Plasticity in leaf traits of 38 tropical tree species in response to light; relationships with light demand and adult stature

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Summary

1. The sun–shade acclimation and plasticity of 16 functional leaf traits of 38 tropical tree species were studied in relation to their light demand, maximum adult stature and ontogenetic changes in crown exposure.

2. Species differed significantly in all leaf traits, which explained a large part of the observed variation (average $R^2 = 0.72$). Light had a significant effect on 12 traits and species showed a similar proportional response to light, indicating that the species ranking in trait performance is largely maintained in different light environments.

3. Specific leaf area, leaf nutrient content and chlorophyll : nitrogen ratio showed the largest plasticity to irradiance. These traits are important for maximizing growth in different light conditions because they are closely linked to the photosynthetic capacity and carbon balance of the plant.

4. Plasticity is generally thought to be greatest for pioneer species that occupy early successional habitats with a large variation in irradiance. This hypothesis was rejected because short-lived pioneers showed the lowest plasticity to irradiance.

5. An alternative hypothesis states that plasticity is largest for tall species that experience large ontogenetic changes in irradiance during their life cycle. Yet plasticity was barely related to adult stature or ontogenetic changes in crown exposure. Short-lived pioneers that experience consistently high light levels did have low plasticity, but shade-tolerant species that experience consistently low light levels had high plasticity.

6. Tropical rainforest species show a large variation in plasticity. Plasticity is a compromise between many factors and constraints, and all of these may explain the observed patterns to some extent.

Key-words: acclimation, adult stature, Bolivia, functional leaf traits, shade tolerance

Introduction

As sessile organisms, plants should possess a tremendous capacity to adjust to the environment in which they have been dispersed. In tropical rainforests, light is one of the most limiting resources for plant growth and survival (Whitmore 1996). Irradiance is a very heterogeneous resource, and can be as high as 47 mol m^{-2} day^{-1} above the canopy and as low as 0·15 mol m^{-2} day^{-1} at the forest floor (Chazdon 1988). Moreover, the light environment changes continuously over time, from minutes in the case of sun flecks, to years in the process of canopy-gap closure (Chazdon 1988). Plants

adjust continuously to the changing light environment: photosynthetic induction occurs within minutes (Rijkers *et al*. 2000); photosynthetic adjustments in days (Cai, Rijkers & Bongers 2005); morphological changes take weeks or months (Ackerly 1997); whereas architectural changes may have a time lag of years (Sterck *et al*. 1999). Modelling approaches show that such acclimation responses enhance the growth (Sims, Gebauer & Pearcy 1994), survival (Sterck *et al*. 2005) and, ultimately, fitness of the plant (Bradshaw 1965).

Perhaps the most efficient way to acclimate and forage for light is by adjusting the leaf characteristics. Sun and shade leaves differ predictably in a number of functional traits (Bongers & Popma 1988). Sun leaves grow in the exposed conditions of the canopy, and because the amount of light is not limiting they can

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maximize their photosynthetic capacity by producing thick leaves to increase nitrogen content on an area basis and the volume of photosynthetic machinery per unit leaf area (Björkman 1981; Gulmon & Chu 1981). Overheating of leaves due to excessive light capture needs to be prevented, which can be done through convective cooling of the leaves or by heat loss through transpiration. Sun leaves increase convective heat loss by reducing the boundary-layer resistance (Givnish 1984), which may be realized with small or slender leaves (Parkhurst & Loucks 1972; Bongers & Popma 1988). Heat loss through high transpiration rates is supported by a large water supply to the leaves, possibly facilitated by relatively thick internodes in proportion to leaf area (cf. Westoby & Wright 2003).

