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Structural and physiological adaptation to light environments in neotropical *Heliconia* (Heliconiaceae)

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ABSTRACT. Influence of habitat on physiological and structural characteristics was investigated for broad-leaved tropical monocotyledons in the genus *Heliconia* (Heliconiaceae). Seven species were selected from three different light regimes, enabling an analysis of the extent to which this genus has adapted its photosynthetic strategies and morphological characteristics to different daily photon flux densities (PFD). Predictably, light response curves showed a clear gradient with respect to light saturation and rates of maximum net assimilation (A_{max}). *Heliconia latispatha*, an open site species, showed saturation at higher PFD (1400 μmol m^{-2} s^{-1}) and higher A_{max} (14–16 μmol m^{-2} s^{-1}) than *H. mathiasiae*, a forest edge species (PFD 1000 μmol m^{-2} s^{-1}; A_{max} 7.5–8.5 μmol m^{-2} s^{-1}) and *H. irrasa* of deep-shade forest understorey (PFD 250 μmol m^{-2} s^{-1}; A_{max} 3.5 mol m^{-2} s^{-1}). Leaf blade areas were largest in open sites, and leaf specific mass was also significantly higher, but leaf support efficiency was highest in understorey species. Species in open sites had thicker leaves with more chlorenchyma, whereas deep-shade species had very thin leaves and low stomatal densities. These rapidly growing herbaceous perennials appear to allocate much of their above-ground biomass to leaf tissues and have a relatively low investment in support tissues. This contrasts with understorey palms, in which leaf form and structural investment has been interpreted as a trade-off between economy and protection against tissue loss from falling branches. Presence of below-ground rhizomes in *Heliconia* may provide the key to this difference.

KEY WORDS: carbon allocation, Costa Rica, *Heliconia*, leaf anatomy, leaf morphology, light saturation, Neotropics, tropical rain forest

INTRODUCTION

In wet tropical forests, leaves exhibit morphological and anatomical differences related to light environments of the habitats (Bongers & Popma 1990, Rollet

1990, Roth 1984, Rundel & Gibson 1996). Sun-adapted canopy leaves of the climax forest and pioneer trees of gaps have well-developed palisade mesophyll and significantly higher rates of photosynthesis in comparison with leaves formed under conditions of dense shade (Rundel & Gibson 1996, Zotz & Winter 1996). However, when expressed on the basis of unit leaf mass, sun-adapted leaves have similar rates of maximum assimilation ($A_{\max}$) to the thinner shade-habitat leaves (Sims & Pearcy 1994). Early studies indicated that understorey species are inherently less adapted to changes in light environment than sun-adapted species (Björkman & Holmgren 1963, Björkman 1981, Bazzaz & Carlson 1982), but it now appears that such species may have an equal capacity for acclimation as that known for sun-adapted species (Sims & Pearcy 1989).

For broad-leaved tropical monocotyledons, the larger sizes of sun leaves logically require not only greater thickness, but also a greater investment in petioles and major veins to support large foliar area, and increased root and below-ground shoot biomass may be adaptations to supply necessary water and nutrients to the leaf (Chazdon 1985; 1986a, b; 1988). It has therefore been hypothesized that adaptation to light environments may rely less on photosynthetic acclimation than on morphological changes in plant architecture and associated carbon allocation patterns (Sims *et al.* 1994). Comparative data on tropical forest herbs, particularly field data, are relatively limited, and have not addressed the question of physiological acclimation and morphological adaptation of sun- and shade-grown leaves. For this type of study, one productive avenue of research is to investigate within a single genus whether physiological and structural adaptations have adaptively radiated along a gradient of habitats from full sun to deep-shade forest understorey.

