

VARIETY OF PHOROPHYTE SPECIES COLONIZED BY THE NEOTROPICAL EPIPHYTE, *LAELIA RUBESCENS* (ORCHIDACEAE)

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ABSTRACT. Epiphytes comprise ca. 10% of all vascular plant species and therefore contribute substantially to plant diversity, particularly in tropical and subtropical regions. Little is known, however, about the specificity of the relationship between epiphytes and their phorophytes. Phorophyte specificity is assessed for the neotropical epiphytic orchid, *Laelia rubescens* Lindley, in the tropical dry forest of Costa Rica. A rating system was used to account for local abundance of tree species supporting *L. rubescens* as well as for the geographic distribution of the orchid-phorophyte association. A nonspecific relationship was observed with *L. rubescens* growing on 33 tree species and, at one site, limestone rock. In every case where the orchid was locally abundant on a phorophyte, the association also was geographically widespread; however, 70% of the orchid-phorophyte associations were locally sparse. Of these, 35% were widespread, and 65% were restricted.

Key words: phorophyte specificity, Costa Rica, tropical dry forest, *Laelia rubescens* Lindley

INTRODUCTION

Vascular epiphytes contribute substantially to global plant diversity (Dressler 1981), accounting for ca. 10% (30,000) of all vascular plant species (Madison 1977, Kress 1986) and an estimated 70% of orchid species (Gentry & Dodson 1987). Epiphytes are particularly important in tropical and sub-tropical regions where they represent as much as 25% of all vascular plant species (Nieder et al. 2001). Highest epiphyte species diversity occurs in the neotropics (Richards 1957, Madison 1977, Gentry & Dodson 1987). Epiphytes experience substantial environmental stress that is greatly alleviated by the high moisture levels characteristic of many tropical habitats.

Holo-epiphytism (non-parasitic plants that spend their entire life cycle on other plants) has been reported for 83 vascular plant families and has evolved independently many times (Kress 1986). The Orchidaceae contains 60% of all epiphytic species and ten times as many epiphytic species as any other family of vascular plants (Kress 1986). Although epiphytes are a significant component of overall plant diversity, relatively little is known about the specificity of the association between epiphytes and their host trees (phorophytes). This association is of particular interest since epiphytes are confined to a patchy and discontinuous distribution of suitable

substrate. The specificity of the orchid-phorophyte relationship may have direct bearing on the abundance of epiphytic taxa, particularly as increasing rates of anthropogenic-related habitat disturbance exacerbate the patchiness of suitable substrate.

Epiphytes enjoy a unique suite of environmental advantages and challenges. Perhaps of most importance, they can compete better for sunlight than terrestrial herbaceous plants (Dressler 1981). Since air movement within the tree canopy is nearly constant, an epiphyte can tolerate direct sunlight without overheating. Epiphytes also can better avoid predation, attract pollinators, and capitalize on the wind to disperse their seeds (Dressler 1981); however, epiphytes and particularly those in drier habitats also must cope with the challenges of obtaining adequate moisture and nutrients. Successful seedling establishment on a phorophyte in a patchy and stressful environment depends on numerous biotic and abiotic factors. The most critical biotic factor for orchids is whether suitable mycorrhizae are present on the substrate on which seeds land. Because orchid seeds lack endosperm, they depend on an obligate endomycorrhizal association for carbon uptake before germination can begin.

Bark substrate characteristics also are of primary importance to seedling recruitment. These include bark texture, whether the bark is stable or exfoliating, its water-holding capacity, porosity, and bark chemistry (pH, growth inhibiting

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exudates, and/or leachates; see ter Steege & Cornelissen 1989). The more textured the bark, the more substrate recesses available to catch seeds and accumulate nutrients. Such pockets and fissures harbor humus and retain moisture. Light levels within the tree canopy vary considerably, also influencing recruitment. Not only will different parts of the tree canopy receive varying light exposure, but branch inclination affects light and moisture levels. Increased inclination is associated with reduced water, light, and nutrient accumulation (ter Steege & Cornelissen 1989).

