

## LIGHT-DEPENDENT LEAF TRAIT VARIATION IN 43 TROPICAL DRY FOREST TREE SPECIES<sup>1</sup>

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Our understanding of leaf acclimation in relation to irradiance of fully grown or juvenile trees is mainly based on research involving tropical wet forest species. We studied sun–shade plasticity of 24 leaf traits of 43 tree species in a Bolivian dry deciduous forest. Sampling was confined to small trees. For each species, leaves were taken from five of the most and five of the least illuminated crowns. Trees were selected based on the percentage of the hemisphere uncovered by other crowns. We examined leaf trait variation and the relation between trait plasticity and light demand, maximum adult stature, and ontogenetic changes in crown exposure of the species. Leaf trait variation was mainly related to differences among species and to a minor extent to differences in light availability. Traits related to the palisade layer, thickness of the outer cell wall, and  $N_{\text{area}}$  and  $P_{\text{area}}$  had the greatest plasticity, suggesting their importance for leaf function in different light environments. Short-lived pioneers had the highest trait plasticity. Overall plasticity was modest and rarely associated with juvenile light requirements, adult stature, or ontogenetic changes in crown exposure. Dry forest tree species had a lower light-related plasticity than wet forest species, probably because wet forests cast deeper shade. In dry forests light availability may be less limiting, and low water availability may constrain leaf trait plasticity in response to irradiance.

**Key words:** Bolivia; crown exposure; leaf traits; light acclimation; plasticity; tropical dry deciduous forest.

Trees are long-lived and sessile organisms that subsist in a spatially and temporally highly heterogeneous environment. Trees should therefore possess the capacity to adjust their leaves to their environment. In tropical wet forests light is considered to be the most limiting resource for tree growth and survival (Whitmore, 1996) and a major axis of differentiation for tropical tree species. In contrast, studies on leaf trait variability from (semi-)arid woody vegetations, such as the Mediterranean maquis (e.g., Gratani and Varone, 2004) and the Californian chaparral (e.g., Ackerly, 2004), have generally focused on leaf traits of shrub species in relation to water availability. Recently, several studies have focused on leaf trait acclimation in response to both light and water availability, thus more closely approximating the reality in the field (Sack et al., 2003; Sánchez-Gómez et al., 2006; Quero et al., 2006). Although authors found that shaded conditions enhance seedling tolerance to drought (Quero et al., 2006) and that the impact of drought on seedling survival and growth rates was stronger in high light than in low light conditions (Sánchez-Gómez et al., 2006), clear functional types of species

able to tolerate a combination of shade and drought are not yet clearly defined (Sack et al., 2003).

Our current knowledge of leaf responses to irradiance in the tropics is mainly based on research conducted in wet forests (e.g., Bongers and Popma, 1988; Poorter et al., 2000) or on small seedlings. Sun leaves grow in a high resource environment and are often relatively thick and small with a low surface to volume ratio. Thicker leaves have a reduced light absorption per unit biomass (Agusti et al., 1994) and an increased photosynthesis per unit leaf area (Björkman, 1981; Klich, 2000). Photosynthetic capacity is enhanced through investment in thicker and/or extra layers of palisade parenchyma tissue and increased nitrogen concentration per unit leaf area (Björkman, 1981; Poorter et al., 1995; Poorter, 1999). Overheating might be a severe problem in high light when leaf temperatures exceed the photosynthetic optimum, especially if water availability is low (Smith, 1978). Smaller, and/or slender leaves have a reduced boundary layer resistance (Givnish, 1984) and are thus capable of regulating their temperature through better convective cooling of the leaf area (Parkhurst and Loucks, 1972). Leaf cuticles and epidermides may reduce water loss through evaporation (Gamage et al., 2003; Mendes et al., 2001) and protect the photosynthetic tissue from excessive irradiance through increased reflectance (Roth, 1984). High radiation loads and high vapor pressure deficits result in greater transpiration rates of sun leaves, and thus a large water flow to the leaves is needed. This can be facilitated by large xylem conduits (Zimmermann, 1983), relatively thick internodes in relation to the leaf area (cf. Westoby and Wright, 2003), and a high leaf hydraulic conductance (Sack et al., 2005).

Light is a limiting resource for growth in the shaded understory. Trees growing in the shaded understory enhance their light interception through the formation of relatively large, thin leaves with a low leaf mass per unit leaf area (LMA) (Evans and Poorter, 2001). They may forage for light and minimize self shading through the formation of cheap petioles with a high petiole length per unit petiole mass. Respiratory

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carbon losses are reduced through low protein and nitrogen concentrations (Sims and Pearcy, 1989).

The magnitude of acclimation that a species can realize in response to differences in irradiance can be referred to as plasticity. Plasticity enhances plant performance and is thought to differ predictably among functional groups. Pioneer species that regenerate in open areas and forest gaps were hypothesized to have a higher plasticity than shade tolerant species, because they grow in a more variable environment. (Bazzaz, 1979; Bazzaz and Wayne, 1994). It is a certainty that formed gaps will close, allowing for selection on high acclimation potential. The high resource availability in early successional habitats allows pioneer species to support the carbon investment costs that come along with a higher acclimation potential. Still there is little consensus about this hypothesis. Some studies found plasticity to be similar for pioneer and shade tolerant species (Sims and Pearcy, 1989; Kitajima, 1994), while others actually found less plasticity in pioneers than in shade tolerant species (Popma et al., 1992). Grubb (1998) suggested that these apparently contradictory results might have been found because pioneers in the seedling stage are more plastic, whereas in the adult stage shade tolerant species are more plastic. Contradictory results may also partly be explained by the fact that in many studies only a few species and a few leaf traits have been evaluated and differing methods were used to calculate and define plasticity. In addition, researchers have often assigned species arbitrarily to functional groups, without an objective, quantitative measure of the light demand of the species.

Popma et al. (1992) argued that pioneers do not need to have a high plasticity because they always grow in high light and do not survive deep shade. Instead, plasticity should be highest for tall species that establish in the shaded understory and are subject to large ontogenetic changes light availability during their life cycle (cf. Thomas and Bazzaz, 1999; Poorter et al., 2005). Close relations of leaf trait plasticity with maximum adult stature and ontogenetic crown exposure may thus be expected.

The magnitude of plasticity is likely smaller in tropical dry forest than in tropical wet forest tree species. Tropical dry forests are characterized by a prolonged dry season in which the vegetation is subject to low soil water availability and high vapor pressure deficit of the air (Bullock et al., 1995). Light penetration in dry forests is relatively high compared to wet forests (5–10% in the wet season in dry forests vs. 0.4–2.0% yr-round in wet forests; Coomes and Grubb, 2000), due to a low and open canopy and low stem densities. These levels are even higher during the dry season, when many canopy and subcanopy species shed their leaves (Parker et al., 2005). Leaf trait acclimation in response to light availability is therefore likely to be less pronounced in tropical dry forests than in wet forests.

In this study we evaluate leaf characteristics and evaluate sun-shade plasticity of 43 tropical dry forest tree species. Twenty-four morphological, anatomical and chemical leaf traits that are important for the heat, water, and carbon balance of the plant are assessed. Leaf trait plasticity is related to quantitative measures of maximum adult stature, juvenile crown exposure, and ontogenetic changes in crown exposure of the species. We made the following three predictions: (1) Functional groups of species related to shade tolerance differ in leaf trait plasticity in response to irradiance. Pioneer species grow in a more variable habitat with higher resource availability and are thus expected to have high leaf trait plasticity, whereas shade tolerant species tend to spend their

entire life cycle in the low resource environment of the forest understory, with a marginally positive carbon balance, and therefore should have less potential to acclimate and less plasticity. (2) There is a positive relationship between leaf trait plasticity and maximum adult stature, juvenile crown exposure, and ontogenetic changes in crown exposure of the species. Tall species establish in the shaded forest understory, but, during their life cycle, endure more changes in light availability than small species. This requires a greater ability to adjust to their changing growth environment. (3) Dry tropical forests tree species will have smaller leaf trait plasticity in response to irradiance than tree species from wetter forest types. As light is less of a limiting factor in dry forests, the necessity of a high light-related plasticity is smaller for dry forest tree species.