Shade leaves grow in the shaded understorey, where light is a limiting resource. Shade leaves increase the efficiency of light capture through a high specific leaf area (SLA) (Evans & Poorter 2001) which, in combination with a high chlorophyll content on a mass basis, leads to a similar chlorophyll content on an area basis compared with sun leaves (Chazdon *et al.* 1996; Poorter *et al.* 2000). Shade leaves therefore realize a similar light capture to sun leaves at lower biomass investment. Shade leaves reduce their respiration costs through a lower N content on an area basis (Björkman 1981; Sims & Pearcy 1989). To enhance light capture, they invest more N in chlorophyll at the expense of investment in Rubisco, which is reflected in a high chlorophyll : nitrogen ratio (Hikosaka & Terashima 1995; Poorter & Evans 1998). Shade leaves are thin (Björkman 1981) and less tough, as wind and desiccation stress are lower in the understorey.

Plasticity is defined as the differential response of a genotype to different environments (Bradshaw 1965). The requirements for optimal leaf functioning differ between low and high irradiance. Generally it is assumed that leaf traits showing high plasticity in response to irradiance are more important to plant functioning in different light environments than traits that show little or no plasticity (Bongers & Popma 1988; but cf. Rice & Bazzaz 1989). The magnitude of plasticity differs among leaf traits and species: physiological traits were found to have higher plasticity than morphological traits (Valladares *et al.* 2000).

Plasticity is thought to be greatest for early successional pioneer species, as they occur in variable, heterogeneous environments (caused by rapid gap formation and closure) with a high resource availability (Bazzaz 1979; Bazzaz & Wayne 1994; Valladares *et al.* 2000). The high resource availability provides early successional species with sufficient carbon and nutrients to be able to invest rapidly in acclimation to changing light conditions (Grime, Crick & Rincon 1986). Acclimation is defined here as the morphological and physiological adjustments made by individual plants to (changes in) the environment. Pioneer species have short-lived leaves (Reich, Walters & Ellsworth 1992), therefore they can rapidly track changes in the light

environment by replacing old leaves at a high rate (Ackerly 1997; Valladares *et al.* 2000). This may explain their high short-term acclimation potential at the whole-tree level, but not the magnitude of the plastic response at the leaf level. A clear consensus on the link between plasticity and successional stage has not been reached, as greater (Strauss-Debenedetti & Bazzaz 1991, 1996); similar (Sims & Pearcy 1989; Kitajima 1994); and lower leaf plasticity (Popma, Bongers & Werger 1992) has been found for pioneers compared with shade-tolerant species.

It has been suggested that plasticity in leaf traits depends not only on the regeneration niche of a tree species, but also on the changes in irradiance it experiences during its life cycle (Popma *et al.* 1992). Tall, late-successional species that start in the shaded understorey and grow to the exposed conditions of the forest canopy experience large ontogenetic changes in light availability, and should have a large capacity for plastic responses. Such species were indeed found to have higher plasticity compared with species that always remained in the understorey, or pioneer species that always remained in the high light conditions of gaps (Popma *et al.* 1992). Tall species make larger ontogenetic shifts in crown exposure than small species (Poorter *et al.* 2005), therefore a close association has been found between plasticity in leaf traits and the maximum height of the species (Thomas & Bazzaz 1999; Cai *et al.* 2005).

In general, differences between sun and shade leaves and plasticity have been investigated using a rather low number of species or leaf traits (but cf. Bongers & Popma 1988; Popma *et al.* 1992), making sound generalizations difficult. Also, species have often been classified subjectively into different functional groups (early *vs* late-successional, shade tolerant *vs* pioneer), without a proper quantification of the light demand of the species and the ontogenetic changes therein.

Here we evaluate the differences between sun and shade leaves for 38 tropical moist forest tree species, and link them to a quantitative measure of the juvenile and adult crown exposure (CE) of the species. We focus on 16 morphological and physiological leaf traits that are important for the C, water and heat balance of the leaves. The following questions were addressed: (1) How do sun and shade leaves differ in their leaf traits? (2) Does plasticity differ among leaf traits? (3) Is plasticity related to the juvenile CE, adult CE, ontogenetic change in CE, or maximum adult stature of the species?

