BIOTROPICA 37(2): 238–244 2005 10.1111/j.1744-7429.2005.00032.x

Inner-crown Microenvironments of Two Emergent Tree Species in a Lowland Wet Forest[1]

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ABSTRACT

Vascular epiphyte communities, comprising up to 25 percent of tropical forest flora, contribute to plant diversity and thus ecosystem-level processes; however, one of the proximal determinants of those communities, microclimate, is little studied. Here we present the first comprehensive study of microclimates in the inner crowns of two emergent tree species, *Hyeronima alchorneoides* and *Lecythis ampla*, at La Selva Biological Station, Costa Rica. We examined photon flux density, temperature, vapor pressure, and humidity in inner-crown branches during the wet and dry seasons and during the wet-season leafless phase of *Lecythis*. In both seasons, the percentage daily PFD in foliated *Lecythis* crowns (9%, wet season; 11%, dry season) was significantly higher than in *Hyeronima* crowns (5%, both seasons), with the leafless wet-season PFD of *Lecythis* reaching 23 percent of full sun. Temperature and vapor pressure varied less in *Hyeronima* than in *Lecythis* crowns during the dry season. Microenvironmental conditions for epiphytes within *Hyeronima* crowns were more spatially and temporally homogeneous and were more buffered from ambient conditions than within *Lecythis* crowns. Growing conditions within the crowns of the same trees and among different trees were measurably different and are likely to affect the structure and composition of the resident epiphyte communities.

RESUMEN

Las epífitas vasculares representan el 25 por ciento de la flora vascular en bosques tropicales. Sin embargo, existe poca información sobre el microclima en que estas plantas habitan. Comparamos flujo fotosintético (PFD), temperatura, presión de vapor y humedad en las ramas interiores de dos especies de árboles emergentes, *Hyeronima alchorneoides* y *Lecythis ampla*, en la Estación Biológica La Selva, Costa Rica. En cada estación, se encontró una diferencia significativa entre el por ciento PFD en el dosel de *Lecythis* (9%, estación lluviosa; 11%, estación seca) y el por ciento PFD registrado en *Hyeronima* (5.6%, los dos estaciones), con por ciento PFD de *Lecythis* en la época sin hojas llegando a 23 por ciento. Las copas de *Hyeronima* mostraron menos variación en temperatura y presión de vapor que las copas de *Lecythis* durante la época seca. El microclima en el dosel de *Hyeronima* fue más homogéneo espacialmente y temporalmente y más regulado en comparación con el microclima en *Lecythis*. Las condiciones de crecer en el dosel de un árbol y entre diferentes árboles son diferentes, y probablemente afectan la estructura y composición de las comunidades de epífitas.

Key words: canopy microenvironment; emergent trees; epiphytes; Hyeronima alchorneoides; Lecythis ampla; *light transmittance; tropical wet forest*.

EPIPHYTES ARE CONSPICUOUS AND IMPORTANT COMPONENTS OF TROPICAL FORESTS, contributing up to 25 percent of the total plant diversity (Nieder *et al.* 2001) and up to 35 percent of the foliar biomass (Nadkarni 1984). Epiphytes have intrigued biologists for centuries, particularly because of their unique adaptations to canopy environments. Moreover, the three-dimensional canopy habitats of epiphytes are more complex and more challenging to study than forest-floor habitats. Within a single tree, different species of epiphytes may grow on horizontal branches, vertical branches, along the trunk, and on the underside of branches. Our functional understanding of epiphyte community composition and canopy dynamics is limited by a poor understanding of microenvironmental variation within crowns and its determinants. Do epiphytes encounter distinct microclimates among tree crowns and tree species analogous to differences encountered by forest-floor species between understory and gap habitats? Differences in forest-floor microclimates can strongly affect species diversity and recruitment (Denslow 1987, Hubbell *et al.* 1999), but these processes are yet to be investigated for epiphyte communities in the forest canopy. In this study, we compared the distribution of photosynthetically active radiation, air temperature, vapor pressure, and relative humidity within the inner crowns of two emergent tree species with different crown characteristics. In addition to examining overall species effects on inner-crown microenvironments, we evaluated specific effects of branch position, leaf phenology, leaf display, and canopy soil organic matter (CSOM) accumulation.