## MATERIALS AND METHODS

**Study area**—This study was conducted in the INPA forest (16°07' S, 61°43' W) in the lowlands of eastern Bolivia. The forest can be classified as a tropical lowland dry deciduous forest, situated at the transition zone between the Amazonian wet forests in the north and the thorn-shrub formations of the Gran Chaco in the south (Killeen et al., 1998; Jardim et al., 2003).

The study area has a mean altitude of 458 m and is located on the Precambrian Brazilian shield. Soils are oxisols and are low in nutrients. Mean annual temperature at Concepción, ca. 40 km from the study site, is 24.3°C, and the mean annual precipitation is 1160 mm with a dry season (<100 mm rainfall per mo) from April until October. From June through September, the potential evapotranspiration exceeds the mean monthly rainfall, which can result in a water deficit. The forest canopy has an average height of 22 m with emergent trees growing up to 30 m. The forest has a density of 437 stems·ha<sup>-1</sup>, a basal area of 19.7 m<sup>2</sup>·ha<sup>-1</sup>, and a species richness of 34 ha<sup>-1</sup> (trees ≥ 10 cm dbh; Instituto Boliviano de Investigación Forestal [IBIF], Santa Cruz de la Sierra, Bolivia, unpublished data). The forests in the region have previously been classified as semi-deciduous forests (Killeen et al., 1998), because most of the subcanopy trees, shrubs and lianas are evergreen or semi-evergreen (Killeen et al., 1998). Because the canopy of the forest at INPA is fully deciduous in the dry season, we chose to classify this forest as a dry deciduous forest in stead of a semi-deciduous forest.

The most dominant species at INPA (listed in decreasing order of basal area [m<sup>2</sup>·ha<sup>-1</sup>] are *Acosmium cardenasii* H.S. Irwin & Arroyo (Fabaceae), *Casearia gossypiosperma* Briquet (Flacourtiaceae), *Caesalpinia pluviosa* DC (Fabaceae), *Neea* cf. *steinbachii* (Nyctaginaceae), *Machaerium acutifolium* Vogel (Fabaceae), *Anadenanthera macrocarpa* Benth (Fabaceae), *Piptadenia viridifolia* (Kunth.) Benth (Fabaceae), and *Centrolobium microchaete* (Benth.) H.C. Lima (Fabaceae) (IBIF, unpublished data). Nomenclature follows that of the nomenclature database of the Missouri Botanical Garden (W<sup>3</sup>TROPICOS; www.mobot.org).

**Study species**—We studied leaf traits of 43 tree species belonging to 40 genera, 24 families, and 19 orders. Among the selected species are some of the most abundant species in this type of forest, as well as several commercially valuable timber species (Table 1). With six species, Fabaceae is the biggest family in this study, which is in line with its dominance in this dry deciduous forest. All species together represent more than 77% of the stems larger than 10 cm dbh in the permanent sample plots (IBIF, unpublished data).

Species varied in leaf form and habit, maximum adult stature, and shade tolerance. Maximum adult stature ( $H_{max}$ ) was calculated for each species as its asymptotic height (cf. Thomas, 1996) using species-specific height-diameter relationships (Verweij, 2004) and the diameter of the third thickest tree in the permanent sample plots (thus avoiding outliers). We classified the species into four guilds of shade tolerance (cf. Finegan, 1992) based on their light requirements and longevity (Jardim et al., 2003; Mostacedo et al., 2003; Justiniano et al., 2004) and additional field observations on the habitat preference of the species (L. Poorter, personal observation). Short-lived pioneers (SLP) are species that need high light to establish and grow to their adult stature and have a lifespan up to 30 yr. These SLP are the “typical” pioneers *sensu stricto*, that can form dense stands in disturbed areas or large treefall gaps (cf. Kammesheidt, 2000). Long-lived pioneers (LLP) need intermediate light to establish and grow to the high light environment of the

TABLE 1. Species list with the scientific names of the 43 studied species. Functional groups related to shade tolerance (Guild; ST = shade tolerant, PST = partial shade tolerant, LLP = long-lived pioneer, and SLP = short-lived pioneer species), mean canopy openness above the sampled individuals per species in the shade ( $CO_{shade}$ ) and sun ( $CO_{sun}$ ), maximum adult stature ( $H_{max}$ ), average crown exposure at 2 m height ( $CE_{juv}$ ), and the ontogenetic change in crown exposure ( $CE_{change}$ ) are given for each species (L. Poorter, unpublished data). Citations follow the nomenclature database of Missouri Botanical Garden (W<sup>3</sup>TROPICOS; www.mobot.org). For *Pouteria gardneriana*, few adult trees were found, so no reliable estimate of  $H_{max}$  and  $CE_{change}$  can be given. *Urera caracasana* is a SLP with a surprisingly low  $CE_{juv}$  (1.58). It seems to establish from seed in disturbed areas. Juveniles die back in the dry season and resprout again in the wet season. Most juveniles in this study were found in the shade and had resprouted from root systems of old individuals that once established in gaps and were overgrown.