Materials and methods

STUDY SITE AND SPECIES

The field work was conducted in the lowland tropical moist forest of La Chonta (15°47′ S, 62°55′ W), Bolivia. The mean annual temperature is 25·3 °C and mean annual precipitation is 1517 mm with a dry season (<100 mm per month) from April until October The forest has an average canopy height of 25 m, stem

Table 1. Characteristics of the 38 study species

	Species	Family	Guild†	H_{max}	$CE_{juvenile}$	CE_{adult}	Plasticity
1	*Alibertia verrucosa*	Rubiaceae	ST	13	1·35	2·43	16·4
2	*Ampelocera ruizii*	Ulmaceae	ST	36	1·35	4·26	14·7
3	*Aspidosperma cylindrocarpon*	Apocynaceae	PST	28	1·75	4·27	11·0
4	*Batocarpus amazonicus*	Moraceae	PST	26	1·35	4·19	18·3
5	*Caesalpinia pluviosa*	Caesalpiniaceae	LLP	27	1·87	4·28	14·0
6	*Cariniana estrellensis*	Lecythidaceae	LLP	42	1·40	4·83	20·5
7	*Cariniana ianeirensis*	Lecythidaceae	PST	44	1·74	4·90	13·0
8	*Cavanillesia hylogeiton*	Bombacaceae	LLP	29	2·16	4·37	16·7
9	*Cecropia concolor*	Cecropiaceae	SLP	33	2·44	4·69	7·7
10	*Centrolobium microchaete*	Fabaceae	LLP	26	1·94	4·49	27·4
11	*Erythrochiton fallax*	Rutaceae	ST	5	1·27	1·40	11·3
12	*Ficus boliviana*	Moraceae	LLP	46	1·93	4·96	19·9
13	*Gallesia integrifolia*	Phytolaccaceae	LLP	42	1·84	4·60	13·6
14	*Guarea guidonia*	Meliaceae	ST	9	1·33	2·23	10·1
15	*Heliocarpus americanus*	Tiliaceae	SLP	22	2·36	4·13	7·9
16	*Hirtella triandra*	Chrysobalanaceae	ST	11	1·28	1·77	11·9
17	*Hura crepitans*	Euphorbiaceae	PST	44	1·62	4·92	10·3
18	*Jacaratia spinosa*	Caricaceae	LLP	21	2·02	3·65	15·6
19	*Licaria triandra*	Lauraceae	ST	14	1·35	3·71	15·8
20	*Myrcianthes* sp.	Myrtaceae	PST	25	1·45	3·59	25·6
21	*Ocotea* sp.	Lauraceae	PST	27	1·37	4·53	20·6
22	*Ocotea* sp.	Lauraceae	PST	20	1·34	3·76	16·1
23	*Peschiera australis*	Apocynaceae	ST	16	1·38	2·97	16·7
24	*Picramnia sellowii*	Simaroubaceae	ST	8	1·34	1·10	16·3
25	*Pourouma cecropiifolia*	Cecropiaceae	PST	20	1·38	3·62	16·2
26	*Pouteria macrophylla*	Sapotaceae	PST	29	1·55	4·46	17·1
27	*Pouteria nemorosa*	Sapotaceae	PST	35	1·57	4·40	14·1
28	*Pseudolmedia laevis*	Moraceae	ST	35	1·32	4·24	17·3
29	*Sapindus saponaria*	Sapindaceae	PST	31	2·23	4·44	15·1
30	*Sapium glandulosum*	Euphorbiaceae	LLP	22	1·63	2·97	22·3
31	*Schizolobium parahyba*	Caesalpiniaceae	LLP	35	2·39	4·89	19·0
32	*Stylogyne ambigua*	Myrsinaceae	ST	10	1·46	1·80	15·9
33	*Sweetia fruticosa*	Fabaceae	LLP	34	1·91	4·46	18·1
34	*Swietenia macrophylla*	Meliaceae	PST	25	1·62	4·64	11·4
35	*Terminalia oblonga*	Combretaceae	PST	34	1·88	4·26	20·7
36	*Trema micrantha*	Ulmaceae	SLP	31	2·52	4·66	7·5
37	*Triplaris americana*	Polygonaceae	LLP	14	1·90	3·48	14·2
38	*Urera caracasana*	Urticaceae	SLP	13	1·99	2·84	8·8