Several investigators have examined the effects of certain tree characteristics on epiphyte distribution and diversity (Todzia 1986, Ter Steege *et al.* 1989, Rudolph *et al.* 1998, Clement & Shaw 1999, Clement *et al.* 1999). Johansson (1974) and Ter Steege and Cornelissen (1989), among others, divided the tree canopy into environmentally distinct zones according to proximity to the trunk. The inner-crown, zone 4, is humid and dark, whereas the outer crown, zone 6, is dry and bright. Pittendrigh (1948) defined tree crown microenvironment in terms of epiphyte-type, for example, shade-loving epiphytes are in the dark humid part of the crown versus exposure epiphytes that are found in the dry and bright part of the crown. It is likely that species-specific differences in tree architecture can strongly influence inner-crown microenvironments. Differences in leaf size, display, and phenology, as well as branch size and bifurcation frequency can alter pathways of light penetration and air movement within the crown, affecting temperature, humidity, and photosynthetic light availability (Meinzer & Goldstein 1996).

Many studies of canopy light environments have focused on horizontal and vertical gradients measured from canopy towers or cranes (Thompson & Hinckley 1977; Parker *et al.* 1996, 2001; Kitajima *et al.* 1997). In a pioneering study on gas exchange in three epiphytes, Zotz and Winter (1994) measured inner-crown photon flux density (PFD) in an emergent *Ceiba pentandra* (Bombacaceae) in a tropical moist forest and found that mean PFD reaching these epiphytes averaged 11.1 and 16.9 mol/m^2/d (263 and 368 μmol/m^2/sec) in the dry season

[1] Received 14 October 2003; revision accepted 21 September 2004.

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and wet season, respectively. PFD values measured within tree crowns in tropical wet forests seem to be in the same range, generally below 400 μmol/m^2/sec (Oberbauer & Strain 1986, Doley *et al.* 1987, Szarzynski & Anhuf 2001). Similarly, Johnson and Atwood (1970) showed a reduction of 94 percent in photosynthetically active radiation from the outer crown to 5 m within the crown in the wet forests of Puerto Rico. Despite progress in measuring environmental conditions in forest canopies (Parker *et al.* 2001), variation within tree crowns remains largely unstudied.

Recent studies suggest that canopy microenvironments can be strongly influenced by epiphyte abundance and by the accumulation of canopy soil organic matter (CSOM) on a branch (Freiberg 1997, 2001). Masses of epiphytes and associated CSOM can decrease the surrounding temperature relative to ambient conditions near the branch, suggesting that epiphyte mats can moderate crown temperature and crown microenvironment in general (Freiberg 1997, 2001). Stuntz *et al.* (2002) at Barro Colorado Island in Panama found that the branch area adjacent to epiphytes was cooler than bare branch areas and evapotranspiration by the tree decreased 25 percent when epiphytes were present. These studies highlight the need for a branch-based approach to study crown microenvironments.

Our study is the first of its kind to quantify inner-crown microenvironment experienced by epiphytes in two emergent tree species. We examined variation in PFD, vapor pressure, humidity, and temperature relative to season, tree phenology, branch orientation, and CSOM depth in the inner crown. The four main questions addressed in this study are: (1) Do epiphytes growing in the same tree experience different microenvironments? (2) Do epiphytes growing on different tree species experience different microenvironments? (3) Are there significant microclimatic differences among seasons and leaf conditions (*i.e.*, leaflessness)? (4) How do inner-crown PFD levels compare to those in forest-floor environments?

METHODS

STUDY SITE AND TREE SPECIES.—This research was conducted at La Selva Biological Station in the Atlantic lowlands of northeastern Costa Rica at 37–100 masl between July 1999 and July 2001. La Selva is categorized as a Tropical Wet Forest under the Holdridge system (Hartshorn & Peralta 1988) and receives approximately 4000 mm of rain per year, with no month having less than 100 mm (McDade *et al.* 1994). Rainfall occurs throughout the year with a noticeably drier period from January to April and from September to October.

We studied the crowns of two emergent canopy tree species: *Hyeronima alchorneoides* Allemao (Euphorbiaceae) and *Lecythis ampla* Miers (Lecythidaceae). We chose emergent tree species to avoid the effects of shading from neighboring trees on microclimates within the crown. These species were chosen because they have similar overall stature, but differ in leaf phenology, leaf morphology, and bark texture. Both species are large trees >50 m tall and bear branches 50–100 cm in diameter that display diverse branch angles ranging from 45 to 90°. Both species support substantial epiphyte loads, although *Hyeronima* hosts a significantly greater abundance of vascular epiphytes than *Lecythis* (Cardelús 2002). *Hyeronima* is an evergreen species with large (~280 cm^2), simple, whorled leaves, borne on whorled, orthotropic branches that produce a multilayered crown (Horn 1971, Menalled & Kelty 2001). The bark of *Hyeronima* is fibrous, spongy, and absorptive. *Lecythis* is a deciduous species with simple, distichously arranged, small (~40 cm^2) leaves borne on orthotropic branches that produce a monolayered effect (Horn 1971). *Lecythis* is leafless for approximately 2 mo during the 9 mo wet season (May–June). In the course of 48 h, *Lecythis* sheds all of its leaves. The older bark of *Lecythis* is rough, relatively non-wetable, and has shallow, longitudinal (1 cm) fissures.

