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BREEDING SYSTEMS, FRUIT SET, AND FLOWERING PHENOLOGY OF EPIPHYTIC BROMELIADS AND ORCHIDS IN A MEXICAN HUMID MONTANE FOREST

PETER HIETZ* AND MANUELA WINKLER

Institute of Botany, Universität für Bodenkultur, Gregor-Mendel-Strasse 33, A-1180 Vienna,
Austria. Email: peter.hietz@boku.ac.at

LETICIA CRUZ-PAREDES

Instituto de Ecología A.C., Apdo. 63, 91000 Xalapa, Veracruz, Mexico.

ANGÉLICA JIMÉNEZ-AGUILAR

Instituto de Ecología A.C., Apdo. 63, 91000 Xalapa, Veracruz, Mexico; Current address: Instituto
Potosino de Investigación Científica y Técnologica, Camino a la Presa San José 2055,
San Luis Potosí, México.

ABSTRACT. Epiphyte pollination is constrained by a stressful habitat that limits the amount of resources to be invested in pollinator attraction. Other constraints are the difficulty of locating conspecific individuals in sometimes highly dispersed populations within the canopy and the ephemeral substrate where branch failure may cut short the time available for successful reproduction. The authors conducted pollination experiments on the relationships of breeding systems, pollination success, flowering phenology, and microhabitat preference in epiphytic orchids and bromeliads in a Mexican humid montane forest. Phenology and fruit set also were observed. The breeding systems ranged from dioecious (*Catopsis sessiliflora*) to largely or entirely self-incompatible and outcrossing (*Tillandsia multicaulis, T. punctulata,* and *Lycaste aromatica*) to partly or mainly self-pollinating (*T. juncea, Jacquiniella teretifolia,* and probably *J. leucomelana*). Fruit set in the field was highest in the orchid *Jacquiniella teretifolia* (76–88%) and in the bromeliad *Catopsis sessiliflora* (71%), both of which grow preferentially on more exposed branches. Ranked next were monocarpic *Tillandsia deppeana* (60%) and xeric *T. juncea* (60%). Fruit set was lower in *J. leucomelana* (29–40%), *T. multicaulis* (41%), and *T. punctulata* (25%) and lowest in long-lived *L. aromatica* (8–11%), plants of which grow mostly on stable branches. The trend for selfing and/or higher fruits sets found in species growing on more ephemeral branches or adapted to more resource-poor conditions suggests that epiphyte pollination reflects adaptations to the diversity of canopy microsites.

Key words: breeding system, Bromeliaceae, epiphyte, fruit set, Mexico, Orchidaceae

INTRODUCTION

In zoophilous plants, investment in pollinator attraction increases the probability of being visited, but current investment in reproduction may reduce future growth or reproduction. Life-history theory suggests that plants invest resources to maximize reproductive output, and that evolution selects plants not limited by pollinators but by resources invested either in attraction or in seed production (Janzen 1977, Ashman et al. 2004). Theory also suggests that plant pollination systems optimize the balance between the chance of an ovule being fertilized by cross-pollination and the genetic disadvantage of inbreeding-depression through self-pollination (Tanaka 1997, Johnsen et al. 2003). Though some species effectively exclude selfing by being dioecious or self-incompatible, others take no risks and self-pollinate, in which case they spare resources for attracting pollinators.

Inbreeding depression is measured as reduced fruit set or reduced seed or embryo numbers in cross-pollinated versus self-pollinated plants. It is stronger in normally outcrossing than in selfing species, suggesting that the main cause of inbreeding depression (deleterious alleles) has been eliminated or reduced in the evolution of selfing species (Tremblay et al. 2005). Thus self-pollination ought to provide a relative advantage where pollinators are scarce or attracting them is too costly or in circumstances where reproduction is severely time-limited. The time-limitation hypothesis has been used to explain why most self-pollinating plants are annuals (Aarssen 2000) and why selfers are over-represented among annuals in particularly time-limited habitats (Snell & Aarssen 2005).

