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## PRIOR AUTONOMOUS SELFING IN THE HUMMINGBIRD-POLLINATED EPIPHYTE *TILLANDSIA MULTICAULIS* (BROMELIACEAE)

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**ABSTRACT.** *Tillandsia multicaulis* is an epiphytic bromeliad found in montane forests from Panama to Mexico. In Veracruz, Mexico, *T. multicaulis* is self-incompatible. However, in Monteverde, Costa Rica, large amounts of self-pollen are transferred autonomously to the stigma before and during floral opening. I hypothesized that *T. multicaulis* is self-compatible and capable of autonomous self-pollination in Costa Rica, and I examined the breeding system of one population in Monteverde. Fruit and seed set were high in open-, self-, and cross-pollinated treatments, and in caged, unmanipulated flowers. Flowers emasculated two days before opening did not set fruit. Therefore, *T. multicaulis* is self-compatible and autogamous, but not agamospermous in Monteverde. Prior selfing occurs during the day before anthesis. Fruit set ranged from 22–32% in emasculation treatments performed the day before anthesis to 78% among flowers emasculated within one hour after floral opening. Although plants in Monteverde offer pollen and nectar rewards and are visited by pollen-collecting bees and hummingbirds, past pollen limitation has likely driven the evolution of self-compatibility. The current potential for fruit set via autonomous self-pollination is high, thus populations may be predominantly inbred. However, mixed mating could be maintained if outcrossed pollen is prepotent or if post-fertilization mortality is higher among inbred offspring.

**Key words:** bromeliad, tropical montane cloud forest, plant breeding system, autonomous self-pollination, hummingbird pollination, reproductive assurance

### INTRODUCTION

Vascular epiphyte species richness is greatest in intermediate elevation neotropical wet forests (Gentry 1982, Cardelús et al. 2006), where their reproductive biology has been examined at several locations. One of the most well-studied locations is the cloud forest of Monteverde, Costa Rica, where approximately 870 species, or 29% of the flora, are epiphytes (Haber 2000). At Monteverde the incidence of self-compatibility among epiphytic taxa greatly exceeds that found in any life form in the tropics (Bush & Beach 1995). All of the 31 epiphytic species tested are self-compatible, including 14 bromeliads (Bush & Beach 1995; Cascante-Marín et al. 2005, 2006; Bush unpubl. data). Many of the bromeliads studied in Monteverde are also capable of autonomous self-pollination, typically because the anthers and stigma are closely associated at anthesis (Bush & Beach 1995; Cascante-Marín et al. 2005, 2006). The underlying factors favoring autonomous self-fertilization, or autogamy, in Monteverde bromeliads are untested. However, one of the presumed benefits of autogamy is to provide reproductive assurance when cross-pollination is unpredictable (Levin 1971). A variety of factors potentially limit opportunities for outcrossing in epiphytic plants (Benzing 1990, Bush & Beach 1995). Most epiphytes are severely resource-limited and plant size is restricted (Benzing 1990). Consequently, epiphytes produce relatively few flowers (Ack-

erman 1986, Benzing 1990) and they may be less attractive to pollinators than terrestrial plants that present larger floral displays (Benzing 1990). The pollination systems of the majority of epiphytes are specialized (Madison 1977, Gentry & Dodson 1987), a trait frequently associated with outcrossing. However, a recent review suggests that autonomously self-pollinating taxa frequently have specialized pollinator relationships (Fenster & Martén-Rodríguez 2007). Perhaps visitation rates are reduced when pollination is limited to a narrow class of vectors, and autonomous selfing serves to ensure reproduction when cross-pollination is insufficient (Fenster & Martén-Rodríguez 2007). Since epiphyte populations are typically hyperdispersed rather than clumped (Ackerman 1986, Benzing 1990), epiphytes tend to be isolated from potential mates. A low density of flowering conspecifics, in addition to limited floral displays, should reduce visitation rates and thus strengthen the selection of autogamy in epiphytes with specialized pollinator relationships. Lastly, selfing may be advantageous in the ephemeral canopy habitat (Benzing 1990, Bush & Beach 1995, Hietz et al. 2006), where survival to reproduction is uncertain due to exfoliating bark, branch falls, and host tree falls (Ackerman 1986, Hietz et al. 2002). Whatever the selective advantage, self-fertilization is important for many bromeliads in Monteverde, despite conditions that favor high species richness.