Studies on the specificity of the relationship of epiphytes with their phorophytes have been minimal, but show that the degree of epiphyte specificity on phorophytes is variable. Some studies have found little host tree specialization in the epiphytes examined (e.g., Johansson 1974, Sanford 1974, Todzia 1986, Ackerman et al. 1989, Zimmerman & Olmsted 1992, Ackerman et al. 1996). Other investigators have found that some vascular epiphytes display phorophyte specificity or preference (e.g., Went 1940, Frei 1973, ter Steege & Cornelissen 1989, Merwin et al. 2003).

The objective of our study was to assess phorophyte specificity of the neotropical epiphytic orchid, *Laelia rubescens* Lindley, in Costa Rica. Allen (1959) reported that, in Panama, *L. rubescens* displayed strong host tree preference. Our research documents the variety of host tree species on which *L. rubescens* was found in the tropical dry forest of Costa Rica over six field seasons. We predicted that orchid establishment shows some preference for host tree species based on the presence of suitable mycorrhizal species, substrate texture, bark compounds, and light and moisture levels within tree canopies. We expected that suitable sites for seedling establishment might be somewhat limited by these factors and that phorophyte preference would be observed.

MATERIALS AND METHODS

Study Species

Laelia rubescens is a long-lived, neotropical, perennial epiphyte ranging from Mexico to Panama (Williams & Allen 1980) in dry habitats below 800 m (Mora de Retana & Atwood 1992). Its bisexual flowers are exclusively animal-pollinated with hummingbirds as the primary agents (D. Trapnell pers. obs.). Each fertilization results in hundreds of thousands of tiny, wind-dispersed seeds. Once established on suitable substrate, *L. rubescens* grows clonally with each fleshy pseudobulb (inflated stem tissue) capable

of producing one or two new pseudobulbs/year. Each pseudobulb bears one, and sometimes two, thick leathery leaves. Clusters can become quite large over time and possess 100 or more pseudobulbs. Each pseudobulb produces a single inflorescence with as many as 20 showy, pink flowers (Halbinger & Soto 1997). Anthesis is over an extended period (January–March) during the dry season. A single inflorescence can produce up to 11 capsules (D. Trapnell pers. obs.).

Study Sites

The study was conducted in the seasonally dry tropical forest of Costa Rica that is characterized by semi-deciduous trees and a 6-month dry season (December–May). *Laelia rubescens* capsules mature and release their seeds for wind dispersal toward the end of the dry season (April–May) when strong, dry, northeasterly winds prevail. Under normal environmental conditions, seeds remain viable for no more than a year (D. Trapnell pers. obs.). Although rainfall during the rainy season is substantial, the dry season is long and harsh. *Laelia rubescens* occurs in habitats ranging from primary forests to highly human-modified landscapes. In less disturbed forests, *L. rubescens* is widely dispersed with relatively few clusters per tree. In the mid-1950s, many of the dry forests of Costa Rica were converted to ranchland (Sader & Joyce 1988), and it is in open pastures that *L. rubescens* reaches its greatest abundance. When the tropical dry forest was cleared for cattle pastures, often one or more shade trees were left. These isolated trees typically have large spreading canopies, and it is on these trees that *L. rubescens* is most abundant with populations of 350 or more clusters. These trees support several other epiphytic species that occur at densities of a few individuals per tree. These include, but are not limited to, two orchids (*Brassavola nodosa* and *Prosthechea fragans*), one bromeliad (*Tillandsia schiedeana*), and a cactus (*Hylocereus costaricensis*).

Methodology

Observations were made throughout the seasonally dry tropical forest of Costa Rica during extensive collection for another study analyzing genetic structure among *Laelia rubescens* populations (Trapnell & Hamrick 2004). We systematically searched for populations from Peñas Blancas near the Nicaraguan border, through Guanacaste Province and much of the Nicoya Peninsula, and as far south as Jaco. When *L. rubescens* was found, the host tree species and

TABLE 1. Frequency of the neotropical epiphyte *Laelia rubescens* (Lr) found on phorophytes locally and over the orchid's geographic range in Costa Rican dry forest. Percentages are of 33 tree species (see TABLE 2) supporting Lr in each classification.