Average crown exposure is given at 2 m height ($CE_{juvenile}$) and at adult height (CE_{adult}), as well as average maximum adult stature (H_{max}, m) (Poorter *et al.* 2006). Average plasticity in leaf traits is indicated (%). 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, multiplied by 100.
†ST = shade-tolerant species; PST = partial shade-tolerant species; LLP = long-lived pioneer species; SLP = short-lived pioneer species.

density of 367 ha⁻¹, basal area of 19·3 m² ha⁻¹, and species richness of 59 ha⁻¹ [all data for trees ≥10 cm diameter at breast height (d.b.h.), Instituto Boliviano de Investigación Forestal (IBIF), unpublished data].

Thirty-eight species differing in maximum adult stature and light demand were selected (Table 1). Study species were abundant, preferably of commercial value, and belonged to the most common species in the forest, in total representing 77% of all stems >10 cm d.b.h. (IBIF, unpublished data). Maximum adult stature (H_{max}) was calculated for each species using the diameter for the third thickest tree in the permanent sample plot (IBIF, unpublished data) and species-specific height–diameter relationships (Poorter, Bongers & Bongers, 2006). Species were assigned to four functional groups based on field observations

of their light requirement and longevity (Table 1; Justiniano *et al.* 2004; L.P., unpublished data). Shade-tolerant (ST) species complete their life cycle in the shade. Partial shade-tolerant (PST) species establish in low light conditions, but need more light at a later stage to continue growth towards the canopy where they experience high light conditions. Long-lived pioneers (LLP) live for >30 years, establish in intermediate light conditions and reach the high-light environment of the canopy. Short-lived pioneers (SLP) live for <30 years and complete their whole life cycle in high light (Finegan 1992). The study included 10 ST, 13 PST, 11 LLP and four SLP species.

In a separate study, Poorter *et al.* (2006) provided an objective, quantitative measure of light demand by analysing the height–light trajectories for each species.

These height–light trajectories describe how CE varies with tree height at the population level. Crown exposure and height were estimated for 662 individuals per species (range 41–9319). The CE varies from 1 if the tree 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, and 5 if it has an emergent crown that receives light from all directions (Dawkins & Field 1978). The CE can be measured repeatedly (average difference between two independent observers = $0 \cdot 1 \pm 0 \cdot 01$ SE; Poorter *et al*. 2006), and there is a good 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 (Poorter *et al*. 2006; cf. Poorter *et al*. 2005). Using the regression equation, we calculated the average CE at 2 m height ($CE_{juvenile}$) and maximum adult stature (CE_{adult}) (Table 1). The absolute difference between $CE_{juvenile}$ and CE_{adult} (CE_{change}) was used as a proxy for the ontogenetic change in light availability of the species.

We used CE and guilds as two complementary approaches to evaluate hypotheses about plasticity. Crown exposure provides a quantitative measure of the light demand of the species, whereas guilds capture both differences in juvenile CE ($CE_{juvenile}$ increased gradually from ST to SLP) and ontogenetic changes in CE (ST and SLP have a lower CE_{change} than the other guilds; see Table 3).

LEAF TRAITS

For 38 species, five sun and five shade individuals were selected randomly. Four leaves per individual were collected, providing a total of 1520 leaves. Trees of 10–20 cm d.b.h., 8–15 m high were selected. Two species – *Erythrochiton fallax* and *Picramnia sellowii* – reached a maximum height of only 5–6 m, and for these the leaves were collected for the tallest individuals. Crown exposure of the tree was estimated independently by two observers. Trees with a CE of 1–2·5 were regarded as shade individuals; trees with a CE ≥3 were regarded as sun individuals. The average CE of the collected shade individuals was $1 \cdot 80 \pm 0 \cdot 03$ (mean ± SE) and of the sun individuals $3 \cdot 40 \pm 0 \cdot 04$ (mean ± SE). Fieldwork was conducted in the wet season from November 2004 to February 2005.

