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Physiological plasticity of epiphytic orchids from two contrasting tropical dry forests

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ABSTRACT

An enormous variation in light, both temporally and spatially, exists in tropical forests, which represents a potential driver for plant physiological plasticity. The physiological plasticity of epiphytic orchids from two tropical dry forests in response to different light environments was experimentally investigated. Plants of five species were growing in a shade-house under three different light regimes (photosynthetic photon flux density; PPFD of 20, 50 and 70% of total daily incident radiation) under watered and drought conditions. Orchids with similar leaf morphology but from different forests responded differently to the same light environment. Linear leaves of *Encyclia nematocaulon* avoided drought stress through stomata control and had a notable increase of photosynthesis, lower osmotic potential, and high photosynthetic efficiency under 50% daily PPFD during both drought and watered periods. In contrast, orchids with cylindrical and oval leaves had a marked decrease of these physiological parameters under 50 and 70% of PPFD during the drought period, but then recovered after rewatering. Oval leaves of *Lophiaris oerstedii* were more sensitive to high light and water availability because they had a strong decrease of their physiological parameters at 70% of PPFD, even during the rewatering period. Contrary to our predictions, *E. nematocaulon* had low plasticity and *Laelia rubescens*, from the deciduous forest, was the most able to acclimate. In general, orchids from the drier forest had higher plasticity than those from the more humid forest, which might help them to tolerate the higher fluctuations of light and water availability that occur there.

1. Introduction

Plasticity is defined as the ability of an organism to adjust its performance by altering its morphology and/or physiology in response to varying environmental conditions (Sultan, 2001; Navas and Garnier, 2002; Pigliucci, 2005). For example, in response to high light, plant leaves increase photosynthetic capacity and thermal dissipation, regulate stomatal aperture and develop smaller leaf area relative to plant biomass (Walters, 2005; Niinemets, 2007). Under low light, however, plants develop a greater relative leaf area, which reflects a reduction of total plant growth (Sultan, 2003). Both responses contribute to the ability of species to occupy diverse and variable microhabitats in different ecosystems (Sultan et al., 1998).

Sun leaves compared to shade leaves have a higher light-saturated photosynthetic capacity per unit leaf area and a greater carbon gain (Lambers et al., 1998; Demmig-Adams and Adams, 1996). Moreover, they are generally smaller, thicker, and contain less chlorophyll per unit leaf mass than shade leaves (Lambers et al., 1998; Demmig-Adams and Adams, 1996). Shade leaves are generally more efficient than sun leaves in capturing light at low

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Abbreviations: CAM, crassulacean acid metabolism; F_v/F_m, maximal quantum efficiency of photosystem II; NPQ, non-photochemical quenching; PPFD, photosynthetic photon flux density; RDPI, relative distance plasticity index; RWC, relative water content; VPD, vapor pressure deficit; ΔH^+, nocturnal acidification; Ψ_s, osmotic potential.

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irradiance because they have larger antennae complexes associated with photosystem II; however, they are more vulnerable to photoinhibition, a process that occurs when absorbed light exceeds that utilized for carbon assimilation (Demmig-Adams and Adams, 1992). Adaptations to irradiance thus involve changes in leaf biochemistry, since a significant fraction of leaf nitrogen is invested in the form of photosynthetic proteins; indeed a strong positive correlation between leaf nitrogen content and irradiance has been demonstrated (Chapin, 1980).

The range of environmental conditions in a location determines which species may survive and reproduce successfully there. Because plant species differ in their acclimation capacity (Brzeziecki and Kienast, 1994), it has been proposed that species with a wide distribution will tend to have larger phenotypical plasticity than species with limited distribution (Sultan, 1995; Niinemets and Valladares, 2004). However, some studies have failed to find an association between ecological distribution and phenotypic plasticity (Baskauf and Eickmeier, 1994; González and Gianoli, 2004).

Epiphytes are a group of plants that occur in a diverse range of microhabitats within the tree canopies. Among the families with epiphytic species, Orchidaceae has the largest number of species, mainly distributed in tropical moist and wet forests (Dressler, 1981; Zotz, 2013), and with lower diversity and abundance in tropical dry forests (de la Rosa-Manzano et al., 2014a). At least half of all epiphytic orchids possess crassulacean acid metabolism (CAM), which is characterized by the temporal separation of CO_2 fixation and its photosynthetic assimilation into organic compounds (Lüttge, 1987). CAM plants show a great variation in their capability for light acclimation, e.g. some CAM plants do hardly acclimate, maintaining similar maximum photosynthesis rates in high and low light (Fetene et al., 1990; Skillman and Winter, 1997), but some exhibit a high plasticity (Maxwell et al., 1999; Haslam et al., 2002). It has been proposed that in habitats with strong environmental stresses the diversity of CAM patterns and the phenotypic plasticity of CAM behavior are low, whereas at sites with lower stress both diversity and plasticity increase (Kluge et al., 2001).