Abundance of Lr on phorophytes at locality	Geographic range of phorophyte/Lr association	
	Widespread (W)	Restricted (R)
Locally abundant (A)	Lr on many trees locally. Association with phorophyte widespread geographically. 12%	Lr on many trees locally. Association with phorophyte restricted geographically to one or few sites. 0%
Locally occasional (O)	Lr on varying number of trees locally. Association with phorophyte widespread geographically. 9%	Lr on varying number of trees locally. Association with phorophyte restricted geographically to one or few sites. 9%
Locally sparse (S)	Lr on one to a few trees locally. Association with phorophyte widespread geographically. 24%	Lr on one to a few trees locally. Association with phorophyte restricted geographically to one or few sites. 46%

location were recorded. Species and family names of phorophyte taxa on which *L. rubescens* was observed follow *Manual de la Flora de Costa Rica* (Instituto Nacional de Biodiversidad & Missouri Botanical Garden 1995). We also noted the number of individuals of that tree species supporting *L. rubescens* at a site. A rating system, similar to that of Rabinowitz (1981), was devised to account for local abundance of trees per species supporting *L. rubescens* as well as the geographic distribution of that orchid-phorophyte association (TABLE 1). For the occurrence of *L. rubescens* on a particular tree species to be rated "locally abundant" (A), several to many individuals of that tree species had to support *L. rubescens* at each site. A "locally sparse" (S) rating indicates that only one to a few trees of that species hosted the orchid at each site. This could be the result of the phorophyte being locally sparse or simply that very few trees within that species support the orchid. A "locally occasional" (O) rating represented cases where some locations had ≤ 3 trees with orchids, while other locations had many trees of that species supporting *L. rubescens*. The geographic distribution of trees possessing *L. rubescens* was recorded for each phorophyte species as widespread (W) or restricted (R).

RESULTS AND DISCUSSION

Laelia rubescens was found growing on 33 tree species and, at one site, on limestone rock (Palo Verde, TABLE 2). This is the second report, of which we are aware, of *L. rubescens* growing (and thriving) as a lithophyte (Allen 1959). Thirty-three species is an underestimate of the actual number of *L. rubescens* phorophyte taxa, be-

cause the dry forest was not comprehensively surveyed; and in a few cases, we were unable to identify the host tree. This ability to establish populations on multiple phorophyte taxa perhaps increases the long-term survival potential of *L. rubescens* by increasing potentially suitable substrate for colonization. This would be particularly advantageous in a landscape that is becoming increasingly altered by human activity.

Four orchid-phorophyte associations (12%) were locally abundant and widespread (TABLES 1, 2). None were locally abundant and restricted. Six orchid-host species associations (18%) were locally occasional; of these three (9%) were widespread, and three (9%) were restricted (TABLES 1, 2). Twenty-three associations (70%) were locally sparse, of which eight (24%) were widespread, and 15 (46%) were observed across a restricted geographic range (TABLES 1, 2). Sparse local abundance of *Laelia rubescens* on some tree species resulted from the sparse occurrence of the phorophyte itself. All locally abundant orchid-phorophyte associations also were widespread. Widespread associations, however, were not always locally abundant; sometimes they were occasional or sparse. Most of the orchid-phorophyte associations (70%) proved to be locally sparse. The largest proportion of orchid-phorophyte associations (46% of total) was locally sparse and distributed across a restricted geographic range.

Samanea saman was by far the most common host tree species. *Laelia rubescens* also was frequently observed on *Crescentia alata* and *Tabeuia* spp. In Panama, *C. alata* was the species with which *L. rubescens* typically associated (Allen 1959). For many tree species, we only recorded a single observation of *L. rubescens*

TABLE 2. Occurrence of phorophyte/*Laelia rubescens* (Lr) association in the Costa Rican dry forest.