Tropical epiphytes are not annuals but, in most cases, polycarpic perennials that live in a

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* Corresponding author.

habitat with severe resource limitation. In addition to the mostly small to moderate size of epiphytes, resources likely limit the potential for pollinator attraction (Ackerman 1986, Benzing 1990). Epiphytes, however, also live in an ephemeral habitat, where exfoliating bark, breaking branches, and falling trees impose limits on life expectancy. Epiphytes that fall to the ground usually die, and branch instability is known to be a factor of mortality and population growth (Hietz 1997, Zotz 1998, Hietz et al. 2001, Zotz & Schmidt 2006). With epiphyte diversity in humid tropical forests high and conspecific individuals often at a distance, pollinator specificity is significant and reflected in a high diversity of floral structures, as illustrated in the largest epiphytic family, the orchids (Ackerman 1986).

In plants where fruit maturation takes a relatively long time, as in most epiphytes, fruit set (proportion of developing fruits to total number of flowers present) is a useful and easy-to-obtain measure of pollination success (Neiland & Wilcock 1998). A higher fruit set does not necessarily result in an increased reproductive output, however, because the investment in more fruits may lead to fewer seeds or reduced vegetative and reproductive growth in the future (Montalvo & Ackerman 1987, Zimmerman & Aide 1989, Ackerman & Montalvo 1990, Bartareau 1995, Melendez-Ackerman et al. 2000). Detailed demographic studies with experimental variation of fruit sets show that the low fruit set found in many orchids does indeed indicate pollinator limitation (Calvo & Horvitz 1990, Calvo 1993). Orchids appear to be often pollinator-limited (Neiland & Wilcock 1998, Tremblay et al. 2005) and Ashman et al. (2004) provide a theoretical framework for pollen limitation. Recent reviews report significantly higher natural fruit set in rewarding than in deceptive orchids, percentages about twice as high in temperate compared to tropical orchids (Tremblay et al. 2005), and no difference between epiphytic and terrestrial species (Neiland & Wilcock 1998).

While many tropical woody plants are self-incompatible (Bawa 1974, Bullock 1985, Kress & Beach 1994, Ward et al. 2005), all 22 epiphytes studied in a Costa Rican cloud forest were self-compatible (Lumer 1980, Bush & Beach 1995). Most orchids, including epiphytes, are also self-compatible (Dressler 1981, Tremblay et al. 2005), and a number are self-pollinating (Catling 1990). Self-incompatibility, however, appears to be common in some groups such as *Pleurothallis* (Borba et al. 2001) and *Epidendroideae* (Tremblay et al. 2005). Self-compatibility also was reported for at least 20 out of 35 Brazilian bromeliads (Martinelli 1994 cited in Benzing 2000) and autogamy for 8 out of 188 bromeliads from the Bolivian Andes (Kessler & Krömer 2000), although the latter data were largely inferred from pollination syndromes and not verified by experiments. Since epiphytes live in a resource-poor and more or less ephemeral habitat, which limits resources and time for reproduction, selection may favor pollination systems that enable successful reproduction in the absence of either a pollinator or a nearby conspecific. In epiphytes from xeric and/or very ephemeral habitats, where plant size is often reduced and the time for successful reproduction is short, the pressure for autogamy or geitonogamy may be particularly high (Benzing 1978, Gilmartin & Brown 1985). For the present study, breeding systems and natural fruit set of eight common epiphytic species in a Mexican humid montane forest were analyzed, looking for relationships between selfing, self-compatibility, phenology, fruit set, and the preferred microhabitat of a species. We hypothesized that mechanisms increasing reproductive output with less investment in pollinator attraction will be more common in the more xeric species and in species preferring thin and short-lived branches.

METHODS

The study was conducted in the Botanical Garden Clavijero and a small forest reserve adjacent to the Instituto de Ecología, 2.5 km south of Xalapa, in central Veracruz, Mexico (19°31′N, 96°57′W) at ca. 1350 m. Average temperature is 19°C, and annual precipitation is 1500 mm, most of which falls in the wet season between June and October. According to the Holdridge life-zone system (Holdridge 1967), the forest is at the transition between premontane and lower montane moist forests. In Mexico, it is commonly classified as 'bosque mesófilo de montaña' (mesophilous montane forest; Rzedowski 1986). Descriptions of the forest structure are given by Williams-Linera (1997) and of the epiphyte community by Hietz & Hietz-Seifert (1995).

