Epiphytic orchids in tropical dry forests of Yucatan, Mexico – Species occurrence, abundance and correlations with host tree characteristics and environmental conditions

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ABSTRACT

Tropical dry forests have been less studied in terms of their resident epiphyte flora compared to wet forests. We studied five species of epiphytic orchids in two dry forest fragments differing in tree composition, stature and rainfall regime. We compared the vertical distribution within the host tree, epiphyte-host associations and seasonal variation in microclimatic conditions in a tropical dry deciduous (Celestún) and a semi-deciduous forest (Kaxil-Kiuic) of the Yucatan Peninsula, Mexico, during the wet, early dry and dry seasons. Light, vapor pressure deficit, air temperature, and dew were measured on two heights (1.5 and 3.5 m) of the host with the highest abundance of orchids. Surprisingly, orchid abundance was higher in the Celestún deciduous forest, the site with low precipitation. High epiphyte abundance in the middle canopy stratum of the hosts in both forests was arguably related to a favorable combination of micro-environmental factors. In both forests, about 90% of all orchids grew on a single host tree species. Although bark roughness and the area of the substrate were the most important host characteristics that influenced the abundance of orchids in the Celestún deciduous forest, this did not explain this preference. Climatic variation was greater among seasons than between microenvironments in the host trees. The most abundant species, *Encyclia nematocaulon*, had a great capacity to occupy different strata in both forests, even in tree tops with very large micro-environmental fluctuations during the year.

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Introduction

The family Orchidaceae comprises about 27,000 species (Zotz, 2013), of which two thirds are epiphytes with a main distribution in tropical forests (Gentry and Dodson, 1987). Their outstanding success in the epiphytic habitat is arguably due to a number of attributes, which allow them to cope with the intermittent water supply in tree crowns. Orchids can optimize water usage through features such as succulent stems and leaves, sunken stomata, CO_2-uptake via crassulacean acid metabolism (CAM), quite impermeable cuticles, or roots with a velamen radicum (a multiple epidermis composed of dead cells surrounding the cortex; Benzing, 1990; Goh and Kluge, 1989; Helbsing et al., 2000; Zotz

and Winkler, 2013). Also, their success depends on specialized pollination systems, relationship with fungi, and mass seed production (Ackerman, 1986; Gravendeel et al., 2004). Most other plant families with a high proportion of epiphytes, e.g. Araceae, Ericaceae, Polypodiaceae, are rarely found in dry forests, while orchids and bromeliads can still be rather common, although both diversity and abundance of epiphytes usually decrease and are biased to few host species in drier forests (Gentry and Dodson, 1987; Vergara-Torres et al., 2010; Zimmerman and Olmsted, 1992); moreover, some of the dry forests in Mexico even lack epiphytes entirely (Rzedowski and Calderon de Rzedowski, 2013).

Dry forests represents around 40% of the tropical and subtropical forests (Holdridge, 1967) and belong to the most endangered tropical ecosystems due to diverse agricultural activities and human invasion (Trejo and Dirzo, 2000). Information on the ecology of the resident epiphytes of these forests is rare. Apart from other studies from Mexico (Reyes-García et al., 2008a) there are a few scattered reports from the Caribbean (e.g. Murphy and Lugo, 1986), from other part of the Americas, e.g. Brazil (Fontoura and Reinert,

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2009), or from Asia (Minagawa, 1997), but none of these studies provides detailed microclimatic information, distributional and plant trait data. However, it is important to generate information about the structure of the epiphytic community in these tropical dry forests, particularly data that allow a functional understanding of the relationship between the physical characteristics of the forest vegetation and the occurrence of orchids, as well as the influence of the microenvironment that may affect richness, abundance and plant traits in these forests.

Successful growth and survival of epiphytes are intimately linked to host tree traits, particularly in stressful environments. Tree architecture, phenology, water absorbing capacity of the bark, bark peeling behavior or differences in bark texture create a vertical stratification of micro-environmental conditions with substantial temporal variation (Callaway et al., 2002; Cardelús and Chazdon, 2005; Castro-Hernández et al., 1999; López-Villalobos et al., 2008). For example, epiphytes at the top of the canopy generally receive much more light and experience more drought than those at lower levels, but this gradient will vary substantially with leaf phenology of the host tree (Cervantes et al., 2005).

In dry forests, most of the trees lose their leaves during the dry season and epiphytes may receive up to nine times more photosynthetic photon flux density (PPFD) compared to the wet season (Graham and Andrade, 2004). Under these conditions, dew and fog interception can be an important source of water for these plants, and can even influence the vertical distribution of epiphytes (Andrade, 2003; Chesson et al., 2004; Graham and Andrade, 2004; Reyes-García et al., 2008b). Increased leaf succulence may also buffer epiphytes from short to medium-term environmental changes in water availability (Reyes-García et al., 2012).