The genus *Heliconia* (200–250 spp., Heliconiaceae) includes large, rhizomatous, herbaceous perennials distributed primarily in the moist forests of the Neotropics, but with outlying species within the Pacific Basin and also reaching Southeast Asia (Berry & Kress 1991; Kress 1984, 1990). Highest species diversity occurs in montane and cloud forests, but their most luxuriant growth is encountered in neotropical lowlands, especially where species are common colonizers in successional growth along roadsides and riverbanks and in tree fall gaps of rain forest. In large open habitats, characterized by high solar irradiance (Chazdon & Fetcher 1984, Chazdon *et al.* 1996), polyaxial heliconias can exceed 6 m in height and form dense stands of 50 shoots or more. The most robust clones of *Heliconia* have a musoid growth form, i.e., pseudostems with semi-erect leaves, and strongly resemble the growth form of successional species in the related families Musaceae and Strelitziaceae of the Old World tropics (Order Zingiberales; Dahlgren *et al.* 1985). *Heliconia* also includes species with a zingiberoid growth form, with distichous horizontal leaves produced along a stiff stem, often colonizers of small gaps, and some low, nearly acaulescent herbs that are climax residents of the forest understorey. Within *Heliconia*, therefore, it is possible to find a gradient of species adapted to light environments ranging from rain forest understorey with extremely low daily photon flux density (PFD, μmol m^{-2} s^{-1}), species from small forest gaps and partially open habitats along creeks, as well as the more typical species colonizing full-sun disturbance sites. Whereas leaf morphology of the genus is fairly uniform, and leaf anatomy shows one basic design (Tomlinson 1959, 1969), there are interesting variations of the tissues involved in photosynthesis, including differences in leaf thickness and mesophyll structure of *Heliconia* (Triplett & Kirchoff 1991), which may, if analyzed, relate to preferred light environments in their native habitats. Using species from different light regimes thus allowed us to study the extent of physiological and structural adaptation to different light environments.

MATERIALS AND METHODS

Study site and species

The La Selva Biological Station of the Organization for Tropical Studies, located in the extremely wet Atlantic lowland of northeastern Costa Rica, provided an excellent gradient of climax rain forest and successional sites for study of *Heliconia*. Twelve species of *Heliconia* are present at La Selva (Wilbur *et al.* 1994), of which the seven common ones were used in this investigation. In open, full-sun successional habitats occurred *H. imbricata* (Kuntze) Baker, *H. latispatha* Benth., *H. pogonantha* Cufodontis, and *H. wagneriana* Peterson; these exhibit a musoid growth form, and shoots commonly reach 6 m in height. Although full-sun species are rapid colonizers in large open sites following a disturbance, clones may persist in shrinking light gaps during late forest succession, when daily PFD of the habitat becomes greatly diminished. *Heliconia mathiasiae* Daniels and Stiles is a moderate-sized zingiberoid colonizer of sites with intermediate PFD, e.g., along stream banks. Two species of the shady understorey in the rain forest at La Selva, *H. irrasa* R. R. Smith ssp. *undulata* Daniels and Stiles and *H. umbrophila* Daniels and Stiles, are low herbs only rarely exceeding 1.5 m in height.

Measurements were taken at beginning of three dry seasons, from late November 1995 to early January 1998, under clear skies but non-limiting water availability, when soil was still at field capacity, relatively humidity typically exceeded 80%, and scattered rains were received during late afternoons and evenings. Climatic conditions and vegetation types at La Selva have been carefully reviewed (McDade *et al.* 1994).

Physiological measurements

Three species were used for gas exchange measurements, *H. latispatha* of open, full-sun sites, *H. mathiasiae* of partial-sun forest edge sites, and *H. irrasa* ssp. *undulata* growing in undisturbed, deep-shade rain forest understorey. Diurnal courses of assimilation (A), stomatal conductance to water vapour (g_s), and transpiration rate (*E*) were determined using a portable photosynthesis system LI-6200 (LI-COR Inc., Lincoln, Nebraska, USA). Light response curves were composited from a series of measurements in 1995 on three to five leaves for each species. An artificial light source with a 12-V projector bulb and cold mirror was utilized to regulate PFD without significantly altering leaf temperature. To vary PFD, neutral-density screens were placed between the natural or artificial light source and the leaf. The leaf was allowed an interval of 15 min to adjust to each new PFD level. Dark respiration was achieved by enclosing the leaf chamber in aluminum foil.