MICROENVIRONMENT MEASUREMENTS.—We studied microenvironments on the two lowest branches of four healthy individuals each of *Hyeronima* and *Lecythis,* except in one individual of *Hyeronima* where a bee's nest limited observations to one branch. The lowest branches were chosen because they are the oldest and largest, and hence, should be supporting the most mature community of epiphytes (Freiberg 1996, Rudolph *et al.* 1998). These lowest branches were also the most accessible by climbing. Trees were accessed using single-rope climbing techniques (Perry 1978). The lowest branches were usually between 20 and 35 m above the ground. The criteria for branch choice also included overall integrity and safety and no evidence of cracking, fungi or bee, wasp or termite nests. Many branches were rejected because they did not meet these criteria. Two transects were established along the two lowest branches of each individual and eight contiguous 0.5 × 0.5 m quadrats were laid out, for a total of 16 quadrats per tree, covering a total area of 4 m^2. This area corresponds to the inner crown, zone 4 and part of zone 5 (Ter Steege & Cornelissen 1989). Aspect, height, diameter, and angle were measured in the center of each quadrat. Quadrat aspect was measured with a compass; quadrat height was measured from the forest floor to the center of the quadrat with a tape measure, and quadrat angle from the horizontal was measured with a protractor with a mounted level. Depth of the highly organic humus layer, or canopy soil organic matter (CSOM), was recorded using a caliper. For CSOM depth measurements, each plot was subdivided into twenty 125 cm^2 subplots and the caliper's metal rod was placed in each subplot until it touched the bark. CSOM depth was averaged across subplots within each quadrat.

Four microclimate parameters were measured within each quadrat: photosynthetically active radiation, air temperature, vapor pressure, and relative humidity using a single CR23X micrologger and an AM416 16-channel multiplexer (Campbell Scientific, Logan, Utah). Trees were measured sequentially for a period of 7–20 d during both the wet season and the dry season as well as during the leafless phase of *Lecythis*. Sensors were mounted on a module that consisted of a 12-cm long PVC pipe, 5 cm in diameter, with a 0.08 amp fan inserted at one end to provide air circulation for an aspirated thermocouple. Each module contained a gallium arsenide photodiode to measure PFD, an aspirated thermocouple (wet bulb and dry bulb) for measuring humidity, and an unaspirated (dry bulb) thermocouple for measuring air temperature. The thermocouple wires stood approximately 3 cm away from each other in the center of the PVC tube. Thermocouples were shaded from direct light and the reservoir for the wet bulb wick was located underneath the PVC pipe within a smaller PVC pipe. The module was placed on top of the branch in the center of each quadrat.

Photodiodes were calibrated against a 190SA Quantum Sensor (LI-COR, Lincoln Nebraska) every 3 mo. Any drift was corrected using

a multiplier. One photodiode was mounted on each sensor module and placed within 5–10 cm from the branch surface. Each light sensor was leveled and braced to the tree to prevent movement. Spectral response of the GaAsP Photodiodes (type no. G1118) is 300–680 nm; peak wavelength is 610 nm (±30 nm, Hamamatsu Corporation, Bridgewater, New Jersey). Photon flux density and air temperature were measured at 5-sec intervals; the data logger computed 5-min averages of these measurements as well as minimum and maximum values every 5 min.

Air temperature measurements were made with a 24-gauge copper/constantan thermocouple wire. Copper/constantan thermocouples were chosen because their temperature accuracy is $\pm 1^{\circ}$ at all humidity levels, which reduces measurement error. Thermocouples were referenced against a 107 Temperature Probe (Campbell Scientific, Logan, Utah) located in the crown. Measurements of the dry thermocouple were recorded every 5 sec with 5-min averages recorded. Humidity measurements were collected every 15 min; wet- and dry-bulb thermocouples were aspirated for 5 min prior to the instantaneous reading. From the instantaneous wet and dry thermocouple readings, saturated vapor pressure, vapor pressure, and humidity were calculated and recorded. After instantaneous light and temperature measurements were collected, 30 min, hourly, and daily averages from 0600 to 1800 h were computed. For humidity and vapor pressure we computed 30-min hourly and daily averages.