We studied these relationships in two tropical dry forests of the Yucatan Peninsula, Mexico, taking advantage of the gradient of increasing rainfall from north to south. In the north we find there tropical dry deciduous forests with higher levels of radiation and low rainfall, whereas farther south, we find tropical semi-deciduous forests, with higher precipitation and lower levels of radiation due to increased canopy height and also increased cloud cover. The objectives of present investigation were: (a) to compare the vertical distribution and abundance of epiphytic orchids in two tropical dry forests with different precipitation regimes; (b) to characterize the micro-environmental gradients in which the epiphytic orchids grow and (c) to relate epiphytic orchid abundance to both the structural features of the host and the microclimatic gradients. We tested the following hypotheses: (i) orchid abundance will be greater in the semi-deciduous forest because of higher rainfall (Gentry and Dodson, 1987), (ii) there will be fewer individuals in the upper canopy of the host trees in both forests because micro-environmental conditions are more stressful compared to the middle and lower parts of the host trees, (iii) orchid leaf succulence will be greater and more variable in the deciduous forest than in the semi-deciduous one.

Materials and methods

Study sites and species

Field measurements were conducted at two sites in Yucatan, Mexico: (1) Celestún (20°50′53″ N, 90°14′17″ W), which receives an average annual rainfall and air temperature of 770 mm and 27 °C, respectively; and (2) Kaxil-Kiuic Biocultural Reserve (20°06′33″ N, 89°32′55″ W), with a mean annual rainfall and air temperature of 1200 mm and 26 °C (Orellana, 1999). The first site is characterized by a low-statured tropical dry deciduous forest of 8–10 m height. Most trees (>90%) drop their leaves during the dry season (March to May). The second site is characterized by a tropical dry semi-deciduous forest with taller trees (between 13 and 18 m). There, only 50–75% of the tree species drop their leaves during the dry season (Dupuy et al., 2012). In both forests the dry period alternates with a wet period (June to October), and an early dry period (November to February), known locally as "nortes", which is characterized by strong winds (>80 km h^{-1}), scattered rains (20–60 mm in total) and daily average temperatures below 20 °C (Orellana, 1999).

In total, we found six species of epiphytic orchids in the two forests, but *Brassavola appendiculata* A. Rich & Galeotti, which we found in the Celestún deciduous forest, was too rare to be included in our study. The five remaining, more common, species were *Encyclia nematocaulon* (BC Rich.) Acuña, *Cohniella yucatanensis* Cetzal and Carnevali and *Laelia rubescens* Lindley in Celestún deciduous forest; and *E. nematocaulon*, *Cohniella ascendens* (Lindley) Christenson and *Lophiaris oerstedii* (Rchb. f.) A. Jimenez, Carnevali and Dressler in Kaxil-Kiuic semi-deciduous forest. The orchids *C. ascendens*, *L. rubescens* and *L. oerstedii* are found in Mexico and Central America, *E. nematocaulon* in Mexico and the Caribbean, whereas *C. yucatanensis* is endemic to the Yucatan Peninsula.

Vertical distribution and abundance

At each study site, we randomly selected four 100 m² plots in a location with a relatively high density of epiphytic orchids; tree species identity, total tree height, diameter at breast height (dbh); the presence of orchids was determined for all trees with a dbh > 5 cm. Individual orchids were classified according to their size, "small" comprising plants with leaves up to 10 cm length and "large" used for all those with leaves exceeding 10 cm. For each orchid, we recorded species name, orientation and height above the forest floor. We randomly chose 20 individuals of each orchid species at each forest and measured leaf length and width. Leaf surface area was calculated as an ellipse (both surfaces) for *E. nematocaulon*, *L. rubescens* and *L. oerstedii* and as a cylinder area for *C. yucatanensis* and *C. ascendens*. Succulence, defined as water content per unit area was determined for all species during each of the three seasons at two heights (1.5 and 3.5 m height; $n = 5$) after Andrade (2003). For succulence, we chose leaves without damage from different plants of similar plant size at each season.

At each study site, we also determined the most abundant trees species. These were *Chloroleucon manguense* (Jacq.) Britton & Rose, *Gliricidia sepium* (Jacq.) Walp., *Guettarda elliptica* Sw., *Gymnopodium floribundum* Rolfe, *Malpighia lundellii* C.V. Morton and *Sebastiana adenophora* Pax & Hoffm. in Celestún deciduous forest and *Eugenia axillaris* (Sw.) Willd, *G. floribundum*, *Jatropha gaumeri* Greenm, *Machaonia lindeniana* Baill, *Neomillspaughia emarginata* (H. Gross) S.F. Blake and *Thouinia paucidentata* Radlk. in Kaxil-Kiuic semi-deciduous forest. To know which host species can offer more area for epiphyte colonization, three tree individuals per species were randomly chosen and we estimated their total bark area (stem and branches, calculated as the area of a cylinder). Additionally, a roughness index of the bark was also measured in a vertical gradient along the host at 1 m intervals. This index was calculated as interstitial circumference/total circumference (Carrascal and Telleria, 1989), and takes a minimum value of one (zero roughness) without a defined upper limit. Both determinations were restricted to 6 m (shorter forest) and 7 m (taller forest) above ground because no epiphytic orchids were found above those heights. We focused on the traits of *G. floribundum* for the multiple regressions because it was the most important host for orchids in both forests. To test if *E. nematocaulon* abundance was different on the most common host, *G. floribundum*, we chose eight mature trees of this species in each forest and compared the abundance of large individuals of *E. nematocaulon*.