Structural studies

Morphological and anatomical studies of leaf structure and biomass were conducted on the seven species. For each species, leaf characteristics were obtained by sampling five mature leaves from several clones. Because the 'trunk' of a musoid plant is a pseudostem, formed by overlapping leaf bases, a specific protocol was adopted by harvesting a petiole from the point where it became structurally free from the main axis. This point serves as the fulcrum for mechanical support of the foliar area. Photosynthetic surface area of each fresh leaf was determined using a LI-3100 leaf area meter (LI-COR Inc., Lincoln, Nebraska, USA), after carefully trimming blade portions from the midvein. The leaf blade with detached midvein and petiole were dried separately at 70 °C to obtain dry weight. Dry weight measurements were used to calculate mean specific leaf mass (g m^{-2} leaf), blade weight-to-petiole weight ratio (g g^{-1}), and blade area-to-petiole weight ratio (m^2 g^{-1}). The latter measure has been termed leaf-support efficiency (Chazdon 1986a).

Thin free-hand sections using a razor blade were prepared from near the tip (highest daily PFD) of the harvested canopy leaves, to standardize measurements on anatomical features that are highly variable under partially shaded conditions. At 2 cm from the leaf margin, thin leaf transections and paradermal sections of adaxial and abaxial surfaces were obtained, each mounted in water on a microslide and examined under a light microscope equipped with an optical micrometer. Stomatal densities were obtained from six fields (× 400) per leaf surface, along one transect, for each of five leaves. Leaf segments of each species were also liquid-preserved in formalin-acetic acid-alcohol and later dehydrated in an ethanol series, critical point dried, coated with 200 nm gold-palladium, and then examined with an ETEC Autoscan scanning electron microscope at 10 kV.

RESULTS

Assimilation rates peaked in the morning hours for both *H. latispatha* and *H. mathiasiae*, and then declined sharply throughout the afternoon, when the adjacent forest canopy shaded this site (Figure 1). Peak morning assimilation rate

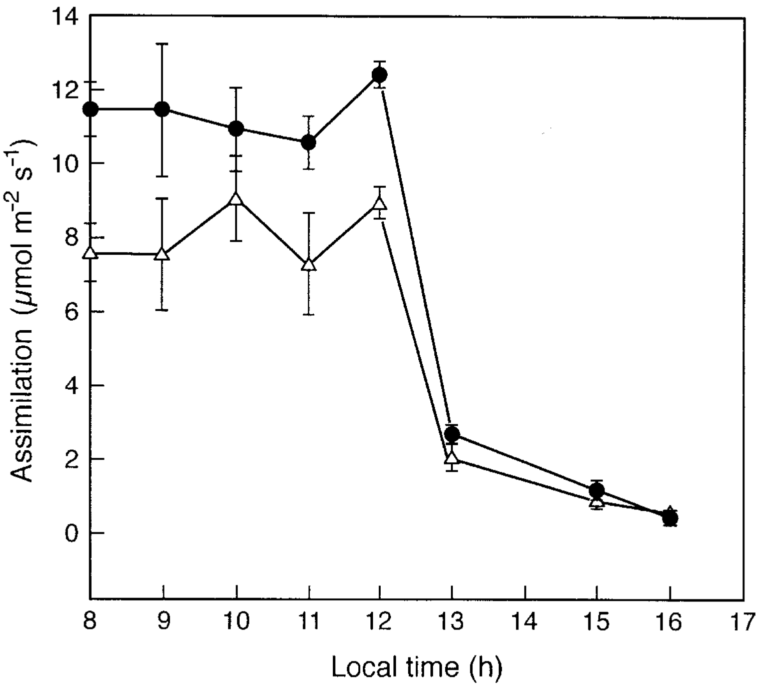

Figure 1. Assimilation rates for *Heliconia latispatha* (solid circles) and *H. mathiasiae* (open triangles) growing in a clearing at La Selva Biological Station, Costa Rica. Measurements were taken on 3–4 December 1995, beginning in full sun but experiencing shade from the adjacent forest canopy throughout the afternoon. Mean and SE of replicate measurements of assimilation rates are plotted.

for *H. latispatha* was 12.4 μmol m^{-2} s^{-1}, as compared with 9.1 μmol m^{-2} s^{-1} for *H. mathiasiae*.