Three orchid and five bromeliad species were studied (TABLE 1). *Jacquiniella teretifolia* (Sw.) Britton & P.Wilson has caespitose erect stems with distichous, almost terete leaves and yellowish-green flowers, ca. 2 cm long, without distinct fragrance. *Jacquiniella leucomelana* (Rchb. f.) Schltr. is of similar habit, but stems and leaves are usually less than half as large and flowers measure only 3 mm. *Lycaste aromatica* (Graham ex Hook.) Lindl. has thin, drought-deciduous leaves at the top of a broad pseudobulb, with dark-yellow flowers arising from the base of the pseudobulb. The flowers emit a strong smell of

TABLE 1. Average number of flowers per flowering shoot (orchids) or ramet (bromeliads), average diameter of branches occupied by reproductively mature individuals, and probability of a reproductively mature individual to fall with its breaking branch within a year.

Epiphyte species	Flowers per shoot or ramet No. (SD; *N*)	Branch diameter cm (SD; *N*)	Probability of epiphyte falling with branch
Bromeliaceae			
Catopsis sessiliflora	29.3 (22.8; 41)	3.9 (4.7; 88)	0.205
Tillandsia deppeana	74.3 (11.7; 8)	5.5 (2.5; 20)	0.120
Tillandsia juncea	16.4 (7.2; 17)	11.1 (8.1; 635)	0.063
Tillandsia multicaulis	12.9 (5.6; 19)	7.8 (6.7; 606)	0.106
Tillandsia punctulata	13.4 (7.4; 34)	8.4 (4.9; 794)	0.079
Orchidaceae			
Jacquiniella leucomelana	2.6 (27; 188)	7.4 (4.9; 43)	0.115
Jacquiniella teretifolia	2.9 (3.2; 39)	7.6 (8.0; 432)	0.103
Lycaste aromatica	4.3 (3.1; 157)	16.8 (9.6; 22)	0.023

Source: Data on branch diameter (Buchberger 2004), data on branch stability (Hietz 1997).
Note: No. = average number of flowers per shoot; SD = Standard deviation; *N* = number of plants.

cinnamon and are pollinated by euglossine bees (Dressler 1968). *Tillandsia deppeana* Steud. produces a large impounding rosette and a pinnate inflorescence, up to 80 cm tall, with reddish bracts and blue to violet corollas. *Tillandsia multicaulis* Steud. also has bright reddish bracts and blue corollas, but a smaller rosette and several sessile spikes, not exceeding the leaves. *Tillandsia punctulata* Schltdl. & Cham. is of tank-atmospheric intermediate habit; the inflorescence is about as long or slightly longer than the leaves and composed of few, densely digitate spikes with red bracts and dark violet petals with a white apex. *Tillandsia juncea* (Ruiz & Pav.) Poir. has filiform, fasciculate leaves; the inflorescence is rather small, composed of few, dense spikes; the bracts are reddish but less conspicuous than in the congeners studied; and the petals are violet. Although not growing on more exposed branches, *T. juncea* is clearly the most xeric of the bromeliads and the only species exhibiting Crassulacean acid metabolism (CAM). In contrast to the other species that are hermaphroditic, *Catopsis sessiliflora* (Ruiz & Pavón) Mez is dioecious; the leaves form small and narrow tanks; the inflorescence is pinnate or bi-pinnate with ca. 1 cm long creamish flowers and small and inconspicuous green bracts. *Tillandsia deppeana* is largely monocarpic, and the other species are polycarpic. The average number of flowers per ramet or individual and the diameter of branches, upon which reproductively mature individuals were growing are presented in TABLE 1.

Plants with developing inflorescences but without open flowers were collected in the forest with as much substrate (branch or bark) as possible and transferred ca. 50 m from the forest edge to the Botanical Garden Clavijero, where they were watered only by rainfall and were not fertilized. Light conditions were similar to those in the mid canopy, but more uniform than in the forest. Transplantation stress and differences in microclimate or pollinator presence may affect the reproductive output. This effect, however, was considered insignificant, since the pollination experiments in the garden were designed mainly to test for self-pollination and self-compatibility and not for reproductive success under natural conditions. Between March 2002 and May 2003, controlled pollination experiments were conducted for all species except *Tillandsia deppeana,* where inflorescences died before producing fruits and dioecious *Catopsis.*