DATA ANALYSIS.—We examined the main effects of species and season on inner-crown light, temperature, and vapor pressure. We standardized the data to minimize the effects of daily and seasonal fluctuations in weather conditions on species and microsite comparisons using data from the La Selva Micrometeorological Station located at a 2 m height in a large clearing. The weather station PFD was measured with a LI-COR LI-190SA quantum sensor (Lincoln, Nebraska) and averaged every 30 min and temperature and humidity were measured with a Campbell HMP35C sensor (Logan, Utah) and averaged every hour. We standardized crown PFD to percent daily transmittance (crown PFD 30 min/simultaneous weather station PFD 30 min × 100). From these data, we calculated total daily percent transmittance. Both the weather station and our light sensor were calibrated using the same light source (LI-COR 1800-2). Temperature was standardized with the weather station's simultaneous readings by subtracting the weather station's readings from the crown readings (crown temperature 60 min − simultaneous weather station temperature 60 min). Saturate vapor pressure (SVP) and VP for the weather station were calculated from the temperature using the following equations: $\mathrm{SVP} = a \exp(bT/T + c)$ and $\mathrm{VP} = \mathrm{SVP} \times$ relative humidity, where $T =$ Celsius temperature, $a = 0.611$ kPa, $b = 17.502$, and $c = 240.97^{\circ}$C (Campbell & Norman 1998). Subsequently, vapor pressure difference between the crown and weather station was calculated as for temperature. All analyses were performed using 30-min averages for percent transmittance and 60-min averages of temperature and vapor pressure.

Separate, multi-factor ANOVAs were performed within each species to analyze the effects of season and branch azimuth on branch microclimate (SAS 1999). Branch, rather than individual, was examined because branches were significantly different from one another in most cases. Analyses were performed for *Lecythis* with and without data from the wet-season leafless period. Thus, effects of the leafless period in *Lecythis* could be assessed independently of seasonal effects.

To examine differences between tree species and season, coding the leafless phase of *Lecythis* as a season, we performed ANOVA with species and season as main effects, with a species × season interaction term. A *post hoc* Tukey analysis was performed on all ANOVA models to assess the differences between species and seasons. Differences in CSOM depth between species were evaluated using a *t*-test.

RESULTS

Mean daily PFD reaching the inner crown of *Hyeronima* was higher in the dry season than in the wet season, but values of total percent transmittance were similar for both seasons (Table 1). *Lecythis* inner crowns received more PFD than *Hyeronima* during both the wet and dry seasons, with the highest daily average PFD during the wet-season leafless phase (Table 1). Average temperature was higher in the dry season than in the wet season for *Hyeronima*, while for *Lecythis* the highest maxima and the greatest temperature variability occurred during the wet-season leafless phase (Table 1). Vapor pressure was high in both the dry and wet seasons in *Hyeronima,* and was highest in the wet-season leafless phase in *Lecythis* (Table 1). For *Hyeronima,* relative humidity was highest in the wet season, whereas for *Lecythis* relative humidity was highest during the wet-season leafless phase (Table 1).

In *Hyeronima* there was no significant effect of season or branch azimuth on percent light transmittance, temperature difference, or vapor pressure difference (Table 2). Although there was not a significant effect of temperature difference between seasons, there was greater variation between inner crown and ambient conditions in the dry season than the wet season (Fig. 1b). *Lecythis* trees in full leaf showed no significant

TABLE 1. *Five-minute mean, minimum and maximum values for PFD μmol/m²/s¹), percent transmittance (%T), temperature (°C), vapor pressure (kPa), and relative humidity (%) measured along transects in both* Hyeronima *(HA) and* Lecythis *(LA) in both the wet season (May–December) and the dry season (January–April) and the leafless phase of* Lecythis *(May–June).*

Species	Season	PFD	%T	Temperature	Vapor pressure	% Humidity
HA	Dry	43.0 (25.0–73.9)	5.9 (4.3–9.6)	26.4 (25.0–27.5)	3.3 (3.1–3.4)	89 (84–93)
HA	Wet	24.3 (10.0–31.3)	5.7 (3.1–7.2)	25.4 (25.1–26.2)	3.1 (3.0–3.3)	95 (91–98)
LA	Dry	66.4 (39.3–124.1)	11.1 (7.16–15.6)	25.0 (22.8–27.0)	3.0 (2.7–3.3)	86 (75–92)
LA	Wet (foliated)	49.0 (30.8–75.0)	9.4 (4.4–12.6)	24.7 (23.7–26.0)	2.9 (2.6–3.4)	86 (66–97)
LA	Wet (leafless)	103.4 (52.9–161.7)	23.2 (10.4–52.1)	26.9 (24.0–28.8)	3.3 (2.9–3.9)	89 (81–94)