Light response curves for the open-site species *H. latispatha*, the forest edge species *H. mathiasiae*, and the understorey species *H. irrasa* showed a clear gradient in their saturating PFD intensities and assimilation rates. *Heliconia latispatha* became light saturated at PFD of 1400 μmol m^{-2} s^{-1}, a level equivalent to about 70% full solar irradiance, and had a maximum rate of assimilation of 14–16 μmol m^{-2} s^{-1} (Figure 2a). In *H. mathiasiae*, light saturation occurred at PFD of 1000 μmol m^{-2} s^{-1}, i.e., half full solar irradiance, and maximum assimilation rates were 7.5–8.5 μmol m^{-2} s^{-1} (Figure 2b). In *H. irrasa*, light saturation was achieved at 250 μmol m^{-2} s^{-1}, and maximum rate of assimilation was only 3.5 μmol m^{-2} s^{-1} (Figure 2c) under non-limiting light conditions. Such a level of illumination is only experienced in the understorey during brief sunflecks. When compared on a leaf dry weight basis, maximum assimilation rates of the three species showed a decrease from the species of open sites to the deep shade; *H. latispatha* was 221 nmol g^{-1} s^{-1}, *H. mathiasiae* was 164 nmol g^{-1} s^{-1}, and *H. irrasa* was only 95 nmol g^{-1} s^{-1}.

Morphological characteristics of sampled heliconias showed clear patterns in relation to their typical light environment. Tall species of open, early successional sites had the largest leaves; mean blade area ranged from 0.68–0.72 m^{2}

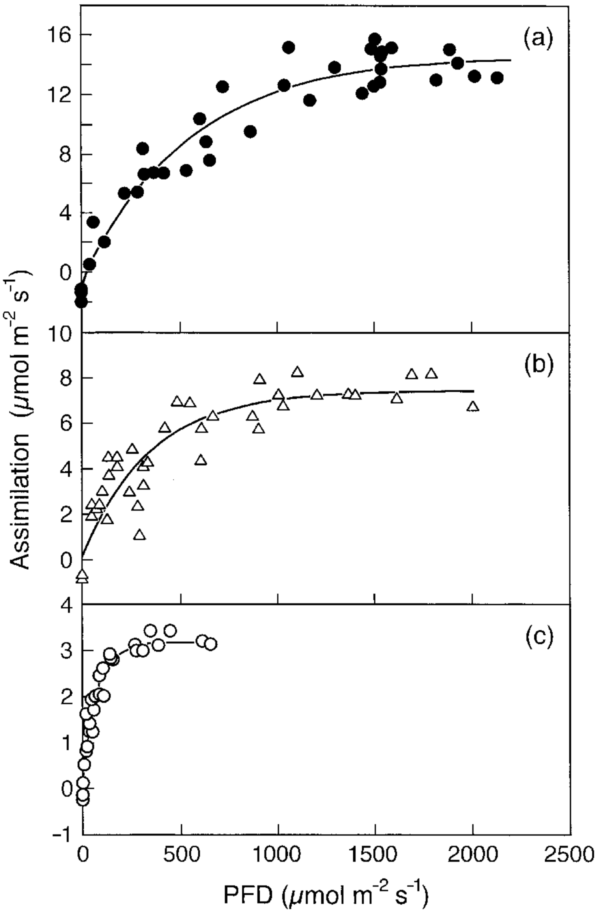

Figure 2. Rates of assimilation as measured at different photon flux densities (PFD) for three species of *Heliconia* at La Selva Biological Station, Costa Rica, taken in early December1995: (a) *Heliconia latispatha* (solid circles) from an open site; (b) *Heliconia mathiasiae* (open triangles) from a forest edge site; (c) *Heliconia irrasa* ssp. *undulata* (open circles) from deep shade in forest understorey.

for three species and 0.38 m^2 for *H. latispatha* (Table 1). The two understorey species had small blades, ranging from 0.06–0.08 m^2. *Heliconia mathiasiae*, having a zingiberoid growth form, cannot be directly compared in leaf area, because its small leaves (0.05 m^2) were displayed horizontally from a main aerial stem.