Species	Family	Guild	$CO_{shade}$ (%)	$CO_{sun}$ (%)	$H_{max}$ (m)	$CE_{juv}$	$CE_{change}$	Plasticity
<i>Acosmium cardenasii</i> H.S. Irwin & Arroyo	Fabaceae	ST	7	54	25	1.44	2.86	14.86
<i>Actinostemon conceptionis</i> (Chodat & Hassl.) Hochr.	Euphorbiaceae	ST	5	47	5	1.40	0.62	16.72
<i>Ampelocera Ruizii</i> Klotzsch	Ulmaceae	PST	11	38	20	1.59	1.36	14.75
<i>Aspidosperma cylindrocarpon</i> Müll. Arg.	Apocynaceae	PST	12	57	25	1.31	2.74	9.27
<i>Aspidosperma tomentosum</i> Mart.	Apocynaceae	PST	11	54	23	1.31	2.86	11.88
<i>Astronium urundeuva</i> (Allemao) Engl.	Anacardiaceae	LLP	9	72	28	2.42	2.30	8.63
<i>Bougainvillea modesta</i> Heimerl	Nyctaginaceae	LLP	14	45	23	2.12	-0.01	17.05
<i>Caesalpinia pluviosa</i> DC.	Fabaceae	PST	11	49	28	1.81	2.82	16.57
<i>Capparis prisca</i> J.F. Macbr.	Capparaceae	ST	15	64	16	1.59	1.01	12.79
<i>Cariniana ianeirensis</i> R. Knuth	Lecythidaceae	PST	13	46	28	1.90	2.75	10.96
<i>Casearia gossypiosperma</i> Briq.	Flacourtiaceae	PST	13	43	18	1.71	2.10	10.32
<i>Ceiba speciosa</i> (A. St.-Hil.) Ravenna	Bombacaceae	LLP	14	55	21	1.64	2.06	20.51
<i>Centropogon microchaete</i> (Mart. ex Benth.) Lima ex. G. P. Lewis	Fabaceae	LLP	7	61	28	1.93	2.46	29.53
<i>Chrysophyllum gonocarpum</i> (Mart. & Eichler) Engl.	Sapotaceae	ST	16	42	14	1.42	0.82	16.99
<i>Combretum leprosum</i> Mart.	Combretaceae	ST	16	57	22	1.92	2.01	20.04
<i>Eriotheca roseorum</i> (Cuatrec.) A. Robyns	Bombacaceae	LLP	11	59	25	1.64	2.64	12.11
<i>Erythroxylum daphnites</i> Mart.	Erythroxylaceae	ST	6	50	2	2.19	1.00	10.33
<i>Esenbeckia almawillia</i> Kaastra	Rutaceae	ST	3	59	2	1.64	0.02	12.95
<i>Galipea ciliata</i> Taub.	Rutaceae	ST	6	64	11	1.49	0.48	20.51
<i>Gallesia integrifolia</i> (Spreng.) Harms	Phytolaccaceae	PST	7	49	22	1.81	1.78	17.70
<i>Guibourtia chodatiana</i> (Hassl.) J. Leonard	Fabaceae	ST	11	73	25	1.87	2.93	10.33
<i>Jacaratia</i> sp.	Caricaceae	ST	7	30	2	1.51	0.00	16.45
<i>Manihot guaranitica</i> Chodat. & Hassl.	Euphorbiaceae	SLP	13	84	6	2.67	0.34	13.93
<i>Myrciaria cauliflora</i> (Mart.) O. Berg	Myrtaceae	ST	5	58	6	1.70	0.06	20.23
<i>Myrciaria</i> sp.	Myrtaceae	PST	11	59	10	1.64	0.61	26.90
<i>Neea cf. steimbachii</i>	Nyctaginaceae	ST	8	42	12	1.63	0.56	16.65
<i>Ouratea</i> sp.	Ochnaceae	ST	8	60	11	1.78	0.56	9.41
<i>Phyllanthus</i> sp. nov.	Euphorbiaceae	ST	6	26	7	1.60	0.38	22.02
<i>Phyllostylon rhamnoides</i> (J. Poiss.) Taub.	Ulmaceae	PST	9	55	26	1.49	2.78	12.99
<i>Platymiscium ulei</i> Harms	Fabaceae	LLP	9	70	27	2.52	1.85	13.20
<i>Pogonopus tubulosus</i> (A. Rich.) K. Schum.	Rubiaceae	ST	6	53	9	1.67	0.51	15.39
<i>Pouteria gardneriana</i> (A. DC.) Radlk.	Sapotaceae	ST	8	65		1.44		15.16
<i>Simira rubescens</i> (Benth.) Bremek. ex Steyerl.	Rubiaceae	ST	7	59	16	1.62	1.20	13.45
<i>Solanum riparium</i> Pers.	Solanaceae	SLP	33	74	15	3.00	0.49	23.48
<i>Spondias mombin</i> L.	Anacardiaceae	LLP	9	63	25	2.40	1.75	11.01
<i>Sweetia fruticosa</i> Spreng.	Fabaceae	PST	11	55	24	1.70	2.60	17.52
<i>Tabebuia impetiginosa</i> (Mart. ex DC.) Standl.	Bignoniaceae	LLP	5	57	30	2.42	2.20	15.46
<i>Tabebuia serratifolia</i> (Vahl) G. Nicholson	Bignoniaceae	LLP	8	55	28	1.27	3.44	26.46
<i>Talisia esculenta</i> (A. St. Hil.) Radlk.	Sapindaceae	ST	9	39	15	1.81	1.19	23.90
<i>Trichilia elegans</i> A. Juss.	Meliaceae	ST	6	54	24	1.24	2.27	15.78
<i>Urera baccifera</i> (L.) Gaudich. ex Wedd.	Urticaceae	SLP	10	82	10	2.29	0.47	22.53
<i>Urera caracasana</i> (Jacq.) Gaudich. ex Giseb.	Urticaceae	SLP	15	79	16	1.58	0.95	16.51
<i>Zanthoxylum monogynum</i> A. St. Hil.	Rutaceae	ST	6	75	10	1.46	-0.16	13.69

forest canopy. They live longer than 30 yr. LLP are pioneers sensu lato that can establish under a wider range of light conditions. Partial shade tolerant species (PST) can establish in the shaded understory, but need more light in later stages of their lifecycle to reach their maximum stature in the high light environment of the canopy. Shade tolerant species (ST) are species that can complete their entire life-cycle in the shade. We included 20 ST species, 10 PST species, nine LLP species, and four SLP species.

Data from a separate study (L. Poorter, unpublished data) provided an objective and quantitative measure of light demand, based on the analysis of height–light trajectories of each species. For a median of 133 (range 16–9064) individuals per species ranging from seedlings to adult trees, the height and crown exposure (CE) were estimated. The CE varies from 1 if the tree crown does not receive any direct light, to 2 if it receives lateral light, 3 if it receives overhead light on part of the crown, 4 when it receives overhead light on the whole crown, to 5 if it has an emergent crown that receives light from all directions (Dawkins and Field, 1978). CE can be measured repeatedly, and

there is a close relation between CE and both canopy openness (Davies et al., 1998) and incident radiation (Clark et al., 1993). For each species, we related CE to tree height, using a multinomial regression analysis (L. Poorter et al., unpublished manuscript; cf. Poorter et al., 2005) and calculated the average crown exposure at 2 m height ( $CE_{juv}$ ) and maximum adult stature ( $CE_{adult}$ ). The difference between  $CE_{juv}$  and  $CE_{adult}$  was used to estimate the ontogenetic change in CE for each species ( $CE_{change}$ ) (Table 1). It should be emphasized that these values indicate the average CE values at the population level. At a given height, individuals of the same species may be found under a wide range of crown exposures, and we used these extreme individuals as sun and shade trees for the sampling of leaves used in the present study. We used the CE and guilds as two complementary approaches to evaluate hypotheses about plasticity. The CE is a quantitative measure of light demand, whereas the guilds capture both juvenile crown exposure and ontogenetic changes in crown exposure (PST and LLP have larger  $CE_{change}$  than the two other guilds).

**Leaf collection**—Sun and shade leaves of each species were collected in the wet season of 2003–2004, by sampling five trees per species in full sunlight and five trees growing in shaded conditions. Sun and shade trees were selected based on the canopy openness (CO) above their crowns. CO was estimated for every sample tree as the percentage of the hemisphere above the tree crown that is not covered by crowns of other trees. Although the maximum and minimum CO at which individuals could still be found is rather species-specific, we applied the rule of thumb that the CO of sun individuals was at least 50% and that of shade individuals at most 15%. For species that could not be found within these ranges, the most highly and least illuminated individuals found were sampled. Average CO of the sampled sun individuals was  $56.5 \pm 0.3\%$  (mean  $\pm$  SE) and of the shade individuals  $9.8 \pm 0.1$  (mean  $\pm$  SE) (Table 1). Leaves were sampled from trees between 10–20 cm dbh and 10–20 m height, to reduce the confounding effect of tree size on leaf traits (Koch et al., 2004). *Jacaratia* sp., *Erythroxylum daphnites*, *Esenbeckia almawillia*, *Actinostemon conceptionis*, *Myrciaria cauliflora*, *Manihot guaranitica*, *Phyllanthus* sp. nov., and *Pogonopus tubulosus*, reached only a maximal height of 2–9 m (Table 1). For these species, the leaves were collected from the tallest individuals. For every sample tree, we estimated the diameter at breast height (dbh), total height, and the percentage canopy openness. To minimize trait variation related to the position of sampled leaves within the crown of the individual trees, we selected trees of the same height (especially within species) and sampled five leaves per tree from the outer leaf shell midway between the top and bottom of the crown. All sun leaves were collected from the most exposed side and all shade leaves from the least exposed side of the crown. Leaves were cut with a pair of extendable pruning shears and transported to the field station in plastic bags. To minimize leaf trait variation caused by the age of the sampled leaves, we selected leaves that were young and fully expanded. We also selected leaves with minimal signs of herbivore or pathogen damage.

In the field station a cross-section of one leaf per tree was stored in 70% ethanol (EtOH) for anatomical analysis. For compound and lobed leaves, a cross-section was made of an average-sized foliole or lobe.