Young flowers, spikes, or entire inflorescences received the following treatments: (A) some were emasculated, enclosed in fine-mesh bags, and pollinated with pollen from the same flower; (B) some were emasculated, bagged, and self-pollinated with pollen from a different flower of the same individual; (C) some were emasculated, bagged, and cross-pollinated with pollen from another plant; and (D) some were left untouched and bagged. With the very small flowers of *Jacquiniella,* hand-pollination was not possible; and flowers were either bagged and untouched (D) or remained open (E) as controls. Between August 2001 (wet season) and February 2004 (dry season), to assess pollination success under field conditions, counts were made of peduncles or dried flowers and fruits on orchid individuals that are part of a long-term population study. Because, in this study, observations of bromeliad inflorescences were not made over

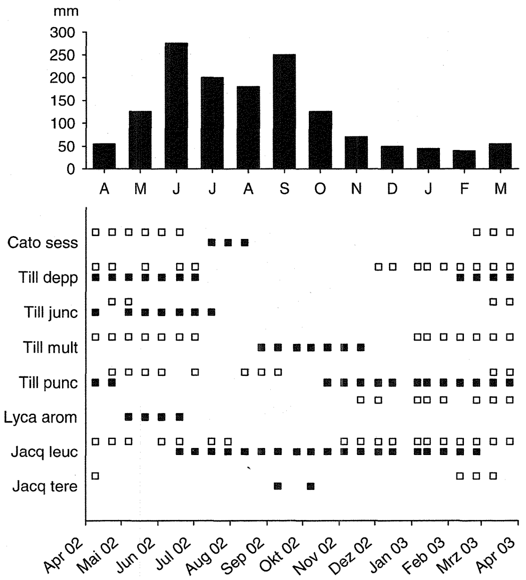

FIGURE 1. Rainfall (top) and phenology (bottom) of flowering (full symbols) and presence of mature seeds (empty symbols) of epiphytes studied in a Mexican humid montane forest. For species abbreviations see TABLE 1.

an extended period, we counted the number of flowers per ramet once (TABLE 1) and the number of fruits on different ramets later in the year, and calculated fruit set as the average number of capsules/average number of flowers per ramet.

The phenology of flowering and fruiting was observed by qualitatively recording the state of inflorescences along trails in the field in biweekly intervals between April 2002 and March 2003.

To assess the impact of branch size and stability on survival, we compared the branch-size distribution of reproductively mature individuals (data from Buchberger 2004) with the probability that a branch of a given size breaks within a year (data from Hietz 1997) to calculate the probability for a reproducing individual of a species to fall with its supporting branch within a year (TABLE 1).

RESULTS

Flowering phenology was diverse. The deciduous *Lycaste aromatica* flowered at the beginning of the rainy season prior to leaf production, *Jacquiniella teretifolia* towards the end of the rainy season, *J. leucomelana* during most of the year, *Tillandsia punctulata* and *T. deppeana* mainly during the dry season, and *T. multicaulis* and *Catopsis* during the wet season (FIGURE 1). Fruits had matured and seeds were dispersing mostly from the dry season to the beginning of the rainy season.

Out of the three species of *Tillandsia* tested, one (*T. juncea*) is self-compatible, with fruit sets similar in self- and cross-pollinated flowers (fruit sets 67–89%, TABLE 2). *Tillandsia juncea* also is capable of self-pollination, though self-pollination resulted in a somewhat lower fruit set (48%). *Tillandsia punctulata* and *T. multicaulis,* which are clearly not self-pollinating, also are largely self-incompatible, with self-pollination resulting in only about 3% of flowers producing fruits. Whether flowers were pollinated with pollen from the same flower, or from a different flower but the same individual (treatments A and B) made no difference. Whereas fruit sets of bagged *Jacquiniella teretifolia* and open controls were equally high, only 2 out of 57 flowers in bagged *J. leucomelana* self-pollinated, but pollination of open controls was also low in this species. In *Lycaste aromatica,* no self-pollination occurred, and only one flower each in treatments A and B set fruit, whereas 39% of cross-fertilizations were successful (TABLE 2).