Distinctive patterns of leaf structure and allocation were also found consistently between open site and understorey species of *Heliconia*. Leaf specific mass was significantly higher for open-site species, ranging from a low of 68 g m^{-2} in *H. latispatha* to a high of 91 g m^{-2} in *H. wagneriana*, whereas understorey species values were substantially lower, with 36 g m^{-2} in *H. irrasa* and 46 g m^{-2} in *H. umbrophila* (Table 1). Leaf specific mass was also comparatively low in *H. mathiasiae* (49 g m^{-2}).

Ratio of blade weight to petiole weight, leaf-support efficiency, varied from

Table 1. Morphological and anatomical characteristics (means ± SE) of seven species of *Heliconia* at La Selva Biological Station, Costa Rica. Each leaf morphology value is a mean of five measurements for each species. Leaf mechanical support data for *H. mathiasiae*, a zingiberoid growth form, were not applicable (NA).

Species	Mean maximum height (m)	Leaf area (m^2)	Specific leaf mass (g m^{-2})	Blade weight/ petiole weight (g g^{-1})	Blade area/ petiole weight (m^2 g^{-1})	Mean intercostal blade thickness (µm)	Mean mesophyll thickness (µm) (no. of palisade layers)	Mean abaxial stomatal density (stomata mm^{-2})
Open sites								
H. imbricata	4–6	0.683 ± 0.062	77.8 ± 4.4	1.9 ± 0.2	0.020 ± 0.005	251 ± 3	174 ± 3 (2)	227 ± 27
H. latispatha	2–4	0.378 ± 0.010	67.9 ± 6.5	4.9 ± 0.7	0.078 ± 0.013	212 ± 15	138 ± 2 (2–3)	158 ± 9
H. pogonantha	3–5	0.690 ± 0.028	89.0 ± 17.2	2.3 ± 0.5	0.027 ± 0.009	211 ± 3	151 ± 4 (2)	188 ± 21
H. wagneriana	4–6	0.715 ± 0.089	91.4 ± 20.9	1.7 ± 0.2	0.021 ± 0.007	288 ± 22	203 ± 3 (2–3)	167 ± 36
Forest edge sites								
H. mathiasiae	2–3.5	0.052 ± 0.010	48.7 ± 6.3	NA	NA	189 ± 6	107 ± 5 (2)	110 ± 17
Forest understorey								
H. irrasa spp. *undulata*	0.5–1	0.060 ± 0.011	35.8 ± 5.5	6.2 ± 0.9	0.199 ± 0.030	154 ± 8	69 ± 2 (1)	52 ± 13
H. umbrophila	1–2	0.082 ± 0.013	45.8 ± 6.1	5.6 ± 1.0	0.246 ± 0.035	174 ± 8	88 ± 3 (1)	65 ± 4