**Leaf morphology**—For each tree, four leaves were measured for the length (LL) and width (LW) of the leaf blade. Folioles were considered to be functional equivalents of simple leaves and were treated accordingly in this study. Average-sized folioles were used in the case of compound leaves. The length of the petiole and the length and diameter of the internode section, below the corresponding node, were also measured. Leaf thickness (LT;  $\mu\text{m}$ ) was measured with a micrometer. Leaves were rehydrated overnight in wet tissue in a refrigerator, dried with a tissue, and weighed to determine the saturated fresh mass. Leaves and folioles were scanned with a desktop-scanner, and their surface area (LA;  $\text{cm}^2$ ) was determined using pixel-counting software (Van Berloo, 1998). Leaf toughness (LTO) was determined with a penetrometer (punch-head;  $\phi$  3 mm; 7 mm<sup>2</sup>). With this device, the leaves were punctured between the veins with the head of a nail. The nail was connected to a reservoir, which was gradually filled with water to increase the mass on the nail until the lamina finally ruptured. The mass at the moment of penetration was converted to a measure for leaf toughness ( $\text{N}\cdot\text{cm}^{-2}$ ), a proxy for leaf toughness. Leaf toughness was not determined for *Caesalpinia pluviosa* because its folioles were too small. Thereafter, the leaves, petioles and internodes were oven dried for 48 h at 65°C and measured again for their dry mass.

From these measurements, we calculated the following morphological traits: leaf density [LD; leaf dry mass/(leaf area  $\times$  leaf thickness);  $\text{g}\cdot\text{cm}^{-3}$ ], leaf slenderness (LS; leaf length/leaf width;  $\text{cm}\cdot\text{cm}^{-1}$ ), leaf mass per area (LMA; leaf dry mass/leaf area;  $\text{g}\cdot\text{m}^{-2}$ ), leaf dry matter content (LDMC; leaf dry mass/fully saturated leaf fresh mass;  $\text{g}\cdot\text{g}^{-1}$ ), specific petiole length (SPL; petiole length/dry petiole mass;  $\text{cm}\cdot\text{g}^{-1}$ ), and the internode to leaf area ratio (ILAR; internode cross-sectional area/leaf area;  $\text{cm}^2\cdot\text{cm}^{-2}$ ) (Table 2). LTO is an indicator of resistance to herbivory, the LS of the capacity to reduce overheating by a reduction of the boundary layer. LDMC indicates the amount of dry mass invested per unit leaf fresh mass and LMA, the amount of biomass a plant invests to produce a unit leaf surface for light capture. Both are proxies for leaf construction costs. SPL indicates the light foraging capacity given a fixed amount of biomass for petiole construction, and the ILAR is an estimate of the water supply capacity to the leaf.

**Leaf anatomy**—Stored leaf samples were dehydrated and embedded in paraffin. The embedded samples were then cross-sectioned with a retraction microtome (Microm HM350; Zeiss, Walldorf, Germany) and mounted on a microscope slide with glycerin-gelatin. After de-waxing the paraffin from the tissue with tert-butyl alcohol and an ethanol series, the tissue sections were

TABLE 2. The 24 leaf traits included in this study and the abbreviations used.

Trait	Abbreviation	Unit
<b>Morphology</b>		
Leaf length	LL	cm
Leaf width	LW	cm
Leaf area	LA	$\text{cm}^2$
Leaf thickness	LT	$\mu\text{m}$
Leaf toughness	LTO	$\text{N}\cdot\text{cm}^{-2}$
Leaf density	LDE	$\text{g}\cdot\text{cm}^{-3}$
Leaf shape index	LS	$\text{cm}\cdot\text{cm}^{-1}$
Leaf mass per unit leaf area	LMA	$\text{g}\cdot\text{m}^{-2}$
Leaf dry matter content	LDMC	$\text{g}\cdot\text{g}^{-1}$
Specific petiole length	SPL	$\text{cm}\cdot\text{g}^{-1}$
Internode to leaf area ratio	ILAR	$\text{mm}^2\cdot\text{cm}^{-2}$
<b>Anatomy</b>		
Thickness of the outer cell wall	TOC	$\mu\text{m}$
Upper epidermis thickness	UET	$\mu\text{m}$
Palisade parenchyma thickness	PPT	$\mu\text{m}$
Spongy parenchyma thickness	SPT	$\mu\text{m}$
Lower epidermis thickness	LET	$\mu\text{m}$
Palisade to spongy parenchyma ratio	PSPR	$\mu\text{m}\cdot\mu\text{m}^{-1}$
Xylem conduit diameter	XCD	$\mu\text{m}$
Xylem conduit density	XCDE	$\text{mm}^{-2}$
No. of palisade parenchyma cell layers	PPL	
<b>Chemistry</b>		
N content concentration per unit leaf mass	$N_{\text{mass}}$	$\text{mg}\cdot\text{g}^{-1}$
P concentration content per unit leaf mass	$P_{\text{mass}}$	$\text{mg}\cdot\text{g}^{-1}$
N concentration content per unit leaf area	$N_{\text{area}}$	$\text{mmol}\cdot\text{m}^{-2}$
P concentration content per unit leaf area	$P_{\text{area}}$	$\text{mmol}\cdot\text{m}^{-2}$

stained with 0.01% toluidine blue in demineralized water. Images of the cross-sectional lamina and mid-rib were digitized using a microscope camera and analyzed with Image J (freeware, <http://rsb.info.nih.gov/ij/>).

From the digital images, we measured the thickness of the outer cell wall (TOC;  $\mu\text{m}$ ), upper epidermis (UET;  $\mu\text{m}$ ), palisade parenchyma (PPT;  $\mu\text{m}$ ), spongy parenchyma (SPT;  $\mu\text{m}$ ), and lower epidermis (LET;  $\mu\text{m}$ ) and counted the number of palisade parenchyma cell layers (PPL). We measured the diameter of the five largest xylem conduits (XCD;  $\mu\text{m}$ ) in the midrib of the leaf as the average of two perpendicular diameters and determined the xylem conduit density (XCDE;  $\text{mm}^{-2}$ ) by counting the number of conduits in a given cross-sectional area of the xylem tissue. Additional observations were made whether additional tissue layers, such as a hypodermis, were present. From these data, we calculated the palisade to spongy parenchyma ratio (PSPR; palisade parenchyma thickness/spongy parenchyma thickness;  $\mu\text{m}\cdot\mu\text{m}^{-1}$ ) (Table 2).

Finally, we determined for each species the mass-based nitrogen concentration ( $N_{\text{mass}}$ ;  $\text{mg}\cdot\text{g}^{-1}$ ), with the Kjeldahl microassay protocol (Archibald, 1958), and the phosphorus concentration ( $P_{\text{mass}}$ ;  $\text{mg}\cdot\text{g}^{-1}$ ) for pooled leaf samples per light environment. From these data, we calculated the area-based nitrogen ( $N_{\text{area}}$ ;  $\text{mmol}\cdot\text{m}^{-2}$ ) and phosphorus concentration ( $P_{\text{area}}$ ;  $\text{mmol}\cdot\text{m}^{-2}$ ).

**Statistics**—For each leaf trait, an arithmetic average was calculated per tree from four sampled leaves. PPL was untransformed, LDMC was arcsine-transformed and the other leaf characters were  $\log_{10}$ -transformed prior to analysis to improve normality and homoscedasticity.

Leaf traits of sun and shade leaves were compared using a full factorial two-way ANOVA with species and light level as fixed factors. The amount of variation explained ( $\eta^2 \times 100\%$ ) by the species, light, and the interaction effect was calculated as the sum of squares of the effect divided by the total sum of squares of the model.  $\eta^2$  is an equivalent of  $R^2$ . If species have a smaller among-species variance of a leaf trait in one light environment compared to another, then this would be an indication that species show a convergent evolution of the trait in that light environment (cf. Bongers and Popma, 1988). We therefore analyzed the differences in variance between sun and shade leaves with a two-tailed  $F$  test, using the mean trait values per species in each light environment. Leaf trait plasticity was calculated for each species based on the mean leaf trait values in the sun and in the shade (cf. Valladares et al., 2000b).