Selfing also can result in lower fruit set in species that are not 100% self-incompatible. This effect is quantified by the index of self-incompatibility, which is the ratio of the fruit set of hand self-pollinated to the fruit set of hand cross-pollinated flowers (Bullock 1985). By combining self-pollination and geitonogamy (treatments A and B), the index of self-incompatibility is >1 for *Tillandsia juncea,* 0.06 for *T. multicaulis,* 0.09 for *T. punctulata* and 0.11 for *Lycaste aromatica.*

Natural fruit set (TABLE 3) in the potentially self-pollinating *Tillandsia juncea* was somewhat higher than with experimental exclusion of pollinators. Fruit set in the other species that are not selfing was between 70% in dioecious *Catopsis* and 25% in *T. punctulata.* Natural fruit set among the orchids was always lowest in *Lycaste aromatica* (8–11%); in *Jacquiniella teretifolia,* it was slightly higher than in the bagged and open controls exposed in the Botanical Garden (76–88%); and in *J. leucomelana,* it was substantially higher (29–40%) than in the experimental plants (FIGURE 2). In the orchids, fruit set was relatively constant in three consecutive years, though *J. leucomelana* could not be evaluated during the last observation in the dry season when flowers of this species were largely absent.

DISCUSSION

A prolonged flowering season could increase the probability of pollination, which should be

TABLE 2. Results of pollination experiments with the following treatments: A. Emasculated, bagged, and self-pollinated with pollen of the same flower. B. Emasculated, bagged, and self-pollinated with pollen from a different flower of the same individual. C. Emasculated, bagged, and cross-pollinated with pollen from another plant. D. Untouched and bagged. E. Open controls, exposed in the Botanical Garden Clavijero, Veracruz, Mexico.

Epiphyte species	Treatment	No. flowers/ individuals	Fruit set	
			Mean	(SD)
Tillandsia juncea	A	28/5	0.67	(0.41)
	B	35/5	0.89	(0.15)
	C	37/13	0.67	(0.38)
	D	167/6	0.48	(0.25)
Tillandsia multicaulis	A	45/15	0.03	(0.13)
	B	50/13	0.02	(0.06)
	C	42/11	0.56	(0.40)
	D	94/5	0.00	(0.00)
Tillandsia punctulata	A	42/10	0.00	(0.00)
	B	41/14	0.06	(0.18)
	C	42/15	0.42	(0.44)
	D	64/5	0.00	(0.00)
Jacquiniella leucomelana	D	57/11	0.02	(0.04)
	E	171/27	0.16	(0.28)
Jacquiniella teretifolia	D	37/25	0.75	(0.43)
	E	34/16	0.72	(0.37)
Lycaste aromatica	A	24/6	0.08	(0.20)
	B	21/3	0.07	(0.12)
	C	25/4	0.39	(0.28)
	D	24/4	0.00	(0.00)

an advantage for species growing on ephemeral substrates that may not live to the next flowering season. Among the species on thinner branches *Jacquiniella leucomelana* flowered for most of the year, but flowers of *Catopsis* and *J. teretifolia* each were observed only during a 2-month period; and the length of the flowering season did not appear to be related to habitat preferences.

Large inflorescences or showy flowers may attract more pollinators, but no apparent relationship was found between flower or inflorescence size and fruit set. Flower or inflorescence size is relatively large in *Lycaste* and *Tillandsia deppeana,* small in *Catopsis* and *Jacquiniella* spp., and intermediate in the other bromeliads.

The eight epiphytes investigated have diverse breeding systems: *Catopsis sessiliflora* is dioecious, *Tillandsia multicaulis, T. punctulata,* and *Lycaste aromatica* are largely or entirely self-incompatible and outcrossing, and *T. juncea* and *Jacquiniella teretifolia* are partly or mainly self-pollinating. The low fruit set of bagged and the moderate fruit set of openly pollinated *J. leucomelana* would suggest this species to be outcrossing. Observations that the minute flowers are nearly closed, do not produce nectar, and that fruit sets in the field were much higher than in the experimental control plants, questions the results of the pollination experiment and points to self-pollination, as reported earlier for this species (Catling 1990). The mesh bags of the pol-

TABLE 3. Numbers of flowers and capsules per inflorescence and fruit set under natural conditions in epiphytic bromeliads.