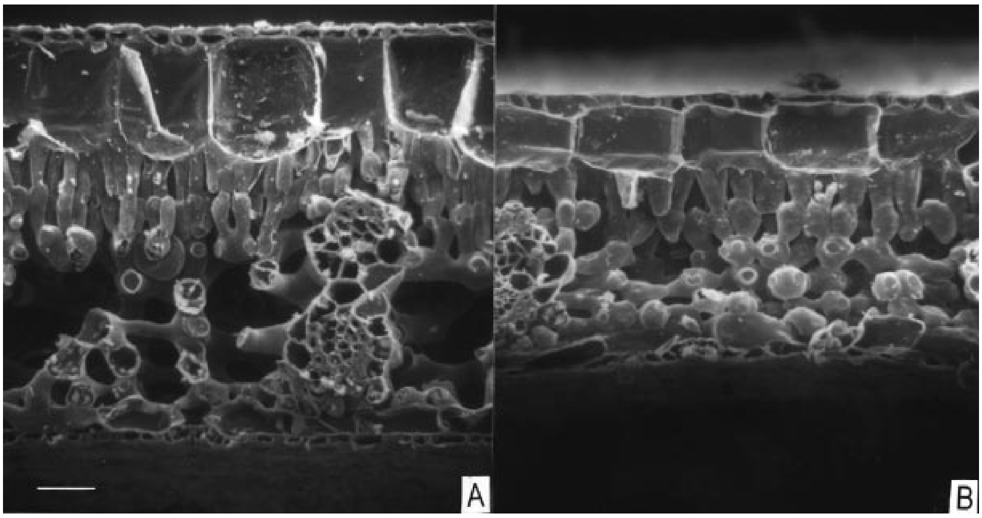

Figure 3. Scanning electron photomicrographs of leaf transections. A. *Heliconia wagneriana* of full-sun open site, showing two layers of palisade mesophyll beneath the large-celled adaxial hypodermis. B. *Heliconia umbrophila* of deep-shade forest understorey; the upper layer of mesophyll consists of funnelform chlorenchyma cells, not palisade cells, and the leaf is much thinner than the full-sun leaf of *H. wagneriana*. Magnification bar = 30 μm.

1.7 to 4.9 g g^{-1} in open sites species but was significantly higher (5.6 to 6.2 g g^{-1}) in the two understorey species (Table 1). Open-site heliconias were able to support 0.020-0.078 m^2 leaf area g^{-1} dry weight of petiole as compared with significantly higher values of 0.199–0.246 m^2 g^{-1} in the two understorey species.

Open-site species also showed consistent differences in leaf anatomical features (Table 1). Leaf thickness, measured for intercostal regions (between veins) and mesophyll thickness were greatest in open-site species, which had two, sometimes three, layers of palisade parenchyma (Figure 3a), and chlorenchyma comprised approximately two-thirds of the leaf transection (mean mesophyll thickness/mean intercostal blade thickness in Table 1). *Heliconia mathiasiae* possessed a similar sun-leaf design but had thinner leaves, and mesophyll comprised slightly more than half of the leaf transection. The thinnest leaves occurred in species inhabiting deep shade; in these, chlorenchyma comprised less than half of the leaf transection, and a single layer of funnelform chlorenchyma cells with prominent, large chloroplasts replaced palisade parenchyma (Figure 3b). Full-sun leaf samples of open-site species sometimes formed three adaxial palisade mesophyll layers, and these particular samples tended to have the highest abaxial stomatal densities plus some adaxial stomata as well, i.e., they were amphistomatic, whereas shade species and shade leaves were strictly hypostomatic. Stomata were typically absent opposite major and minor veins of the blade, thus producing stomatic and astomatic strips on the abaxial epidermis. Guard cell length was 25–27 μm for all species examined, hence maximal stomatal pore dimensions showed no interspecific or light environment differences.

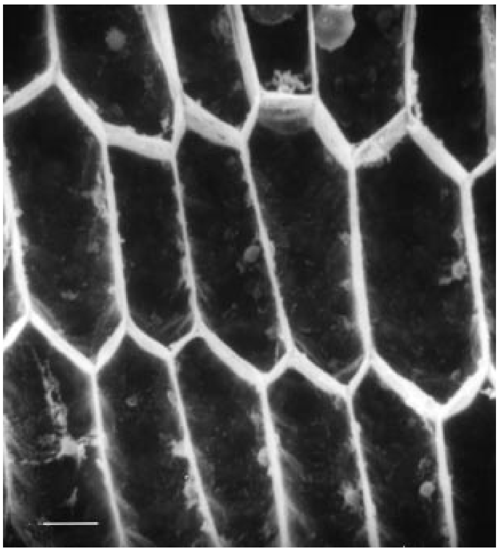

Figure 4. Scanning electron photomicrograph of adaxial hypodermis, viewed in paradermal section in a leaf of *Heliconia wagneriana*. Hexagonal cells of this tissue have somewhat thickened primary cell walls but no intercellular air spaces. Magnification bar = 15 μm.