TABLE 3. Two-way ANOVA with the effect of species ( $N = 35\text{--}43$ ) and light level ( $N = 2$ ; SH = shade, SU = sun) on leaf traits (total  $N = 360\text{--}380$ ).  $F$ -values and the level of significance (\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ ), and the  $\eta^2$  of the effects and the total model are given.  $\eta^2$  is an equivalent of  $R^2$  and was calculated as the sum of squares of the effect in proportion to the total sum of squares (\*100%). The back-transformed mean is given for pooled individuals of sun and shade leaves. The plasticity in leaf traits was calculated as the absolute difference between the maximum average trait value in one of the light environments and the minimum trait value in the other light environment, divided by the maximum value (\*100%). PPL was untransformed; LDMC was arcsine transformed and all other leaf traits were  $\log_{10}$ -transformed prior to analysis. The Pearson correlation coefficients indicate the correlation between trait values of the species in sun and shade ( $N = 35\text{--}43$ ). The two-tailed  $F$  test tests for differences in among-species variance between shade and sun leaves. See Table 1 and Table 2 for the definitions of abbreviations.

Trait	<i>n</i>	Species			Light			Interaction			$\eta^2$ Total	SH Mean	SU Mean	Plasticity (%)	Pearson <i>r</i>	<i>F</i> test	
		<i>F</i>	<i>P</i>	$\eta^2$	<i>F</i>	<i>P</i>	$\eta^2$	<i>F</i>	<i>P</i>	$\eta^2$						Variance	<i>P</i>
<b>Morphology</b>																	
LL (cm)	37	100	***	89.9	20	***	0.5	2	***	1.9	93.0	9.90	9.17	7.4	0.96		
LW (cm)	37	149	***	93.4	13	***	0.2	2	**	1.2	95.1	4.85	4.52	6.9	0.97		
LA (cm <sup>2</sup> )	37	125	***	91.8	15	***	0.3	2	***	1.7	94.1	30.2	26.0	14.0	0.96	shade > sun	*
LT ( $\mu\text{m}$ )	37	25	***	69.0	42	***	3.2	2	**	5.1	77.6	165	184	10.5	0.84		
LTO ( $\text{N}\cdot\text{cm}^{-2}$ )	36	38	***	79.6	3	ns	0.2	2	*	3.3	83.3	27.0	28.6	5.4	0.92		
LDE ( $\text{g}\cdot\text{cm}^{-3}$ )	37	26	***	95.1	2	ns	0.0	2	***	1.1	96.5	0.07	0.08	6.0	0.96		
LS ( $\text{cm}\cdot\text{cm}^{-1}$ )	37	63	***	87.3	1	ns	0.1	1	ns	1.2	89.2	2.05	2.04	0.5	0.96		
LMA ( $\text{g}\cdot\text{m}^{-2}$ )	37	35	***	75.0	60	***	3.6	2	**	3.8	82.1	49.0	57.6	15.0	0.88		
LDMC ( $\text{g}\cdot\text{g}^{-1}$ )	37	19	***	65.4	13	***	1.3	1	ns	4.9	71.6	0.28	0.30	6.7	0.88		
SPL ( $\text{cm}\cdot\text{g}^{-1}$ )	37	40	***	80.2	3	ns	0.2	2	**	3.8	85.4	119	109	8.8	0.89		
ILAR ( $\text{mm}^2\cdot\text{cm}^{-2}$ )	37	5	***	33.6	4	*	0.9	1	ns	10.3	44.7	0.09	0.11	15.7	0.52	shade > sun	***
<b>Anatomy</b>																	
TOC ( $\mu\text{m}$ )	35	32	***	71.4	106	***	6.9	2	*	3.8	83.6	0.93	1.17	20.2	0.84	shade < sun	*
UET ( $\mu\text{m}$ )	36	21	***	69.6	9	**	0.9	1	ns	3.5	75.0	8.88	9.56	7.2	0.89		
PPT ( $\mu\text{m}$ )	36	22	***	61.8	122	***	9.9	2	***	5.9	78.9	21.0	27.9	24.6	0.85		
SPT ( $\mu\text{m}$ )	36	31	***	75.5	1	ns	0.1	2	***	5.1	81.6	35.6	36.8	3.2	0.85		
LET ( $\mu\text{m}$ )	36	20	***	68.7	6	*	0.6	1	ns	4.9	74.9	6.16	6.46	4.6	0.87		
PSPR ( $\mu\text{m}\cdot\mu\text{m}^{-1}$ )	36	25	***	66.7	72	***	5.5	3	***	7.6	80.0	0.59	0.76	22.2	0.79	shade < sun	**
XCD ( $\mu\text{m}$ )	35	57	***	86.7	1	ns	0.1	1	ns	2.0	89.2	9.98	9.69	2.9	0.95		
XCDE ( $\text{mm}^{-2}$ )	35	47	***	83.2	1	ns	0.1	2	***	3.8	87.6	5959	6323	5.8	0.92		
PPL	36	20	***	63.2	59	***	5.4	2	***	7.1	76.6	1.32	1.63	18.8	0.80		
<b>Chemistry</b>																	
$N_{\text{mass}}$ ( $\text{mg}\cdot\text{g}^{-1}$ )	43	14	***	93.4	1	ns	0.1					3.10	3.15	1.5	0.87		
$P_{\text{mass}}$ ( $\text{mg}\cdot\text{g}^{-1}$ )	43	10	***	90.9	0	ns	0.0					0.15	0.15	0.3	0.82		
$N_{\text{area}}$ ( $\text{mmol}\cdot\text{m}^{-2}$ )	43	9	***	82.9	33	***	7.6					108	129	16.3	0.79		
$P_{\text{area}}$ ( $\text{mmol}\cdot\text{m}^{-2}$ )	43	7	***	83.1	15	***	4.4					2.38	2.81	15.3	0.74		

This plasticity index was calculated as the absolute difference between the maximum trait value in one of the light environments and the minimum trait value in the other light environment, divided by the maximum value, and multiplied by 100% (cf. Valladares et al., 2000b). Total plasticity per species was expressed as the average plasticity of all 24 leaf traits. Using Pearson correlation analyses, we investigated the relations between sun and shade values of the leaf traits and the relations between leaf trait plasticity and  $CE_{\text{juv}}$ ,  $CE_{\text{change}}$ , and  $H_{\text{max}}$  using the species average. Statistical analyses were performed with SPSS 12.0.1 (SPSS Inc. Chicago, Illinois, USA).

RESULTS

**Species and light environment**—Species and light environment had a large effect of leaf morphology, anatomy, and chemistry (Table 3). All leaf traits differed strongly among species ( $P < 0.001$ ), which explained most of the leaf trait variation (mean 77%, range 34–95). Light had a significant effect on 16 of 24 leaf traits and explained considerably less of the variation in leaf traits (mean 3.4%, range 0.2–10). There was a significant species and light interaction effect for 14 of 24 leaf traits. For these traits, species responses to light explained an additional 3.9% of the variation (range 1.1–7.6). Light did not have a significant direct or interaction effect on leaf slenderness and xylem conduit diameter. Light did not have a significant effect on the chemical traits  $N_{\text{mass}}$  and  $P_{\text{mass}}$  either, and no

interaction effect could be calculated here because  $N$  and  $P$  were determined for each species based on pooled leaves. An absence of a significant species-light interaction effect indicates that all species have a similar response to light. Species thus had a similar response to the light for leaf slenderness, LDMC, internode to leaf area ratio, upper and lower epidermis thickness, and xylem conduit density.

**Differences between sun and shade leaves**—Light had a significant effect on 16 of the 24 leaf traits and explained an average 3.4% of the leaf trait variation (Table 3). Light explained the largest proportions of variation for palisade parenchyma thickness (9.9%),  $N_{\text{area}}$  (7.6%), thickness of the outer cell wall (6.9%), palisade to spongy parenchyma ratio (5.5%), and the number of palisade parenchyma cell layers (5.4%).