*Tillandsia multicaulis* Steud. is a geographically-widespread epiphytic bromeliad found in primary and secondary forests of Monteverde. Large quantities of pollen are transferred autonomously to the stigma before and during anthesis in *T. multicaulis* found in Monteverde, similar to many other autogamous bromeliads in this locale. However, in the moist montane forest of Veracruz, Mexico, *T. multicaulis* is strongly self-incompatible and fruit set is moderate in natural populations (Hietz et al. 2006). The relative positioning of the anthers and stigma in Mexican *T. multicaulis* has not been described, and previous studies make no mention of either the presence or the absence of the autonomous transfer of self-pollen in Veracruz populations (Hietz et al. 2006, Ordano & Ornelas 2004). The breeding systems of epiphytes studied in Veracruz contrast with those examined in Monteverde. Three of six species examined in Veracruz are self-incompatible, including two of the three bromeliads tested (Hietz et al. 2006). Selfing breeding systems and higher rates of natural fruit set were associated with species growing on more ephemeral branches and in resource-limited canopy microsites, suggesting that selfing is adaptive in ephemeral epiphytic habitats (Hietz et al. 2006). While *T. multicaulis* may be self-incompatible in Monteverde as well, the large amount of self-pollen transfer suggests a self-compatible breeding system. Self pollen can impede cross pollination by clogging stigmas and by interfering with pollen export or receipt (Webb & Lloyd 1986); therefore, the majority of outcrossing plants maintain mechanisms that separate male and female function (Lloyd & Webb 1986) to minimize the interfering effects of self-pollen. If *T. multicaulis* is self-incompatible in Monteverde, the large quantity of self pollen transferred autonomously could significantly reduce fecundity. Alternatively, if self-compatible in Monteverde, autonomous self-pollination may be important in ensuring seed set. I hypothesized that Costa Rican *T. multicaulis* are self-compatible and capable of autonomous self-pollination. I tested the breeding system in one Monteverde population of *T. multicaulis*, including the potential for, and possible timing of, autonomous self-pollination.

*Tillandsia multicaulis* ranges from Mexico to Panama, and is generally found in forests from 1200 to 1900 m in elevation (Smith & Downs 1977). It is a common species in Costa Rica, where specimens have been collected from 950 to 2300 m (Morales 2000). The biology and ecology of *T. multicaulis* have been studied extensively in the humid montane forest of Veracruz, Mexico (elevation 1350 m), including its nectar production (Ordano & Ornelas 2004),

breeding system (Hietz et al. 2006), and role in the epiphyte community (Hietz et al. 2002; Flores-Palacios & García-Franco 2004; Winkler et al. 2005, 2007). *Tillandsia multicaulis* is a tank bromeliad that has the capacity for clonal growth. In Veracruz it is slow-growing and reaches fertility after 9–16 years (Hietz et al. 2002, Winkler et al. 2007). Veracruz populations flower during the wet season (July to November) (Ordano & Ornelas 2004, Hietz et al. 2006), while flowering in Costa Rica has been reported between February and April (Morales 2000). The floral morphology of *T. multicaulis* is characteristic of pollination by long-billed hummingbirds (Haber 2000): approximately 7 cm long, tubular, nectar-containing, and with orange and purple coloration. Gardner (1986) suggested that the high production of pollen in *T. multicaulis* is characteristic of bee pollination. Pollen-collecting bees and hummingbirds were observed visiting flowers in Veracruz populations of *T. multicaulis* (Ordano & Ornelas 2004, Hietz et al. 2006). The floral bracts of *T. multicaulis* vary from red to orange (Morales, 2000), while the petals are deep purple. The bracts produce a slimy fluid of unknown function that envelopes unopened buds and developing fruits (Gardner 1986). In Veracruz, *T. multicaulis* responded to nectar removal by replenishing with more than three times the volume of the initial nectar removed (Ordano & Ornelas 2004). There was no relationship between the deposition of pollen on stigmas by hand and subsequent nectar production, nor was nectar reabsorbed following pollen deposition (Ordano & Ornelas 2004). However, there was a significant cost associated with nectar replenishment, as nectar removal reduced seed set by 50% (Ordano & Ornelas 2005). Hummingbird flower mites consume pollen and nectar from *T. multicaulis* plants in Veracruz (García-Franco et al. 2001).