A colourless, uniseriate adaxial and abaxial hypodermis occurred in all species of *Heliconia*, and cells were hexagonal in paradermal view and arranged in distinct longitudinal files (Figure 4). Hypodermal tissue lacked intercellular air spaces, and the long axis of each hypodermal cell was oriented perpendicular to the files of the groundmass epidermis and, likewise, perpendicular to the vascular bundles. Adaxial hypodermis was commonly three or more times taller in transection than the abaxial hypodermis (Figures 3a–3b), which tended to be tabular. Height of adaxial hypodermis varied between species, but there was no obvious pattern in height of hypodermis along the light environment gradient, except that in understorey species the water-storing hypodermal layer comprised nearly half of the leaf transection. Anticlinal cell walls of hypodermis were straight, evenly thickened apparently with structural polysaccharides, each up to 1.5 μm thick and substantially thicker than cell walls of either the photosynthetic mesophyll or the epidermis. These geometrically regular cells of hypodermis strongly contrasted the epidermis, composed of smaller cells with sinusoidal anticlinal walls.

Major and minor vascular bundles of leaf blades included clusters of lignified adaxial and abaxial bundle fibres. Although understorey species appeared to have greater fibre mass per transection of leaf blade, no attempt was made to quantify values for species because age of leaf would be an important factor to analyze intraspecific and interspecific variations; however, the observation is consistent with the result that shade species had higher ratios of blade weight to petiole weight (Table 1).

DISCUSSION

Detailed studies of shade tolerance and photosynthetic acclimation in tropical forest herbs have largely come from research on an Australian species of *Alocasia* (Björkman & Holmgren 1963, Björkman 1981, Chow *et al.* 1988, Mulkey & Pearcy 1992; Sims & Pearcy 1989, 1994; Sims *et al.* 1994). Under low PFD, characteristic of the forest floor environment, light saturation observed under laboratory conditions occurs at an irradiance of *c.* 250 μmol m^{-2} s^{-1}, and field studies with understorey species of *Streptochaeta*, an herbaceous bamboo (Mulkey 1986), and three understorey palms (Chazdon 1986b) have found saturation levels of 100–150 μmol m^{-2} s^{-1}. These results are similar to our observations for *Heliconia irrasa*, which grows abundantly in the same microhabitat at La Selva as the understorey palms. Under conditions of high PFD, however, as might be expected to occur when an understorey area is exposed to direct sun after treefall creates a light gap, *Alocasia macrorrhiza* G. Don showed a strong ability to acclimate physiologically by producing sun-adapted leaves that had light saturation instead at 800 μmol m^{-2} s^{-1} and a photosynthetic capacity raised to 12 μmol m^{-2} s^{-1}, three times the rate present in shade-adapted leaves (Chow *et al.* 1988, Mulkey & Pearcy 1992, Sims & Pearcy 1989).

Leaves for light saturation found in our study for *H. latispatha*, a species that colonizes open sites in full sun, are high (1400 μmol m^{-2} s^{-1}), and thus similar to saturation values reported for early successional trees on Barro Colorado Island, Panamá (Hogan *et al.* 1995). Nevertheless, it has been suggested that pioneer tropical trees typically become light saturated for photosynthesis at PFD levels of only about 25% full sun (Strauss-Debenedetti & Bazzaz 1996). *Ceiba pentandra* (L.) Gaertn., a persistent pioneer species of tropical forest, has been found to saturate at *c.* 500 μmol m^{-2} s^{-1} (Zotz & Winter 1994). Full-sun conditions in large forest gaps or clearings may cause photoinhibition in tropical plants, with recovery occurring over several hours in the afternoon (Kraus & Winter 1996). Steep leaf angles in *Heliconia* have been shown to be an adaptation to reduce midday levels of incident radiation (He *et al.* 1996), and they ensure rain runoff while permitting the abaxial surface to remain relatively dry during rainstorms.

Anatomical features of these seven Costa Rican species showed trends of an important gradient in photosynthetic apparatus along a light gradient, at a field location where species were growing within a km^2 under the same rainfall regime. Full-sun leaves of open-site species have substantially thicker leaves, with proportionately greater investment in chlorenchyma, especially having development of more palisade parenchyma and apparent reductions in air space volume within the spongy parenchyma. To improve CO_2 diffusion into full-sun leaves that are equipped with high internal mesophyll surface area, species in open sites have higher stomatal densities, and some leaves are amphistomatic, providing an extra stomatal conductance from the adaxial surface (Mott *et al.* 1982). Amphistomaty, although not studied to any degree in the wet tropics, should also be expected to occur in early successional colonizers of high PFD gaps, as well as full-sun herbs, and there are scattered reports of low adaxial stomatal densities even in certain pioneer trees (Ashton & Berlyn 1992). In contrast, deep-shade heliconias, like other understorey herbs, have very thin mesophyll and low stomatal density, matching the low PFD expectations of leaves which receive most daily illumination via light flecks of short duration (Chazdon & Fetcher 1984).