Sun leaves were shorter, narrower, smaller, and thicker than shade leaves. Sun leaves had a higher LMA, LDMC, and a higher  $N$  and  $P$  concentration per unit leaf area ( $N_{\text{area}}$ ,  $P_{\text{area}}$ ), but sun and shade leaves did not differ in slenderness, leaf toughness and density, or specific petiole length.

Anatomically, the greater thickness of sun leaves could be attributed to their thicker outer cell wall, upper epidermis, palisade parenchyma, and lower epidermis. Sun leaves had a

TABLE 4. One-way ANOVA with plasticity in leaf traits for 43 tropical dry forest tree species from Bolivia. The mean plasticity (in %) is given for each functional group (guild): groups followed by a different letter differ significantly at the 0.05 level (Student's-Newman-Keuls test) (\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ ; ns = not significant). The plasticity in leaf traits per species was calculated as the absolute difference between the maximum and the minimum trait value divided by the maximum value (\*100%). ST = shade tolerant species ( $N = 20$ ), PST = partial shade tolerant species ( $N = 10$ ), LLP = long-lived pioneer species ( $N = 9$ ) and SLP = short-lived pioneer species ( $N = 4$ ). See Table 2 for the trait abbreviations.

Leaf trait	Guild			ST		PST		LLP		SLP	
	<i>F</i>	<i>P</i>	$\eta^2$	Mean		Mean		Mean		Mean	
<b>Crown exposure (CE)</b>											
CE <sub>juv</sub>	10.06	***	43.6	1.62	a	1.57	a	2.00	b	2.40	c
CE <sub>change</sub>	7.60	***	39.4	0.59	a	2.35	b	2.09	b	0.55	a
H <sub>max</sub> (m)	9.85	***	43.8	9.09	a	23.60	b	25.47	b	10.75	a
<b>Morphology</b>											
LL	3.94	*	23.3	13.7	ab	5.5	a	9.1	a	21.3	b
LW	7.66	***	37.1	14.0	a	6.3	a	6.5	a	24.0	b
LA	8.02	***	38.1	25.5	a	9.7	a	15.2	a	43.8	b
LT	1.67	ns	11.4	11.1		7.2		10.5		19.7	
LTO	0.81	ns	6.0	10.8		14.1		11.1		17.7	
LDE	1.18	ns	8.3	16.1		10.5		19.4		27.9	
LS	0.77	ns	5.6	6.1		3.7		6.6		6.6	
LMA	1.71	ns	11.6	14.5		13.6		15.1		28.0	
LDMC	0.35	ns	2.6	11.5		9.5		13.3		11.7	
SPL	2.23	ns	14.7	21.5		21.1		14.8		37.2	
ILAR	0.23	ns	1.8	37.2		41.6		32.2		32.2	
<b>Anatomy</b>											
TOC	0.38	ns	3.0	20.0		20.0		23.1		26.3	
UET	1.86	ns	12.8	14.6		11.2		7.6		20.7	
PPT	0.14	ns	1.1	23.6		22.5		26.5		24.2	
SPT	1.49	ns	10.6	14.0		13.4		21.7		9.7	
LET	0.31	ns	2.4	11.9		11.1		12.3		7.9	
PSPR	2.47	ns	16.3	24.9		15.7		35.1		24.1	
XCD	0.47	ns	3.7	9.4		6.9		10.8		9.6	
XCDE	0.13	ns	1.0	19.0		17.3		19.0		15.2	
PPL	0.52	ns	4.0	16.0		13.0		19.1		25.0	
<b>Chemistry</b>											
N <sub>mass</sub>	1.38	ns	9.6	10.6		4.8		8.1		6.6	
P <sub>mass</sub>	0.02	ns	0.2	15.7		15.1		16.6		15.9	
N <sub>area</sub>	1.42	ns	9.9	16.5		13.6		20.7		27.7	
P <sub>area</sub>	2.34	ns	15.3	19.7		13.3		25.6		32.8	

higher palisade to spongy parenchyma ratio. Part of this increase can be ascribed to the increased number of palisade parenchyma cell layers in sun leaves compared to shade leaves. Sun and shade leaves did not differ in the mean thickness of the spongy parenchyma nor the diameter and density of xylem conduits of the midrib.

For all leaf traits sun and shade values were highly correlated (average  $r = 0.86$ , range 0.52–0.97,  $p < 0.001$  in all cases) (Table 3). Few traits showed differences in species variance between sun and shade leaves. The species variance in leaf area and internode to leaf area ratio was lower in sun leaves than in shade leaves, suggesting convergent evolution in these leaf traits in the sun. The variance in thickness of the outer cell wall and palisade to spongy parenchyma ratio was lower in shade leaves than in sun leaves.

**Leaf trait plasticity in response to irradiance**—For the morphological leaf traits, internode to leaf area ratio (15.7%), LMA (15.0%), leaf area (14.0%), and leaf thickness (10.5%) were among those with the greatest plasticity. LDMC (6.7%), leaf length (6.9%), and width (7.4%) were among the traits with the lowest morphological plasticity, while still being significantly different between sun and shade leaves.  $P_{\text{mass}}$

(0.3%) had the lowest plasticity (Table 3). For the anatomical traits, three of the four that had the highest plasticity were related to the palisade parenchyma tissue, namely palisade parenchyma thickness (24.6%), palisade to spongy parenchyma ratio (22.2%), and the number of palisade parenchyma cell layers (18.8%). Also the thickness of the outer cell wall (20.2%) had a high plasticity. The thickness of the lower and upper epidermis (4.6% and 7.2%) had the lowest plasticity, while still significantly different between sun and shade leaves. Xylem conduit diameter (2.9%) had the lowest plasticity among all anatomical traits (Table 3). Morphological, anatomical, and chemical traits did not differ significantly in their mean plasticity (ANOVA:  $F_{3, 20} = 0.7$ ;  $P > 0.05$ ).

**Plasticity among functional groups**—Plasticity in leaf length, width, and area differed significantly among functional groups related to shade tolerance, while all other plasticity in leaf traits did not (Table 4). Short-lived pioneers had greater plasticity in these traits than the three other functional groups.

**Plasticity in relation to adult size and crown exposure**—Plasticity was generally not correlated to maximum adult stature or ontogenetic changes in crown exposure. Plasticity in

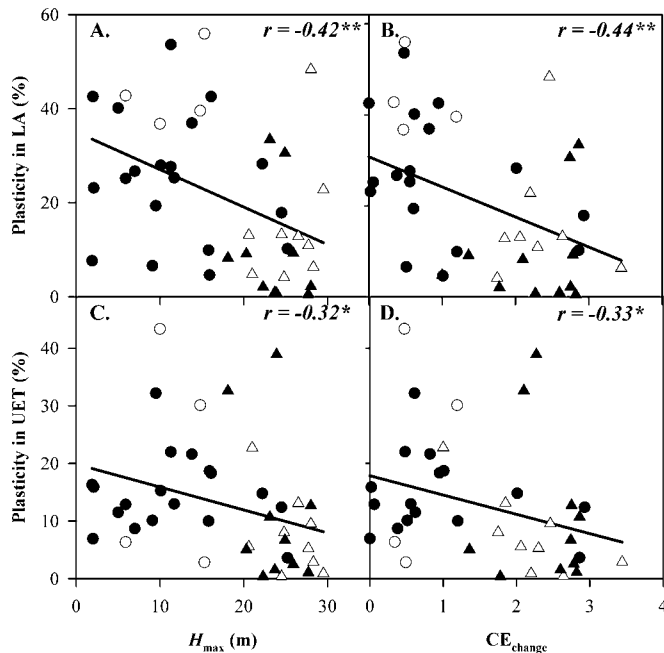


Fig. 1. Correlations between leaf trait plasticity, adult stature ( $H_{\max}$ ), and ontogenetic changes in crown exposure ( $CE_{\text{change}}$ ) of 43 tropical dry forest tree species. Plasticity in leaf area (LA) with (A)  $H_{\max}$  and (B)  $CE_{\text{change}}$  and plasticity in upper epidermis thickness (UET) with (C)  $H_{\max}$  and (D)  $CE_{\text{change}}$  are shown. Leaf trait plasticity is calculated as the absolute difference between the maximum average value in one light environment and the minimum average trait value in the other light environment divided by the maximum value ( $\times 100$ ). Functional groups related to shade tolerance are indicated with different symbols: shade tolerant species (filled dots), partial shade tolerant species (filled triangles), long-lived pioneers (open triangles) and short-lived pioneers (open dots). Regression lines and Pearson correlations are shown. \*  $P < 0.05$ , \*\*  $P < 0.01$ .

leaf size parameters (LL, LW, and LA) and upper epidermis decreased with  $H_{\max}$  and  $CE_{\text{change}}$ , (Fig. 1). No significant correlations were found between leaf trait plasticity and juvenile crown exposure.