## METHODS

The present study was conducted at approximately 1500 m on Pacific Ocean-facing slopes of the Cordillera de Tilarán, in Monteverde, Costa Rica (10°18'N, 84°48'W). The forest community is classified as lower montane wet forest (Holdridge 1967), and receives an average of 2500–3500 mm of rainfall per year (Haber 2000) which is concentrated in the rainy season lasting from May through October. Mist and cloud-water are frequent throughout the remainder of the year, which includes a windy-misty season (November to January) and a dry season (February to April) (Clark et al. 2000). The plants in the population studied in Monteverde were confirmed as *T. multicaulis* by a local bro-

omous self-pollination occurred in the bud stage during the day before anthesis. Pollen-collecting bees of the genus *Trigona*, and the long-billed hummingbird *Phaethornis guy* were observed visiting open flowers. During 9.1 hours of observation, there were 16 bee visits and one hummingbird visit. The mean nectar volume of the four flowers tested was 6.6  $\mu$ l, and the mean total sugar production per flower was 1.3 mg, both similar to that found previously in Veracruz (Ordano & Ornelas 2004).

### DISCUSSION

The breeding system of *Tillandsia multicaulis* in Monteverde differs greatly from the self-incompatible Veracruz population. In Veracruz, the proportion of *T. multicaulis* flowers producing fruit in the hand self-treatment was 6% of that in the cross-pollinated treatment (Hietz et al. 2006), while in Monteverde fruit set was slightly higher following self-pollination (85%) than after crossing (77%). No fruiting occurred in bagged and unmanipulated flowers in Veracruz, compared to 79% fruit set in similarly treated flowers in Monteverde. Fruit set was much higher in open-pollinated flowers in Monteverde, 91%, compared to only 41% in Veracruz. In contrast to the variation in self-incompatibility, the pollination of *T. multicaulis* appears relatively similar in Costa Rica and Mexico. In both locations plants present nectar and pollen rewards and are visited by hummingbirds and bees. However, the foraging behavior of pollen-collecting bees is very different from that of long-billed hummingbirds. *Trigona* bees typically collect pollen from a wide variety of plants, at times indiscriminately visiting any plant with accessible pollen (Lobo 2000). Although bees were the most common visitors in Monteverde, they are likely to effect cross-pollination only among clumped individuals in secondary forests, or among the co-habitants of one tree in an abandoned field. Long-billed hummingbirds are capable of moving pollen over much greater distances, such as those that typically separate *T. multicaulis* individuals in primary forest. Hummingbird trapliners typically forage among widely-spaced individuals, traveling specific routes several times per day in their search for high-quality nectar rewards (Linhart et al. 1987). Although only one hummingbird visit was observed, foraging behaviors, nectar production, and floral morphology suggest that hummingbirds are the primary pollinators of *T. multicaulis*.

One of the most common evolutionary trends in flowering plants is the shift from outcrossing to selfing, which may transpire when the level

of cross-pollination is insufficient for the fertilization of all of the ovules within a flower (Stebbins 1974). Pollen limitation is typically estimated via the comparison of seed set of supplemental hand pollinations to that of open-pollinated flowers. By this estimate, *Tillandsia multicaulis* is not presently pollen-limited in Monteverde, as the open-pollinated and hand cross-pollinated treatments did not differ significantly. However, this comparison does not shed light on the extent of current cross-pollen limitation in Monteverde; the level of fruit set in open-pollinated flowers detected in this study could potentially be achieved either via autonomous selfing or by cross-pollination. The conclusions that can be drawn from comparisons between open-pollinated treatments in Monteverde and Veracruz are limited, as the studies were done in different years and included only one population per study. Nevertheless, for open-pollinated flowers, fruit set was much lower in the self-incompatible Veracruz population than in Monteverde. Perhaps formerly self-incompatible *T. multicaulis* populations were pollen limited in Costa Rica, and self-compatibility evolved to ensure adequate fruit set. Pollen limitation and self-compatibility are often associated with marginal or isolated habitats (Stebbins 1957, Rick et al. 1977). Monteverde would generally not be considered marginal epiphytic habitat, given the species richness and abundance of epiphytes, and also because the altitudinal limit of *T. multicaulis* in Costa Rica is approximately 800 m higher than Monteverde. Furthermore, the high fruit and seed set observed in Monteverde suggests that reproduction in *T. multicaulis* is not greatly limited by resources at present. Therefore, present or past pollen limitation is likely the cause of the evolution of autonomous selfing in Monteverde. One factor that may have contributed to a reduction in the efficiency of cross-pollination in *T. multicaulis* in Monteverde is climate change. Over the past 30 years in Monteverde, daily minimum and maximum temperatures have increased across all seasons (Pounds et al. 2006), and the elevation at which clouds form has likely increased as well (Still et al. 1999). The number of days without mist precipitation during the Monteverde dry season, during which *T. multicaulis* flowers, has increased dramatically since the 1970s (Pounds et al. 1999). The change in mist frequency in Monteverde is associated with changes in the local distributions of birds, reptiles, and amphibians (Pounds et al. 1999). Perhaps the change in climate has also modified the pollination environment of *T. multicaulis*. Bromeliad phenology can be altered by aspects of climate change that are similar to those that have occurred in Mon-