Young, fully expanded leaves without epiphylls or significant damage by herbivores were selected from the outer leaf layer halfway the crown. The sample included the petiole and corresponding internode (twig section between two nodes). The following characteristics were determined: leaf length (LL, cm), leaf width (LW, cm), leaf area (LA, cm^2), fresh and dry mass (g), leaf toughness (LTO, N cm^{-2}), thickness (LTH, mm) and chlorophyll content (Chl, SPAD units). Leaf area was determined by scanning the leaves with a flatbed scanner and analysing the pictures with pixel-counting software (SIGMASCAN PRO 5, SPSS Inc.). The leaves were placed between wet paper overnight to reach water saturation of the leaves. Afterwards leaves were superficially dried with a tissue and the leaf fresh mass was determined. Leaf toughness was measured with a penetrometer. The leaves were penetrated between veins with the head of a nail (3 mm diameter). The weight on the nail was gradually increased until the nail penetrated the leaf. The mass at the moment of penetration of the leaf was converted to a measure for leaf toughness (N cm^{-2}). Chlorophyll content per unit leaf area was estimated with a SPAD meter (Konica Minolta). The SPAD value was converted to chlorophyll concentration per unit leaf area (Chl_{area}, μmol m^{-2}) using an average of the regression equations for six temperate herbaceous species ($Chl_{area} = 13 \cdot 9 \times SPAD$-$112 \cdot 9$; Anten & Hirose 1999). The internode diameter was measured in two directions and the cross-sectional internode area (mm^2) was calculated as an ellipse. For each combination of species and light level, nitrogen content (N_{mass}, % DM) and phosphorus content (P_{mass}, % DM) were determined for a pooled sample of leaves.

From these data the following parameters were derived: leaf shape index (LSI, leaf length per unit leaf width, cm cm^{-1}), specific leaf area (SLA, leaf blade area per unit leaf mass, cm^2 g^{-1}), leaf dry matter content (LDMC, leaf DM per unit leaf fresh mass, g g^{-1}), internode : leaf area ratio (ILAR, cross-sectional internode area per unit leaf area, mm^2 cm^{-2}), and chlorophyll : nitrogen ratio (Chl : N, leaf chlorophyll per unit leaf N, mmol mol^{-1}).

SLA is a measure of the amount of leaf area for light capture per unit biomass invested. N_{mass} is a proxy for the photosynthetic capacity of the leaf. Chl : N indicates the amount of leaf N invested in chlorophyll at the expense of investment in other compounds (e.g. Rubisco). The LTO is an indicator for the resistance of plants to herbivory (Coley 1983). The ILAR indicates the capacity of a leaf to sustain transpiration through a larger water supply per unit leaf area. Westoby & Wright (2003) analysed the relation between twig cross-sectional area and the total leaf area on the twig. They found that total leaf area was determined mainly by leaf size, rather than by the number of leaves. Therefore it was assumed that the individual leaf area could be used in the ratio in this study. For each compound leaf, leaf length, width and area were determined for an average-sized leaflet. The leaf area and LSI of leaflets of compound-leaved species and simple leaves were compared; as in comparing convective heat loss among species, leaflets were assumed to be functionally equivalent to simple leaves.

STATISTICAL ANALYSES

In all analyses an arithmetic average was used of the four leaves sampled per individual for the leaf traits. N_{mass} and P_{mass} were arcsine-transformed, the other leaf

characters were $\log_{10}$-transformed prior to analysis to increase normality and homoscedasticity.

Leaf traits of sun and shade leaves were compared using a two-way ANOVA with species and light level as fixed factors. The amount of variation explained by species, light and the interaction was calculated as the sum of squares of the effect in proportion to the total sum of squares of the model, equivalent to R^2. Plasticity in leaf traits was calculated based on the mean leaf trait values in sun and shade. Plasticity 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 (Valladares *et al.* 2000). Total plasticity per species was expressed as the average plasticity of all the leaf traits. Using Pearson's correlation, the plasticity in leaf traits was related to $CE_{juvenile}$, CE_{adult}, CE_{change} and H_{max} of the tree species. All statistical analyses were carried out using SPSS 11·5.