**Leaf trait plasticity in dry and wet forests**—To investigate the assumption that in wet forests leaf trait plasticity would be larger because of stronger light gradients, we compared our leaf trait data set with those of two other multi-species sets from a tropical moist forest (La Chonta, Bolivia, Rozendaal et al., 2006) and a tropical wet forest (Los Tuxtlas, Mexico, Bongers and Popma, 1988). The three forests are distinctly different in mean annual precipitation and length of the dry period (Table 5). The plasticity in all but one of the leaf traits differed among the three forest types (one-way ANOVA, all  $P < 0.001$ , Table 5). Leaf trait plasticity was greatest in the wet forest, but hardly any differences in leaf plasticity were found between the dry and the moist forest (Fig. 2), despite considerable differences in forest structure and canopy openness.

## DISCUSSION

**Leaf trait plasticity in response to irradiance**—Most of the variation in leaf traits could be explained by differences among

species. Light had only a minor effect: for one-third of the traits no effect at all and for two-thirds the effect on leaf trait variation was low, despite large differences in canopy openness (CO) above the sampled sun ( $CO = 56.5 \pm 0.3\%$ ) and shade trees ( $CO = 9.8 \pm 0.1\%$ ). Species respond differently to an increase in light, as indicated by the high number of significant species–light interaction terms (Table 3). Different tree species thus have different ways of coping with resource capture and conservation.

Although the light effect explained minor proportions of the leaf trait variation, sun and shade leaves did differ in most traits. Results are overall in line with past studies reviewing the matter of leaf acclimation to irradiance (see, e.g., Bongers and Popma, 1988; Sims and Pearcy, 1989; Cao, 2000; Evans and Poorter, 2001; Rozendaal et al., 2006). While species differed substantially in their response to irradiance, there is a high correlation between species trait values in the sun and the shade (Table 3). This means that the species ranking for trait values is largely maintained in both light environments and that there is no crossover in trait performance between low and high irradiance. Shade tolerant and pioneer species may therefore specialize for different environments because of differences in their inherent traits (cf. Kitajima and Poorter, in press), rather than through phenotypic differences in trait values at low and high irradiance (cf. Sack and Grubb, 2003).

The among-species variance of four of the 24 traits differed significantly between sun and shade leaves. Bongers and Popma (1989) argued that, if the among-species variance of a trait in a given light environment is smaller, the state of that trait has a greater importance for the performance of the leaf in that environment. A smaller among-species variance therefore indicates convergent evolution in that light environment. We found a smaller variance in leaf area in the sun. Sun leaves are smaller to allow more effective cooling of the leaf area as they have a thinner boundary layer (Parkhurst and Louks, 1972; Givnish, 1984), thus avoiding supraoptimal leaf temperatures for photosynthesis. We also found a smaller variance in the internode to leaf area ratio. Sun leaves have a higher internode to leaf area ratio to compensate for the higher transpiration with an increased water supply (cf. Westoby and Wright, 2003). In this way, plants increase the vessel number, rather than the vessel density or diameter. The variances in thickness of the outer cell wall and in the palisade to spongy parenchyma ratio were smaller in the shade (Table 3). Shade leaves have a thinner upper epidermis with a thinner outer cell wall, apparently because they need less protection than sun leaves. The outer cell wall and upper epidermis protect the leaf as they minimize the damaging effect of high irradiance through reflection of the excessive light (Roth, 1984; Bondada et al., 1996) and reduce cuticular evaporation (Hall and Jones, 1961). Shade leaves have a smaller palisade to spongy parenchyma ratio. The relatively thick spongy parenchyma layer is especially useful to enhance backscattering within the leaf of diffuse understory light. Bongers and Popma (1988) also found smaller variances in palisade to spongy parenchyma ratios in shade leaves in Los Tuxtlas. Sun plants may regulate leaf temperatures through smaller leaves or an increased transpiration. Such a water-spending strategy is counterintuitive, however, given the limited water availability in the dry season. Sun trees may avoid dry-season water stress by exploring deeper soil layers, a larger soil volume for water (Poorter and Hayashida, 2002), or by having a deciduous leaf habit. Of the species included in this study, we observed that at least 22

TABLE 5. One-way ANOVA and *t* test with species plasticity in leaf traits for 2–3 forest types differing in mean annual precipitation. INPA (*N* = 43) is the dry forest described in this study, the moist forest values (La Chonta) (*N* = 39) were derived from Rozendaal et al. (2006) and wet forest values (Los Tuxtlas) (*N* = 62) from Bongers and Popma (1988). The mean plasticity (%) is given for each forest type: values followed by a different letter differ significantly at the 0.05 level (Student’s-Newman-Keuls test) (\* *P* < 0.05; \*\* *P* < 0.01; \*\*\* *P* < 0.001; ns = not significant). The plasticity in leaf traits per species was calculated as the absolute difference between the maximum and the minimum trait value divided by the maximum value. See Table 2 for the trait abbreviations.

Statistics		INPA (dry forest)	La Chonta (moist forest)	Los Tuxtlas (wet forest)
Precipitation		1160 mm	1517 mm	4639 mm
Dry period		6–7 mo	4–5 mo	1–2 mo
Temperature		24.3°C	25.3°C	24.6°C
ANOVA	<i>F</i> <i>P</i>			
LL	11    ***	11.5    a	7.82    a	17.4    b
LW	12    ***	11.6    a	9.54    a	18.7    b
LA	10    ***	21.6    a	15.7    a	30.2    b
LT	22    ***	10.9    a	13.0    a	23.6    b
LDE	21    ***	16.6    a	15.4    a	35.7    b
LS	13    ***	5.68    a	5.43    a	11.8    b
LMA	23    ***	15.7    a	22.7    b	33.4    c
LDMC	7.4    ***	11.4    a	10.4    a	17.2    b
<i>N</i> <sub>mass</sub>	10.1    ***	8.3    a	8.9    a	16.2    b
<i>P</i> <sub>mass</sub>	2.5    ns	15.8    a	13.6    a	19.5    b
<i>N</i> <sub>area</sub>	9.8    ***	17.8    a	23.1    a	31.3    b
<i>P</i> <sub>area</sub>	7.8    ***	20.6    a	22.4    a	32.0    b
<i>t</i> test	<i>t</i> <i>p</i>			
LTO	1.2    ns	12.2	10.1	-
SPL	1.0    ns	21.5	18.4	-
ILAR	1.4    ns	36.7	29.9	-
UET	-3.9    ***	12.9    a	-	25.2    b
PPT	-2.6    *	24.0    a	-	32.1    b
SPT	-5.6    ***	15.1    a	-	32.3    b
LET	-5.6    ***	11.4    a	-	24.0    b
PSPR	-1.9    *	24.8    a	-	32.3    b
PPL	-1.4    ns	16.9	-	22.7

species showed a deciduous leaf habit in the dry season. Despite the fact that light acclimation and dynamic responses to light have been reported vary substantially with leaf longevity (Kursar and Coley, 1993, 1999), leaf trait plasticity did not differ between evergreen (*N* = 14) and deciduous species (*N* = 22) in our study (*t* test:  $-1.45 \leq t \leq 1.32$ ; *P* > 0.05; *df* = 34).