teverde. In a Puerto Rican population of the tropical montane bromeliad *Werauhia sintenisii*, the annual onset of flowering differed by one month between two consecutive years. The shift in flowering was related to increase in mean minimums in temperature and solar irradiation in the months preceding flowering (Lasso & Ackerman 2003). Changes in either the phenology of *T. multicaulis*, or of species with which it shares pollinators, may have increased competition and thus reduced the frequency of visitation to *T. multicaulis*.

The potential for fruit set via autonomous self-pollination in natural populations of *Tillandsia multicaulis* is high; auto-fertility indices averaged greater than one and the reproductive output of the autogamy and open-pollinated treatments were similar. The actual rate of autonomous selfing can be estimated by comparing seed set in emasculated, open-pollinated flowers to seed set in unmanipulated, open-pollinated flowers (Eckert et al. 2006). The actual rate could not be estimated for *T. multicaulis*, due to the damaging effects of emasculation. In the Monteverde population, the anthers must be removed two days before anthesis to ensure that stigmas are self-pollen free. When emasculations were performed at this time in the agamospermy control treatment, floral shape was dramatically altered, floral damage was extensive, and fruit set reduced by approximately 40% relative to supplemental self- and cross-pollinations. In a literature review of autonomous selfing, primarily based upon taxa that self at senescence, Fenster and Martén-Rodriguez (2007) found that estimates of the actual rate of selfing (0.31) are significantly lower than potential selfing rates (0.79). Therefore, the actual rate of autonomous self-pollination in *T. multicaulis* may be lower than the high potential rates estimated from fruit set (0.92) and seed set (1.10).

The timing of self-fertilization influences the amount of reproductive assurance provided by autonomous selfing. Earlier selfing increases the potential that selfing will supersede outcrossing (Lloyd & Schoen 1992), and minimize the reproductive assurance value of selfing. In relation to opportunities for outcrossing, autonomous selfing may be either prior, competing, or delayed (Lloyd & Schoen 1992). In *T. multicaulis* in Monteverde, prior selfing can commence at least 18–20 hours before anthesis. Among flowers emasculated at this time, 22% eventually produced fruit. The anthers tend to grow increasingly close to the stigma and the potential for pollen transfer increases as flower development continues. Thirty-two percent of flowers emasculated 12–14 hours pre-anthesis set fruit, and the mean number of seeds per fruit (269.1) was

greater than the mean number of seeds among flowers emasculated earlier in the day (141.5). By anthesis, the quantity of pollen transferred to the stigma in caged flowers yields mean levels of fruit set (77.7%) and seed production (308.1 per fruit) similar to that produced by either open-pollinated or hand-pollinated flowers. The rates of prior and competing selfing may be high in natural populations, and *T. multicaulis* may be largely inbred. However, prior selfing does not preclude outcrossing in *T. multicaulis*. Since hummingbird visitation rates are high at dawn (Feinsinger 1987) and *Trigona* bees are very active in the morning (Lobo 2000), flowers could receive a mixture of self- and cross-pollen very soon after flowers open. Outcrossed pollen can be competitively superior in pollen tube growth, or prepotent, relative to self-pollen (Darwin 1876, Bateman 1956, Cruzan & Barret 1993). It seems likely that the pollen deposited the day before anthesis, which yielded between 22–32% fruit set in caged treatments, would effect fertilization before cross-pollen under natural conditions. If prepotent, outcrossed pollen deposited closer to the time of floral opening could compete successfully with prior self-pollen. Higher post-fertilization mortality among inbred offspring may also increase the proportion of outcrossed progeny that survive to reproduction. Therefore, selfing could ensure reproduction in the absence of pollinators, and *T. multicaulis* may maintain a mixed mating system in Monteverde.