TABLE 2. *Summarized results of multi-factor ANOVA on the effects of season and branch facing direction (azimuth), on standardized microclimate variables within each tree species, log percent transmittance, air temperature difference (° C) between tree crown and weather station and relative vapor pressure difference (kPa) between tree crown and weather station.* Hyeronima *in both the wet and the dry seasons,* Lecythis *in the dry season and foliated wet season and* Lecythis *in the dry, foliated wet season and leafless wet season. P values shown and values below 0.05 are in bold.*

	Hyeronima dry & wet seasons			*Lecythis* dry & foliated wet season			*Lecythis* dry, foliated & leafless wet seasons		
	Log %T	Temperature difference	Vapor pressure difference	Log %T	Temperature difference	Vapor pressure difference	Log %T	Temperature difference	Vapor pressure difference
Model	0.14	0.41	0.32	**<0.01**	0.50	**0.03**	**<0.01**	0.46	**0.01**
Season	0.24	0.15	0.34	0.31	0.28	0.23	**<0.01**	0.24	0.22
Quadrat azimuth	0.13	0.51	0.30	**<0.01**	0.52	**0.03**	**0.02**	0.54	**0.01**

differences between seasons with respect to percent transmittance, temperature, and vapor pressure; however, azimuth had a significant effect on percent transmittance and vapor pressure difference (Table 2). These trends were also present when the leafless phase was included in the model, with the added significant effect of season on percent light transmittance (Table 2). Leaf loss in *Lecythis* led to a significant increase in light availability and an increase in variability for all microclimate variables in general (Fig. 1; Table 2).

Lecythis inner crowns received a significantly higher percentage of incident daily PFD than did inner crowns of *Hyeronima*. Percent transmittance during the leafless phase of *Lecythis* was significantly higher (23.1%) than both seasons for both species (Table 1, Fig. 1a). *Lecythis* had significantly higher log percent transmittance than *Hyeronima*, with only the *Lecythis* foliated wet season similar to *Hyeronima* during the dry season (Table 3, Fig. 1a). In the ANOVA model, season was a significant main effect for percent transmittance only when the model included the leafless wet season values for *Lecythis* (Table 3). There was a significant species × season interaction for temperature difference only for the model excluding the leafless wet season of *Lecythis* (Table 3). No significant difference was found in temperature or vapor pressure (standardized variables) between the two species.

Maximum, 5-min average, PFD values for all days of each species and season or leaf phase never exceeded 100 μmol m^2/sec in *Hyeronima* for either season, whereas both the dry season and leafless phase of *Lecythis* often exceeded 100 μmol m^2/sec, with highest daily maximum values of 148.3 μmol/m^2/sec and 208.9 μmol/m^2/sec, respectively (Table 1). PFD spikes of instantaneous readings exceeding 1000 μmol/m^2/sec were frequently observed during sunflecks. Sunflecks were noted throughout the day in both tree species, in all seasons and leaf phases. The highest recorded instantaneous values for *Hyeronima* exceeded 1700 μmol/m^2/sec during the dry season, maximum values in *Lecythis* crowns during the dry season were higher and more frequent than those for *Hyeronima,* with a peak value of 1834 μmol/m^2/sec. The leafless phase of *Lecythis* had even higher values than the dry season, with values over 2000 μmol/m^2/sec recorded. For *Lecythis*, values for average daily PFD in the leafless phase were similar to the maximum daily PFD averages in the foliated wet season. The maximum values of PFD followed the same patterns seen with average values, *e.g.*, *Lecythis* during the leafless phase had sunflecks with highest PFD, whereas *Hyeronima* during the wet season had sunflecks with lowest PFD values.

Overall, branch characteristics poorly explained patterns of variation in microclimate variables in the inner crown. Transect height, diameter, and angle were not significant factors in any ANOVA model (data not shown). The only tree characteristic that showed a significant effect within tree species was transect azimuth, but only for *Lecythis* (Table 2). Transect azimuth was a significant factor for percent light transmittance and vapor pressure in all *Lecythis* leaf phases (Table 2). Depth of CSOM in the inner crown was not significantly different between *Hyeronima* (17.8 mm ± 11.5) and *Lecythis* (13.2 mm ± 10.7), although soil depth was more variable in *Lecythis* crowns.