It is useful to compare leaf morphological characteristics and allocation ratios from understorey species of *Heliconia* with values obtained for long-lived understorey fan palms at La Selva (Chazdon 1986a, b). Leaf specific masses in mature individuals of these palm species were 55–70 g m^{-2}, making them similar to open-site heliconias and higher than specific leaf masses of the understorey *H. irrasa* and *H. umbrophila*. Biomass allocation to photosynthetic blade compared with petiole allocation was 53–63% in understorey palms as compared with 85–86% in understorey heliconias. All open-site species of *Heliconia* allocated as much or more leaf biomass to foliar blade area (65–83%) as the understorey palms. Leaf support efficiencies determined for heliconias are also high in comparison with La Selva understorey palms, where mean values ranged from 0.021–0.027 m^2 g^{-1}. Again, the palms had values similar to open-site species of *Heliconia* and only about one-eighth values reported here for understorey heliconias.

The colourless adaxial and thinner abaxial hypodermis of the blade in *Heliconia* is a synapomorphy that occurs in nearly all described leaves of order Zingiberales (Tomlinson 1959, 1969). Probably, sunlight is diminished very little as it passes through adaxial hypodermis with its large water-storing vacuoles to reach the underlying photosynthetic tissue. Also important is the overall lattice-like design of hypodermis, without intercellular air spaces. Skutch (1930) proposed that hypodermis in musoids is the tissue enabling young leaves to unroll. In addition, a hypodermal network may be expected to resist shear during wind action on the leaves (Niklas 1992) and also to produce the characteristic inrolling of older leaves as the hypodermal cells lose turgor and leaf wilting occurs. Strong wind causes tearing of broad monocotyledonous leaves of heliconias and their relatives, but only along the axis parallel to the major veins, because veins are greatly strengthened with bundle fibres. Commonly, large sectors of a wind-damaged leaf remain intact, presumably due to the strength of the hypodermal network, a substitution for the reticulate network of vascular bundles found in dicotyledonous leaves.

The evolution of leaf form and structural investment in understorey palms has been discussed in detail as a trade-off between economy and safety (Chazdon 1985, 1986a). Whereas minimizing investments for support structures would lead to metabolic savings, a compromise in the mechanical structure of a leaf support system would lead to increased chance of early tissue loss from physical or biological stresses. Fallen branches and other heavy plant objects have been shown to be a major cause of mortality in rain forest understorey species (Chazdon 1986a, Clark & Clark 1987, Sharp 1993), clearly establishing the significance of safety for understorey species with slow rates of leaf production. This evolutionary pressure toward mechanical durability in leaf support structures, however, may be less important in rapidly growing herb species that have substantial carbohydrate storage reserves in below-ground rhizomes or corms. Rain forest herbs like *Heliconia* allocate a large percent of above-ground biomass to leaf tissues, and these leaves have a relatively low investment in support tissue in both understorey and open-site species. In understorey environments at La Selva, the relatively low investment in support structure for shade-adapted heliconias may be an important aspect of shade tolerance, but opens these plants to higher risk of catastrophic leaf loss or damage. Data on the relative above- and below-ground allocation of carbon in understorey herbs and palms is still needed to test whether the rhizome storage structure is an alternative strategy of safety.

In most of its physiological and structural features of the leaf blade, *Heliconia mathiasiae* was intermediate between the full-sun and deep-shade strategy, and its gas exchange and well-developed palisade mesophyll probably indicate that this species is basically a heliophilic species. Future studies need to determine the evolution and ecological significance of the zingiberoid growth habit, as is typical of Zingiberaceae, which are most commonly found in shade habitats.

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