Epiphyte species	Flower buds/ inflorescence No. (SD; *N*)	Capsules/ inflorescence No. (SD; *N*)	Average fruit set
Catopsis sessiliflora	29.3 (22.8; 41)	20.4 (10.6; 62)	0.706
Tillandsia deppeana	66.1 (26.1; 9)	44.4 (40.2; 31)	0.597
Tillandsia juncea	16.4 (7.2; 17)	9.8 (9.4; 69)	0.599
Tillandsia multicaulis	12.9 (5.6; 19)	5.3 (4.4; 93)	0.412
Tillandsia punctulata	13.4 (7.4; 34)	3.4 (2.5; 33)	0.254

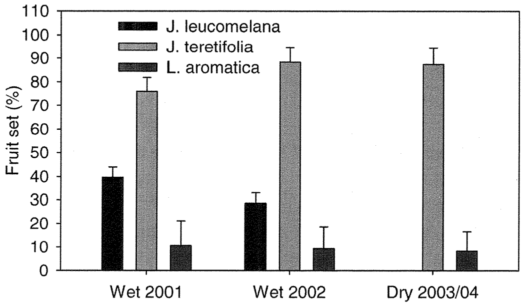

FIGURE 2. Average (±SE) fruit set of *Lycaste aromatica, Jacquiniella leucomelana,* and *J. teretifolia* in a natural forest during a 3-year period.

lination experiment (D) may have prevented self-pollination, if this is facilitated by rain or wind. Rain-facilitated selfing was reported for *Liparis loeselii* (Catling 1980), though the flower of *J. leucomelana* has no similarity with that species. Also a previous report that found *T. deppeana* self-compatible but not selfing (García-Franco & Rico-Gray 1991) is questionable; those pollination experiments largely failed; and not only the self-pollination, but also the cross-pollination produced no fruit at all.

Natural fruit set in bromeliads was highest in *Catopsis,* followed by *Tillandsia juncea, T. deppeana, T. multicaulis,* and *T. punctulata.* In the outcrossing *T. punctulata* and *T. multicaulis* natural fruit set was 74% and 60%, respectively, of hand-cross pollinated individuals; and natural fruit set was ≥60% in the other bromeliads. This is substantially higher than the fruit set in outcrossing *Lycaste aromatica* and in many other orchids (Neiland & Wilcock 1998, Tremblay et al. 2005), suggesting that bromeliads are less pollinator-limited than orchids. In *T. juncea,* fruit set in the field (60%) was not much higher than fruit set of only self-pollinating flowers (48%); thus a substantial proportion of flowers appears to be selfing under field conditions. This is the only atmospheric and certainly the most xeric species tested, and a high frequency of selfing concurs with the trend suggested for extreme epiphytes (Benzing 1978, Gilmartin & Brown 1985). A trend for selfing in xeric bromeliads also is reflected in isoenzyme variation, which shows strong inbreeding in the extremely xeric *Tillandsia recurvata,* a species with very small flowers. In contrast, the semi-xeric *T. ionantha,* which has long violet flowers and showy red bracts, is mainly or entirely outcrossing (Soltis et al. 1987). The floral morphology of *T. punctulata,* where the stigma comes into close contact with the anthers, led to the assumption of self-pollination (Gardner 1986), but this is clearly not the case.

Benzing (2000) states that selfing is most conspicuous in monocarpic *Tillandsia* subgen. *Tillandsia,* but cites only the example of *T. utriculata.* Unfortunately, we could not test the breeding system of monocarpic *T. deppeana*; and an earlier report is dubious. Ensuring high fruit set through selfing or at least self-compatibility would be an obvious advantage for monocarpic species that, like annuals, cannot save resources not used by unpollinated flowers for future vegetative or generative growth. This hypothesis, however, awaits more pollination studies in monocarpic and polycarpic species. Apart from the breeding system, the very attractive inflorescence of *T. deppeana* and its production of ca. twice as much nectar per flower as *T. multicaulis* (Ordano & Ornelas 2004) should favor pollination resulting in the high fruit set observed.