DISCUSSION

In the lowest part of the crown, light environments varied significantly within and between these two emergent tree species, creating a spatially and temporally heterogeneous canopy environment. These crowns also demonstrated high variation in temperature and vapor pressure, depending on the species, season, and leaf phase creating zones of low PFD, above-ambient vapor pressure, and below-ambient temperatures contrasted with zones of high PFD, below-ambient vapor pressure, and above-ambient temperatures. Environments in lower branches of *Hyeronima* were dark, moist, and relatively uniform in all the four individuals measured, while lower branch microenvironments in the inner crowns of *Lecythis* were brighter than *Hyeronima* and more variable in temperature and vapor pressure, particularly during the wet season leafless phase. Thus, for all microenvironmental variables, conditions were more homogenous and more moderated from ambient conditions within crowns of *Hyeronima* compared to *Lecythis*.

The poor predictability of the inner-crown microclimate by tree branch characteristics was surprising. Branch azimuth had a significant effect on percent transmittance in *Lecythis* crowns during both leafless and foliated periods (Table 2) with the south-facing branches receiving higher PFD and percent transmittance than non-south-facing branches. The effect of tree characteristics will likely increase in more exposed parts of the crown. Although no single tree characteristic was a consistently significant factor determining microclimate for either tree species, an effect of tree structure was observed for *Lecythis*. This species provides an excellent model system for studying the effects of crown and branch structure on microenvironment because it has a completely leafless phase.