Results

VARIATION IN LEAF TRAITS EXPLAINED BY SPECIES, LIGHT, AND THEIR INTERACTION

Species differed significantly in all leaf traits (Table 2). There was a significant light effect for 12 out of 16

traits evaluated, and an interaction effect in only one (leaf width) of the 11 traits for which the interaction could be evaluated. This indicates that the tree species showed a similar proportional response to the light level (Sokal & Rohlf 1995), as data for most leaf traits were $\log_{10}$-transformed. The variation in leaf traits explained by species (average $R^2 = 0·76$) was much larger than the variation explained by light (average $R^2 = 0·08$) or the interaction between species and light level ($R^2 = 0·01$) (all average R^2 values mentioned above are based on significant effects only), despite large differences in CE of the sampled sun (average CE = 3·4) and shade (average CE = 1·8) individuals. The effect of light was relatively small, which was also reflected in strong correlations (average $r = 0·86$) between average trait values of species in sun and shade (Table 2). On average, R^2 of the model was 0·84, with a range from 0·62 for Chl_{area} to 0·97 for leaf width.

SUN AND SHADE LEAVES

Many traits (12 out of 16) differed between sun and shade leaves (Table 2). A high proportion (17–23%) of the variation in SLA, N_{area} and Chl : N was explained by light. Leaf length and width were both higher in shade leaves, consequently the LSI did not differ between sun and shade leaves. Also, sun and shade

Table 2. Two-way ANOVA with the effect of species ($n = 38$) and light level ($n = 2$; SH = shade, SU = sun) on leaf traits (total $n = 380$)

Parameter†	Species			Light			Interaction			R^2 total	SH mean	SU mean	r	Plasticity (%)
	F	P	R^2	F	P	R^2	F	P	R^2					
LL (cm)	92·56	***	0·91	7·86	**	0·00	0·86	ns	0·01	0·92	18·37	17·51	0·98	4·7
LW (cm)	231·42	***	0·96	6·42	*	0·00	1·48	*	0·01	0·97	9·79	9·38	0·99	4·2
LA (cm^2)	144·85	***	0·94	4·78	*	0·00	1·23	ns	0·01	0·95	116·52	108·61	0·99	6·8
LSI (cm cm^{-1})	138·57	***	0·94	0·12	ns	0·00	1·40	ns	0·01	0·94	1·88	1·87	0·98	0·4
ILAR (mm^2 cm^{-2})	16·08	***	0·59	81·33	***	0·08	1·15	ns	0·04	0·71	0·08	0·12	0·87	30·8
SLA (cm^2 g^{-1})	11·91	***	0·48	154·94	***	0·17	0·79	ns	0·03	0·67	194·62	149·37	0·88	23·2
LDMC (g g^{-1})	29·08	***	0·73	65·48	***	0·04	0·98	ns	0·02	0·80	0·29	0·32	0·93	10·2
LTH (mm)	30·12	***	0·71	103·42	***	0·07	1·10	ns	0·03	0·81	0·17	0·19	0·92	12·9
LTO (N cm^{-2})	39·27	***	0·80	14·98	***	0·01	1·27	ns	0·03	0·83	33·29	35·65	0·93	6·6
Chl_{area} (μmol m^{-2})	10·90	***	0·57	0·07	ns	0·00	0·93	ns	0·05	0·62	541·88	544·41	0·57	0·5
Chl_{mass} (μmol g^{-1})	16·88	***	0·59	83·92	***	0·12	1·11	ns	0·04	0·75	10·20	8·09	0·78	20·7
N_{area} (mmol m^{-2})	6·43	***	0·66	83·92	***	0·23				0·90	84·49	111·07	0·76	23·9
N_{mass} (% DM)	9·17	***	0·90	0·16	ns	0·00				0·90	2·34	2·36	0·80	1·0
P_{area} (mmol m^{-2})	10·83	***	0·84	38·29	***	0·08				0·92	3·15	4·00	0·85	21·1
P_{mass} (% DM)	15·95	***	0·94	0·83	ns	0·00				0·94	0·20	0·19	0·89	3·0
Chl : N (mmol mol^{-1})	5·12	***	0·68	52·58	***	0·19				0·87	6·43	4·90	0·71	23·8