Tillandsia deppeana, T. multicaulis, and *T. punctulata* were observed being visited by hummingbirds. At least *T. deppeana* and *T. multicaulis* also are visited by bees and butterflies and respond to repeated nectar removal by producing >3 times the nectar than unvisited flowers (Ordano & Ornelas 2004). Their flowers, therefore, are likely to be visited more than once and by more than one pollinating species, resulting in a high fruit set. *Catopsis sessiliflora,* while not of xeric habit, tends to grow on smaller and less stable branches than do the other bromeliads studied, with a corresponding high mortality of reproductive individuals (TABLE 1) and selective pressure to ensure high fruit set. Though the fruit set of *Catopsis* was indeed high, no responsible mechanism was obvious. The genus *Catopsis* includes dioecious and hermaphroditic species. Also within the species *C. sessiliflora,* some populations have perfect flowers, and others are dioecious (Benzing 2000). The population studied was entirely dioecious and therefore obligate outcrossing in contrast to xeric species of *Tillandsia* or *Jacquiniella* growing on relatively unstable branches. Although we did not observe or find reports on pollinators, *Catopsis sessiliflora,* which is certainly pollinated by insects, has the least conspicuous floral display of the bromeliads studied. This contrasts particularly with the low success of *Lycaste aromatica,* which has relatively large (ca. 5 cm), strongly scented, and dark yellow flowers, lasting for many days and pollinated by euglossine bees. While the density of *Lycaste* in the forest is not high, plants tend to grow in clusters on individual branches of trees, so that finding another flowering plant should not be difficult for the bees. Several species of orchids pollinated by

Euglossinae and Melpomini bees have low fruit set in spite of frequent visitation, which is explained by incompatibility, geitanogamous pollination by bees remaining for several minutes at individual inflorescences, and low genetic variability (Singer 2001, Singer & Koehler 2003). If neighboring individuals of *Lycaste* are closely related and share the same alleles determining incompatibility, many cross-pollinations may not result in fertile fruits. This, together with reliance on a specific pollinator, can explain the low fruit set.

Whether resulting from rare pollinators or self-incompatibility, fruit set may be less limiting for *Lycaste,* which is a long-lived species growing on large and rather stable branches, than it is for *Jacquiniella* spp. and *Catopsis,* growing on less stable substrate. Two other orchids, studied in a nearby coffee plantation and also fairly common in the forest, confirm this pattern. While *Maxillaria densa,* which prefers thicker branches, was largely self-incompatible and had a natural fruit set of 18.2%, *Scaphyglottis livida,* growing on thinner and more exposed branches, was self-compatible, though not autogamous, and had a natural fruit set of 35.5% (Solis-Montero et al. 2005).

The time-limitation hypothesis, which states that selfing has evolved as a consequence of strong selection in ephemeral habitats, was confirmed in a review of annual plants, where selfing is generally widespread and occurs in higher frequencies in two of the most severely time-limited habitats—deserts and cultivated habitats (Snell & Aarssen 2005). In epiphytes, in addition to the temporal constraint on ephemeral branches, the potential investment in pollinator attraction is limited by resource availability, which is particularly true for xeric species adapted to dry forests or microhabitats.

In general, results from species studied here and by others (Gilmartin & Brown 1985, Solis-Montero et al. 2005) suggest that perennial epiphytes preferring the more ephemeral branches tend to ensure pollination by being autogamous, or at least increase the chances of pollination by being self-compatible. Breeding systems as well as habitat preferences, however, may also be related to phylogenetic groups. As an example, twig epiphytes among the orchids are mostly related genera within the Oncidiinae and appear to have smaller genome sizes, which may be an advantage in ephemeral and stressful habitats (Chase et al. 2005). Also, self-incompatibility and self-pollination are unevenly distributed within the orchids (Catling 1990, Borba et al. 2001, Tremblay et al. 2005). To sort out which traits are primarily phylogenetic, possibly representing pre-adaptations enabling the colonization of certain habitats, and which have evolved in response to specific habitats, data from a larger number of species is needed.

Epiphyte pollination has received early and widespread attention (Darwin 1888, van der Pijl & Dodson 1966) and remains a worthwhile subject for the study of breeding systems and pollination strategies as adaptations to specific environmental constraints. The present study, while generally supporting the time-limitation hypothesis, does leave open the intriguing question—what is the function of showy flowers, pollinator rewards, and breeding systems that promote pollination, if *Catopsis sessiliflora* achieved the highest fruit set in our study with guaranteed outcrossing and little apparent investment in reproductive structures or pollinator attraction?

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