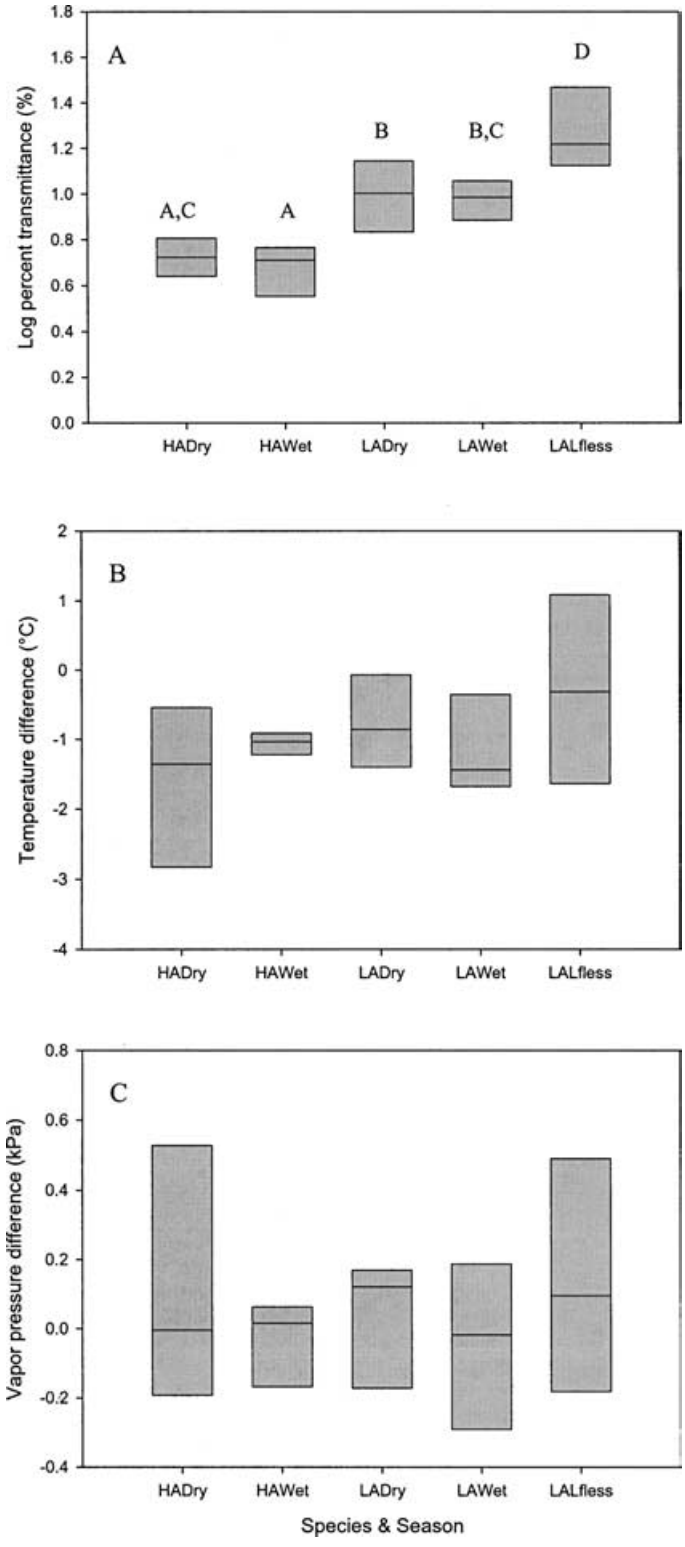

FIGURE 1. Box and whiskers plots, showing median of (A) log percent PFD transmittance, (B) temperature difference (°C), and (C) vapor pressure difference (kPa) for *Hyeronima* (HA) in the wet and dry seasons and for *Lecythis* (LA) in the dry, foliated wet and leafless (Lfless) wet seasons. Different letters indicate significant differences (*post hoc* Tukey analyses).

An effect of within-crown shading was observed during the leafless phase as PFD values were not equivalent to the control open clearing. In the absence of *Lecythis* foliage, lower branches received only 23 percent of full sun (Table 2). This within-crown shading is likely caused by both the branches and other epiphytes above the study quadrats. The branches that were studied ranged in diameter from 50 to 100 cm with comparably sized branches above them. Evergreen lianas were also a likely source of shading as they were clearly visible in hemispherical photographs during the leafless phase of *Lecythis* trees. Another source of shading were the trunks themselves, which ranged from 1130 to 1200 cm at breast height (D. B. Clark, pers. comm.).

Differences in overall PFD levels between *Hyeronima* and *Lecythis* are most likely driven by foliage differences between the two species, which influence crown openness. *Hyeronima*'s larger multilayered leaves, whorled phyllotaxy, and varying petiole lengths increase light capture of individual leaves within the crown and create a thick filter, limiting the amount of PFD reaching the inner, lower branches (Horn 1971, Menalled & Kelty 2001). *Lecythis,* in contrast, has small leaves that are presented high up in the crown and monolayered. The lower crown leaf area index (LAI) allows more light to penetrate to lower branches. Thus, in *Hyeronima*, a denser canopy acts to reduce or wholly eliminate the effects of other tree characteristics, such as branch azimuth.

The combination of low light due to the multilayered foliage combined with spongy bark and a greater abundance of vascular epiphytes contributes to the ability of *Hyeronima* to maintain a less variable temperature and vapor pressure in the dry season as compared to *Lecythis*. Compared to *Hyeronima*, *Lecythis* has fewer traits of moderate inner-crown conditions, specifically non-absorptive bark, monolayered leaves, a lower LAI, and a lower abundance of epiphytes.

For epiphytes, the balance between light availability and desiccation is important for survival (Benzing 1990). *Hyeronima*'s buffering ability is especially critical during dry periods when limited water availability is a greater threat to epiphyte survival than deep shade. In contrast, epiphytes on lower branches of *Lecythis* receive higher light availability year round, and are resident in a crown that is less moderated during the dry season (Figs. 1b and 1c). The most exposed period, the leafless phase, occurs during the wet season when PFD is lowest. During this period, frequent rain maintains high vapor pressure and reduces the risk of desiccation for epiphytes in *Lecythis* crowns. Stress for an epiphyte would be greatest during this leafless wet season in *Lecythis* crowns, however, because the microclimate is more variable as well as more extreme (*e.g.*, higher sunflecks) than during the leafed wet season and dry season (Fig. 1). Based on these microenvironmental differences, we predict that *Hyeronima* inner crowns are more likely to support drought-sensitive epiphytes than *Lecythis.* We also predict that *Hyeronima* would be a more suitable host for generalist epiphytes, since its inner crown offers a more moderated crown microenvironment throughout the year than *Lecythis*. Although epiphyte physiological characters were not measured, the epiphyte species composition between these two tree species was significantly different (Cardelús 2002). For example, *Oleandra articulata* (Dryopteridaceae), a common fern in *Hyeronima* inner crowns, is virtually absent from *Lecythis* inner crowns. This epiphyte has thin delicate leaves suggesting drought sensitivity. Zotz and Winter (1994) have shown that epiphytes living in a wet-season deciduous *Ceiba pentandra* (Bombacaceae) tree make physiological adjustments during the dry

TABLE 3. *ANOVA results on the effect of species, season and species × season, on standardized variables log percent transmittance, air temperature difference (° C) between tree crown and weather station and relative vapor pressure difference (kPa) between tree crown and weather station for* Hyeronima *and* Lecythis *in both the dry and wet seasons, excluding the leafless wet season of* Lecythis*, and including leafless phase of* Lecythis *(leafless). P values shown and values < 0.05 are in bold.*