In the Mexican tropical dry forests of the Yucatan Peninsula, epiphytes undergo extreme changes in light and water availability throughout the year. Specifically, during the dry period (rainfall <60 mm per season), which can last for up to seven months, trees lose their leaves, and solar radiation on the evergreen orchids can increase up to nine times that measured during the wet season (Graham and Andrade, 2004; de la Rosa-Manzano et al., 2014b). In these dry forests, orchid leaves show a substantial seasonal variation in the efficiency of CAM photosynthesis. For instance, during the early dry season compared to the mid-dry and wet seasons, when night temperature and nocturnal vapor pressure deficit are low, both photosynthesis and maximum quantum yield increase (de la Rosa-Manzano et al., 2014b).

Most studies on the responses of orchid leaves to light have focused on morphological and physiological aspects, and the ecological implications of tolerance to the extreme environments (Lin and Hsu, 2004; Shi-Bao et al., 2007; Maxwell et al., 1999; Haslam et al., 2003). No study, to our knowledge, has focused on physiological plasticity. In the present work, we explore the response of orchid leaves to three light environments and water availability regimes for five orchid species with different leaf morphology from a deciduous and a semi-deciduous tropical forest. We address the following two questions: a) what are the physiological responses to variation in light for epiphytic orchids with similar leaf morphology from sites with contrasting precipitation and average light environments? and b) what is the magnitude of physiological plasticity of epiphytic orchids in response to variability in light and water availability? In order to answer these questions, we establish the following hypotheses: i) Species from a drier forest will be more tolerant to high light and lower water availability than those from a wetter forest, even when they have similar leaf morphologies, and ii) Considering the local species densities for the studied orchids, species with higher local abundance on host trees will have higher physiological plasticity than those with lower abundance.

2. Materials and methods

2.1. Plant material and experimental conditions

The experiments were conducted in a shade house at the Centro de Investigación Científica de Yucatán (CICY) in Mérida, Yucatán, México (21° 01′ 47″N, 89° 38′ 14″W). We collected 12 mature and healthy plants of each orchid species in two tropical dry forests of Yucatan, Mexico. For the tropical dry deciduous forest in Celestún, species were: *Encyclia nematocaulon* (A. Rich.) Acuña, *Cohniella yucatanensis* Cetzal & Carnevali and *Laelia rubescens* Lindley; for the semi-deciduous forest in the Kaxil-Kiuic Biocultural Reserve, species were: *E. nematocaulon*, *Cohniella ascendens* (Lindley) Christenson and *Lophiaris oerstedii* (Rchb. f.) A. Jimenez, Carnevali & Dressler. The closely related *Cohniella* species are allopatric, *C. yucatanensis* is distributed in the dry deciduous forest and is endemic to the Yucatan peninsula, while *C. ascendens* is found in more humid sites such as the semi-deciduous forest, and has a broad distribution in Mexico, Belize, El Salvador, Guatemala, Honduras, Nicaragua, and Costa Rica (Cetzal-Ix and Carnevali, 2010). Species were selected because of their leaf shape for comparison and because they have similar abundances and distribution in those forests (de la Rosa-Manzano et al., 2014a).

Both tropical dry forests differ in tree composition, tree stature, and rainfall regime; the dry deciduous forest contains trees between 8 and 10 m height and most of them drop their leaves during the dry season (mean annual rainfall and temperature of 770 mm of 27 °C, respectively), and the semi-deciduous forest has a canopy height between 13 and 18 m, where 50–75% of trees are drought-deciduous (mean annual rainfall and temperature of 1200 mm and of 26 °C, respectively); for more details, see Cach-Pérez et al. (2013) and de la Rosa-Manzano et al. (2014a). *Encyclia nematocaulon* plants possess linear leaves (long, elongate leaves), both congeneric species of *Cohniella* have cylindrical leaves (involute leaves; elongate leaves having the edges rolled over the upper surface), while the leaves of *L. rubescens* and *L. oerstedii* are oval (egg-shaped leaves with the broader end at the base). All leaves are succulent; those from *Cohniella* spp. being the most succulent, followed by those of *L. oerstedii*, *L. rubescens* and *E. nematocaulon* (de la Rosa-Manzano et al., 2014b).

Plants (all with comparable size and five to six pseudobulbs) were individually attached to a piece of wood (~670 cm^3) with a flexible wire at a height of 2 m and all were acclimated for 30 d in a common garden, receiving 20% of daily incident photosynthetic photon flux density (PPFD), which was measured using calibrated photodiodes (Hamamatsu, Bridgewater, NJ, USA). Then, orchids were transferred to a shade house, and assigned randomly to three light environment treatments ($n = 4$ for each light treatment). Artificial shading was created using nylon nets and treatments resulted in light intensities of 20% (7.2 ± 1.3 mol m^{-2} d^{-1}), 50% (19 ± 1.1 mol m^{-2} d^{-1}) and 70% (26 ± 1.5 mol m^{-2} d^{-1}) of incident daily PPFD. These light levels coincide with average light levels for the natural sites during the wet, early dry and dry seasons (de la Rosa-Manzano et al., 2014a).

Air temperature and relative humidity in each treatment were measured with HMP35C-L sensors (Vaisala Campbell Scientific, Inc., Logan, 186 Utah, USA); vapor pressure deficit (VPD) was