Leaf trait plasticity varies between 0.3 and 24.6%. Leaf traits that have the greatest plastic response could be more important for leaf functioning in different light environments (Bongers and Popma, 1988). If this were the case in our forest, palisade parenchyma thickness, palisade to spongy parenchyma ratio, thickness of the outer cell wall, the number of palisade parenchyma cell layers, *N*<sub>area</sub> and *P*<sub>area</sub> are most critical for light acclimation in our species. Three of these traits are anatomical and directly related to the palisade parenchyma tissue. The palisade parenchyma, *N*<sub>area</sub> and *P*<sub>area</sub> all play a distinct role in enhancing the photosynthetic capacity of the leaf (Evans, 1999). The internode to leaf area ratio, the most plastic morphological trait in this study, is related to water supply and the thickness of the outer cell wall is related to water conservation. A high light-related plasticity was also found in *N*<sub>area</sub> and palisade parenchyma thickness of 61 Mexican wet forest species (Bongers and Popma, 1988). Rozendaal et al. (2006) analyzed the plasticity of 39 Bolivian moist forest species and found a high plasticity in internode to leaf area ratio, SLA, *N*<sub>area</sub>, and *P*<sub>area</sub>.

**Plasticity among functional groups**—Plasticity of four leaf traits was greatest for short-lived pioneers, in line with our first hypothesis. Yet, we did not expect that functional groups would differ in the plasticity of so few leaf traits (cf. Sack et al., 2003). Many other studies showed considerable differences among functional groups (Popma et al., 1992; Kitajima, 1994; Strauss-Debenedetti and Bazzaz, 1996; Valladares et al., 2002). We may argue that, for relatively open forests such as tropical dry forests, plant traits and plasticity might be more closely related to drought tolerance than to shade tolerance.

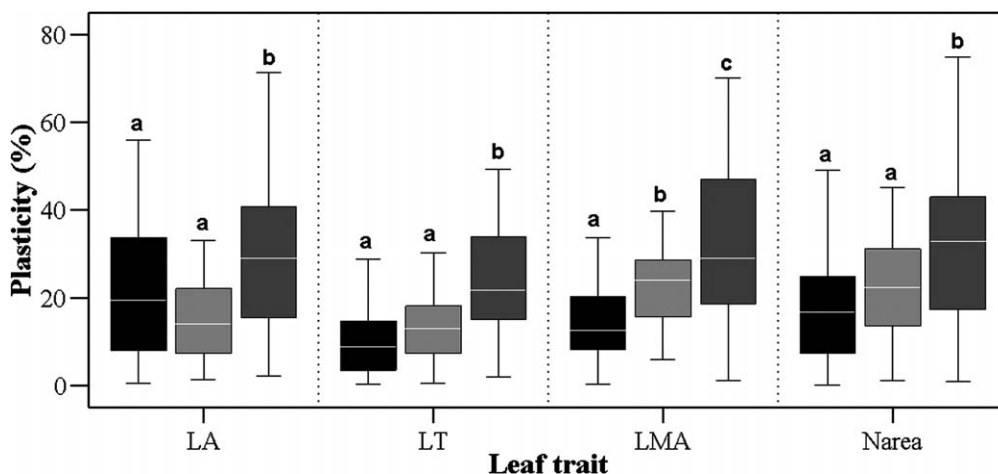


Fig. 2. Leaf trait plasticity for three forest types differing in mean annual precipitation. INPA (black) is the dry forest described in this study, the moist forest values (La Chonta) (light gray) were derived from Rozendaal et al. (2006) and wet forest values (Los Tuxtlas) (dark gray) from Bongers and Popma (1988). The median (white line), interquartile range (upper and lower limits of the boxes; 75 and 25 percentile), and the total variation in plasticity (whiskers) are given for each trait. Boxes indicated with a different letter differ significantly at a *P* level of 0.05 (Student’s-Newman-Keuls test). The plasticity in leaf traits per species was calculated as 100× the absolute difference between the maximum and the minimum trait value divided by the maximum value. See Table 2 for the trait abbreviations.



In our study only the plasticity of leaf size parameters (LL, LW, and LA) and upper epidermis thickness differed among functional groups. For these traits, short-lived pioneer species had the greatest plasticity. This is in line with the hypothesis as formulated by Strauss-Debenedetti and Bazzaz (1996), which assumes that pioneer species have greater plasticity because they grow in more heterogeneous habitats, but in contrast with results from other studies (Sims and Percy, 1989; Popma et al., 1992; Kitajima, 1994; Rozendaal et al., 2006).

**Plasticity in relation to adult size and crown exposure**—Most leaf trait plasticity parameters were not correlated to maximum adult stature or ontogenetic crown exposure of the species. The lack of a relation with  $H_{\max}$  is surprising because tall trees generally have to cope with all the changes in light environment that occur from the understorey to the forest canopy (cf. Poorter et al., 2005). Therefore we expected  $H_{\max}$  and  $CE_{\text{change}}$  to be positively related to plasticity. That this is not the case may be because ontogenetic changes in crown exposure are related to ontogenetic plasticity, rather than the sun–shade plasticity derived from sun and shade trees of similar age. It might also be related to the fact that differences in light availability, especially during the dry period, are less pronounced in the deciduous dry forest, which therefore may not act as the only selective force. Low water availability in the dry season might constrain sun–shade plasticity and partly explain our counterintuitive results.

**Leaf trait plasticity in dry and wet forests**—Although sun and shade leaves differed in most leaf traits, the percentages of explained variation were generally low (Table 3). Only 3% of the total variation in leaf traits could be explained by differences between sun and shade leaves, while the same factor explained 8% of the leaf trait variation of 39 Bolivian moist forest tree species (Rozendaal et al., 2006). The smaller light effect in our study may well be the result of the more open and deciduous character of the dry forest compared to the moist forest.

When we compared the plasticity in leaf characteristics between three forests differentiated by water availability (Table 5), it was clear that the wet forest had greatest plasticity, while the differences between the other two forests were minor (Fig. 2). This is most probably related to variability in light availability, which is much higher in Los Tuxtlas. The vegetation there is much denser with a much deeper shade year-round in the non-gap areas, while the vegetation in the other two forests is rather open. For such forests, leaf trait acclimation to differences in light availability may thus be not well defined, because light is not as limiting as in hyperwet forests. An alternative explanation is that in the wet forest the shade leaves have been sampled in deeper shade. Given that the largest changes in leaf traits occur at the lowest light levels (Poorter, 1999), this might have led to a different observed plasticity among forest types. We acknowledge that water and light availability are often interacting factors, especially in drier ecosystems. Lower water availability has been reported to reduce plant response to irradiance (Quero et al., 2006; Sánchez-Gómez et al., 2006). We do not believe that in this deciduous dry forest, water is a limiting factor during the wet season when these leaves are formed. Still tree species may follow a “conservative resource-use strategy” involving relatively low leaf-level responses to irradiance (cf. Valladares et al., 2000a).

Summarizing, we found that in the deciduous dry forest leaf trait variation is mainly explained by differences among species and only to a minor extent by differences in light availability. Sun–shade plasticity is therefore not large, and as a result, this plasticity is only very sporadically related to (ontogenetic changes in) the light requirements of the species. In relatively open dry forests, light-related plasticity seems to be less essential for species growth and survival than in wet forests, and the low water availability in dry forests may constrain the magnitude of leaf trait plasticity in response to irradiance.

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