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## UPDATED INSTRUCTIONS FOR AUTHORS

With *Selbyana* 30, we have revised the “Instructions for Authors” to make the submission, review, and publication process more efficient and effective. The revised instructions now clearly state how and in what format documents should be submitted and explain what authors can expect during the review process. Authors new to *Selbyana*, as well as those familiar with publishing in our journal, are encouraged to read these revised instructions.

Most notable in the revised instructions are the slight modifications to and greater detail in explaining the format of manuscripts. The need for parallel formatting of manuscripts in a journal may seem self-evident—parallel construction affords a level of continuity in the finished product making the journal a cohesive, recognizable unit. Additionally, uniformly formatted documents allow reviewers and editors to effectively evaluate the content of manuscripts without unnecessary complications from unique and/or arbitrary style.

~John R. Clark, Assistant Editor, *Selbyana*

### INSTRUCTIONS FOR AUTHORS

#### Overview

*Selbyana* (ISSN 0361-185X) is the scientific journal of the Marie Selby Botanical Gardens and is published twice a year by Selby Botanical Gardens Press, 811 S. Palm Ave., Sarasota, FL 34236-7726 USA. Articles published in *Selbyana* are original studies that explore various aspects of tropical forest diversity with an emphasis on epiphytes and their forest canopy habitats. The focus on epiphytes and canopy habitats is considered broadly in *Selbyana* and includes not only epiphyte diversity and ecology but also studies on entire families or groups that partially or wholly contain epiphytic species. Papers on anatomical/cellular/molecular traits of taxa are encouraged for submission as are papers dealing with floristics, natural history, conservation biology, plant-animal interactions, and other related topics.

Editorials address relevant topics of current interest to tropical biologists including discussions on current debates in botany and related fields.

*Horti Selbyani* is an occasional column by prominent researchers working in the field of tropical botany and ecology.

Book Review proposals may be submitted to the Editor for approval.

Announcements are also published.

#### Submission of Manuscript for Review

All manuscripts must be submitted electronically. Hardcopies alone are not accepted. The text must be submitted as a document file, preferably in Microsoft Word format (.doc files). Rich text files (.rtf files) are also accepted. PDF files can not be accepted. Manuscripts can be either emailed to the Editor Wesley Higgins at whiggins@selby.org or burned to a CD or DVD

and mailed, along with a cover letter, to Dr. Wesley Higgins, Editor, Selby Gardens Press, % Marie Selby Botanical Gardens, 811 S. Palm Ave., Sarasota, FL 34236.

**Naming files.** Please name all electronic files beginning with the last name of the first author followed by the date of submission and ending with the file contents (e.g., Smith\_et\_al\_30Dec08\_text.doc, Smith\_et\_al\_30Dec08\_fig1.tif).

**Data.** All data, datasets and other relevant information must be made available to reviewers. Research involving phylogenetic analysis must include corresponding datasets (e.g., nexus format gene sequence matrices, morphological data matrices).

#### Manuscript Formatting

*Selbyana* instructions for authors should be reviewed and followed carefully before submitting a manuscript. Please refer to the most recent issues of *Selbyana* for current styles and formatting. Manuscripts not conforming to the basic formatting and style requirements will be returned to the author(s) for adjustment before the review process can begin.

**Page charges.** Please be concise. Articles of excessive length may be returned for rewrite. Page charges are US\$75 per page. Journal subscribers at the time of manuscript submission or during the year of publication are entitled to five free printed pages per volume. Under special circumstances, concessions are sometimes made for authors that cannot cover page charges. Please contact the editor for details and requirements. Color plates incur additional charges regardless of affiliation.

**Language.** Manuscripts must be submitted in English (please use American spelling; bilingual abstracts are accepted). Authors not fluent in