F values and the level of significance (P) and total R^2 of the model are indicated (*, $P < 0·05$; **, $P < 0·01$; ***, $P < 0·001$). An equivalent for R^2 was calculated as the sum of squares of the effect in proportion to the total sum of squares. The back-transformed mean is given for pooled individuals for sun and shade leaves. r indicates Pearson 's correlations between average, back-transformed trait values of the species in sun and shade ($n = 38$); all correlations were significant at the 0·001 level. 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, multiplied by 100. N_{mass} and P_{mass} were arcsine-transformed, the other leaf traits were $\log_{10}$-transformed prior to analysis. Interaction effects between species and light level could not be evaluated for N_{mass}, N_{area}, P_{mass}, P_{area} and Chl : N as leaf nutrient contents were determined pooled per species and light level.
†LL, leaf length; LW, leaf width; LA, leaf area; LSI, leaf shape index; ILAR, internode : leaf area ratio; SLA, specific leaf area; LDMC, leaf dry matter content; LTH, leaf thickness; LTO, leaf toughness; Chl_{area}, chlorophyll concentration per unit leaf area; Chl_{mass}, chlorophyll content per unit leaf mass N_{area}, nitrogen concentration per unit leaf area; N_{mass}, nitrogen content per unit leaf mass P_{area}, phosphorus concentration per unit leaf area; P_{mass}, phosphorus content per unit leaf mass Chl : N, chlorophyll : nitrogen ratio.
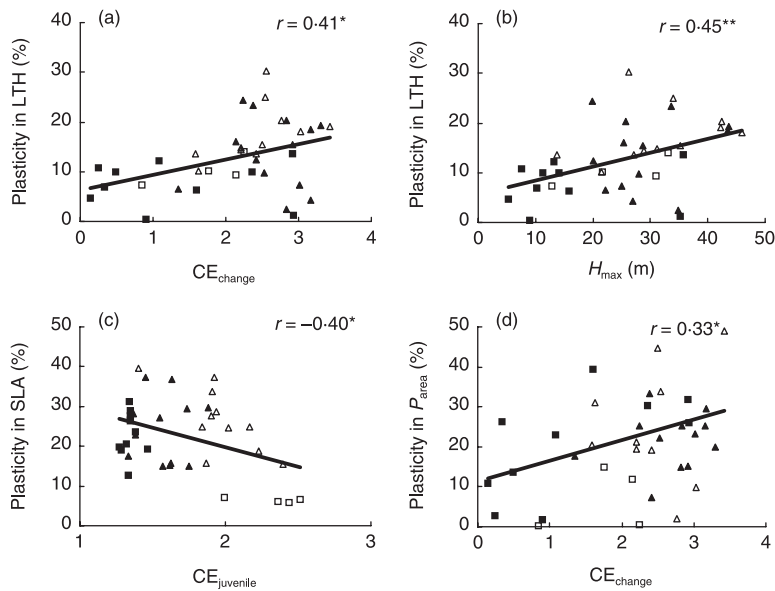
Fig. 1. Relations between plasticity in leaf traits, crown exposure (CE) or adult stature (H_{max}). Back-transformed means of sun leaves of 38 tropical moist forest tree species are shown. Plasticity in leaf traits per species was calculated as the absolute difference between the maximum average value in one light environment and the minimum average trait value in the other light environment divided by the maximum value. ■, shade-tolerant species; ▲, partially shade-tolerant species; △, long-lived pioneers; □, short-lived pioneers. (a,b) Leaf thickness (LTH); (c) specific leaf area (SLA); (d) phosphorus content per unit leaf area (P_{area}).

