to be self-compatible (TABLE I). The proportion of selfed flowers setting fruit was high in all species of Bromeliaceae, Lentibulariaceae, and Lobeliaceae studied, ranging from 62% to 100%. In the Orchidaceae the proportion of self-pollinated flowers setting fruit was lower; however, the proportion of selfed to crossed flowers setting fruit was similar within each species. In eight of eleven species, fruit set in self pollinations was equal to or greater than that produced in cross pollinations, indicating a high level of self-fertility.

Two of the four species tested for autogamy, *Guzmania nicaraguensis* and *Pitcairnia brittoniana,* are readily capable of vectorless self-pollination, based upon the high percentages of fruit set observed in bagged flowers (TABLE II). The percent fruit set observed in bagged flowers of *Burmeistera tenuifolia* was low; however, autogamy was demonstrated. *Drymonia conchocalyx* was found to be incapable of autogamy, as none of the fifteen bagged flowers set fruit.

Discussion

The results reported here and those of Lumer (1980) who had tested self-compatibility in seven species of epiphytes in the Melastomataceae, demonstrate self-compatibility in 100% of the 22 epiphytic species studied in Monteverde. This represents the highest proportion of self-compatible species documented within any life form at any tropical site. The lowest proportion of self-compatibility documented is 21%, in a survey of 34 tree species at a lowland site in Guanacaste, Cost Rica (Bawa 1974). At a premontane wet forest (La Selva, Costa Rica) the incidence of self-compatibility among 57 species of trees, shrubs and herbs surveyed is 49%, with self-compatibility detected among 66% of the understory plants studied (Kress & Beach 1994). The proportion of self-compatible plants is higher in two tropical montane forests, with 56% of 25 species of trees, shrubs, and herbs self-compatible in Venezuela (Sobrevila & Arroyo 1982), and 88% self-compatible in a limited study of eight tree species in Jamaica (Tanner 1982). A trend toward a higher incidence of self-compatibility has not been detected in trees of Monteverde, where all seven species of Leguminous trees tested were found to be self-incompatible (Koptur 1984).

The epiphytic habitat may be a critical determinant in the evolution of the high incidence of self-compatibility within the community. Epiphytic plant size is typically restricted (Ackerman 1986), and resources available for sexual reproduction may be limited (Benzing 1990). Therefore, epiphytes typically produce fewer flowers per day than species of other life forms, possibly limiting plant attractiveness to pollinators when in competition for pollinator service with more floriferous species. Also, epiphyte populations tend to be hyperdispersed and seldom clumped (Ackerman 1986). The epiphytic habitat is often ephemeral and unpredictable, as changes in the size, structure, and also death of the supporting plant may induce epiphyte mortality (Ackerman 1986).

Ackerman (1986) has argued that constraints imposed by the epiphytic habitat may have influenced the evolution of the highly specialized pollinator relationships observed in many epiphytes. Ackerman also suggests that low daily flower production, coupled with highly specialized pollinators, reduces the probability for geitonogamy. Self-compatibility may therefore be selectively neutral in epiphytes (Ackerman 1986), as has also been suggested for tropical understory plants (Kress 1983).

An important benefit of self-compatibility is the increased probability of successful pollination (Bawa 1974), as demonstrated by a higher fruit to flower ratio among open pollinated, self-compatible tree species than in open-pollinated, self-incompatible tree species in a tropical dry forest (Bawa 1974). Hummingbirds are typical of the specialized long distance pollinators which service many epiphytic species. We documented a high frequency of autogamy in two of the four hummingbird pollinated species studied. Vectorless self-pollination has also been documented in many species of orchids with highly specialized pollination systems (Catling 1990). Pollinator visitation may be unpredictable in epiphytes due to limited floral display or plant isolation, thus autogamy or geitonogamy may be favored. Also, as resources available for sexual reproduction may be limited in epiphytes as Benzing (1990) maintains, self-compatibility may be selected for due to the increased probability of pollination it offers. Although aspects of epiphytic reproductive systems likely promote outcrossing, inbreeding through self-fertilization may be significant among epiphytes in tropical forests.

Table 2. Species tested for autogamy.

Species	Proportion of flowers setting fruit (P)	(n)	Autogamous
Burmeistera tenuifolia	(6)	0.16 (12)	Yes
Drymonia conchocalyx	(4)	0.00 (15)	No
Guzmania nicaraguensis	(6)	0.62 (52)	Yes
Pitcairnia brittoniana	(5)	0.91 (79)	Yes

P = number of plants tested.
n = number of flowers tested.

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