	Percent transmittance		Temperature difference		Vapor pressure difference	
	Foliated	Foliated & leafless	Foliated	Foliated & leafless	Foliated	Foliated & leafless
Model	**<0.01**	**<0.01**	0.19	0.11	0.64	0.66
Species	**<0.01**	**<0.01**	0.35	0.42	0.61	0.65
Season	0.32	**<0.01**	0.62	0.25	0.24	0.31
Species × season	0.81	0.84	**0.05**	0.09	0.83	0.85

season in order to survive the dramatic changes in microenvironment, *e.g.*, C_3–CAM switching. Similarly, an epiphyte living in *Lecythis* would be more likely to require physiological adjustments than an epiphyte living in a *Hyeronima* tree because of the dramatic changes in the microenvironment, particularly light, between seasons and leaf phases.

Given that the forest-floor microenvironment is thought to influence the distribution of soil-rooted plants (Denslow 1980), we asked how inner-crown light environments compare to those from the forest floor. Compared to measurements by Chazdon and Fetcher (1984), inner-crown PFD was most similar to microsites in small and large canopy gaps with PFD for *Hyeronima* approaching those measured for the understory with PFD for *Lecythis* approaching those of a gap (Fig. 2). Because light exposure will likely increase to near full sun out on the branches, these results indicate that within the crowns of these trees, light environments span a range equivalent to that of near understory to large clearing. It is therefore likely that crown microenvironment drives epiphyte distribution in much the same way that forest-floor microclimate variation drives forest-floor species distribution (Denslow 1980). With this in mind, the heterogeneity in crown microclimate observed in this study would be even more pronounced with more architecturally contrasting tree species. An important next step will be to understand how epiphytes respond functionally to the different microenvironments imposed by the effects of season, tree phenology, and host species characteristics.

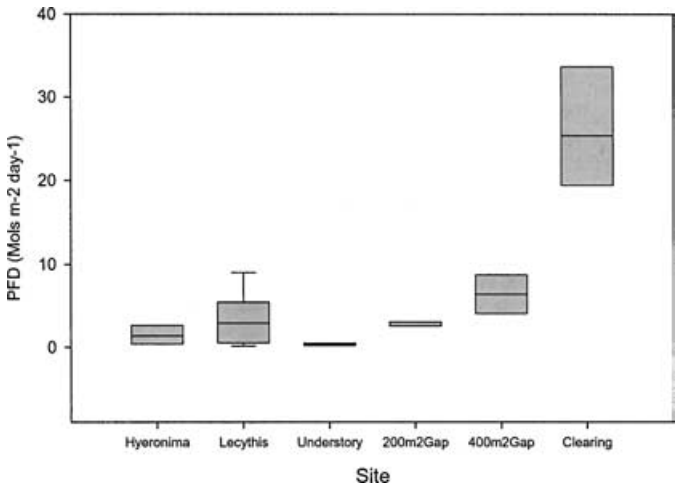

FIGURE 2. Box and whiskers plots, showing median, error bars, and outliers of PFD (mol/m^2/d) in six different light environments at La Selva Biological Station: *Hyeronima* crowns, *Lecythis* crowns, understory, 200 m^2 gap, 400 m^2 gap, and a clearing (data from Chazdon & Fetcher 1984).

ACKNOWLEDGMENTS

Special thanks are due to Dr. K. Holsinger, Dr. C. Schlichting, and Dr. J. A. Silander Jr. who provided vital advice throughout this work. We are grateful to Dr. J. S. Silander, Dr. K. Holsinger, J. E. Watkins Jr., and S. E. Cardelús for advice and comments on earlier versions of this manuscript. We thank two anonymous reviewers and guest editor Steven Oberbauer for valuable comments. We also thank Dr. D. A. Clark and Dr. D. B. Clark for logistical support at La Selva; and R. Gonzalez-Vargas, S. Esquivel, and J. E. Watkins Jr. for field assistance. Dr. D. Penick helped with developing sensors and D. Meeks at Campbell Scientific offered critical programming support. This study was financed by an NSF Graduate Research Fellowship, NSF Dissertation Improvement Grant; Organization for Tropical Studies Pilot and Research Grants; Ronald Bamford Endowment to the University of Connecticut Department of Ecology & Evolutionary Biology; University of Connecticut Natural History Museum; University of Connecticut Graduate School, and University of Connecticut Research Foundation.

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