Phorophyte/limestone	Family	Occurrence of Lr association
<i>Anacardium excelsum</i>	Anacardiaceae	WS
<i>Andira</i> sp.	Fabaceae	RS
<i>Ascosimum panamensis</i>	Fabaceae	RS
<i>Astronium graveolens</i>	Anacardiaceae	RS
<i>Bombacopsis quinatum</i>	Bombacaceae	WO
<i>Brosimum alicastrum</i>	Moraceae	WS
<i>Byrsonima crassifolia</i>	Malpighiaceae	RS
<i>Calycophyllum candidissimum</i>	Rubiaceae	WS
<i>Ceiba pentandra</i>	Bombacaceae	RO
<i>Coccoloba caracasana</i>	Polygonaceae	RS
<i>Crescentia alata</i>	Bignoniaceae	WA
<i>Dalbergia retusa</i>	Papilionoideae	RO
<i>Enterolobium cyclocarpum</i>	Mimosoideae	WS
<i>Ficus</i> sp.	Moraceae	RS
<i>Guazuma ulmifolia</i>	Sterculiaceae	WO
<i>Hura crepetans</i>	Euphorbiaceae	WS
<i>Hymenaea courbaril</i>	Fabaceae	RS
<i>Licania arborea</i>	Chrysobalanaceae	RO
<i>Lysiloma divaricatum</i>	Mimosoideae	WO
<i>Maclura tinctoria</i>	Moraceae	RS
<i>Piscidia carthagenensis</i>	Papilionoideae	RS
<i>Pterocarpus</i> sp.	Papilionoideae	RS
<i>Quercus</i> sp.	Fagaceae	RS
<i>Samanea saman</i>	Mimosoideae	WA
<i>Sciadodendron excelsum</i>	Araliaceae	RS
<i>Sideroxylon capiri</i>	Sapotaceae	RS
<i>Sideroxylon celastrinum</i>	Sapotaceae	WS
<i>Spondias mombin</i>	Anacardiaceae	WS
<i>Sterculia apetala</i>	Sterculiaceae	WS
<i>Swartzia panamensis</i>	Papilionoideae	RS
<i>Tabebuia ochracea</i>	Bignoniaceae	WA
<i>Tabebuia rosea</i>	Bignoniaceae	WA
<i>Terminalia oblonga</i>	Combretaceae	RS
Limestone rock	—	RS

Note: WA = widespread, locally abundant; WO = widespread, locally occasional; WS = widespread, locally sparse; RO = restricted, locally occasional; RS = restricted, locally sparse.

growing epiphytically. Most of the phorophyte taxa shared characteristically rough, fissured, or shaggy bark. It was exceptional to find *L. rubescens* on smooth-barked species, such as *Enterolobium cyclocarpum* and *Hymenaea courbaril*, even though they are common elements of this forest. Also little apparent consistency in light levels was observed within the tree canopy. Typically the orchids were shaded by the host tree's canopy. Often trees obviously dead for quite some time and completely devoid of any leaf cover still had robust clusters of *L. rubescens* apparently thriving and producing fruit. Orchids on one such tree produced fruit for at least 4 years after the tree's death. Although *L. rubescens* persists under these conditions, its seeds most likely cannot successfully colonize such an exposed tree. Of special interest was the frequency with which we observed what appeared to be ideal phorophytes completely devoid of *L.*

rubescens. For example, *S. saman* trees near *L. rubescens* phorophytes of comparable age and growth form often did not support *L. rubescens*. This may indicate that *L. rubescens* seeds have never arrived on such trees, which seems unlikely or that the necessary mycorrhizae had not established on this potential phorophyte. Another possibility is simply that the pressures exerted by this stressful environment have thus far prevented germination and seedling establishment of *L. rubescens* on many suitable phorophytes.

Our findings raise a number of questions. Is the large number of phorophytes documented for this epiphytic orchid a reflection of non-specificity of its mycorrhizal association or the catholic distribution of a specific taxon of mycorrhizae? Is the occurrence of bark sloughing and growth inhibitory substances less common in the tropical dry forest, where epiphyte load is less of a problem for phorophytes than in wetter

tropical forests? Is the observation of so many apparently suitable phorophytes in close proximity to established clusters of *Laelia rubescens* a reflection of the absence of necessary mycorrhizae fungi or simply the result of the harsh realities of surviving in the tropical dry forest? Or could it be that nearby clusters of *L. rubescens* experience little reproduction that could facilitate recruitment of uncolonized trees within close proximity? As is often the case, this investigation has raised a number of questions that warrant further investigation.

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