Table 3. One-way ANOVA on crown exposure, maximum adult stature and plasticity in leaf traits for 38 tropical moist forest tree species

	Guild			ST	PST	LLP	SLP
Parameter	F	P	R^2	mean	mean	mean	mean
$CE_{juvenile}$	37·14	***	0·77	1·34 a	1·55 b	1·95 c	2·32 d
CE_{adult}	11·39	***	0·50	2·36 a	4·16 b	4·38 b	4·00 b
CE_{change}	6·15	**	0·36	0·96 a	2·58 b	2·38 b	1·64 ab
H_{max}	8·57	***	0·43	13·1 a	28·1 b	30·2 b	23·1 b
LL	0·38	ns	0·03	8·76	8·51	6·23	7·63
LW	0·64	ns	0·05	9·31	11·61	7·71	8·36
LA	0·72	ns	0·05	16·21	18·67	12·28	14·36
LSI	0·02	ns	0·00	5·66	5·19	5·43	5·61
ILAR	2·49	ns	0·18	32·83	30·64	33·82	9·44
SLA	8·27	***	0·42	22·90 b	24·48 b	26·48 b	6·37 a
LDMC	2·00	ns	0·15	11·29	10·32	12·07	3·37
LTH	5·54	**	0·33	7·61 a	13·85 ab	17·72 b	10·25 a
LTO	2·19	ns	0·17	6·10	13·14	10·97	7·66
Chl_{area}	0·20	ns	0·02	9·91	12·28	10·43	9·20
Chl_{mass}	2·14	ns	0·16	20·10	21·09	25·51	9·95
N_{area}	3·38	*	0·23	21·96 b	24·19 b	28·45 b	7·57 a
N_{mass}	0·74	ns	0·06	6·58	9·90	11·42	4·15
P_{area}	2·54	ns	0·18	20·59	24·25	27·43	6·94
P_{mass}	0·48	ns	0·04	13·48	13·98	15·55	7·02
Chl : N	2·88	*	0·20	20·97 ab	24·53 ab	30·50 b	10·04 a
Total	6·95	***	0·38	14·64 b	16·66 b	17·64 b	8·00 a

Values of crown exposure at 2 m height ($CE_{juvenile}$), at adult height (CE_{adult}), the ontogenetic change in crown exposure (CE_{change}) and maximum adult stature (H_{max}) were $\log_{10}$-transformed prior to analysis. Mean plasticity (percentage) is given for each functional group (guild): groups indicated with a different letter differ significantly at the 0·05 level (Student–Newman–Keuls test). F values and level of significance (P) and the total R^2 of the model are indicated (*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$). 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. ST = shade-tolerant species ($n = 10$); PST = partial shade-tolerant species ($n = 13$); LLP = long-lived pioneer species ($n = 11$); SLP = short-lived pioneer species ($n = 4$). For parameter definitions see Table 2.

leaves did not differ in LSI when leaflets were used for compound-leaved species and simple leaves for the other species (two-way ANOVA: $F = 0.21$, $P > 0.05$, $n = 38$). Total leaf area was higher in shade leaves, and the same results were found when leaflets were included for compound leaves (two-way ANOVA: $F = 4.27$, $P < 0.05$, $n = 38$). Sun leaves had a higher ILAR. Shade leaves had a higher SLA and lower leaf thickness and toughness. Chl_{mass} was higher in shade leaves, but Chl_{area} did not differ between sun and shade leaves. Sun leaves had a similar N and P content on a mass basis, but higher contents on an area basis, compared with shade leaves. Chl : N was higher for shade leaves.

PLASTICITY IN LEAF TRAITS

Plasticity in leaf traits was large (20–31%) for SLA, Chl_{mass}, N_{area}, P_{area}, Chl : N and ILAR. Leaf traits that were significantly affected by light, but had a low plasticity (4–7%), were leaf toughness and size-related leaf traits (leaf length, width and area) (Table 2). No differences in plasticity between physiological traits (chlorophyll and nutrient contents, Chl : N) and the other nine morphological leaf traits were found (t-test: $t = -0.44$, $P > 0.05$, df = 14). Few significant relationships were found between plasticity, CE and H_{max}. Plasticity in leaf thickness was positively correlated to CE_{adult} ($r = 0.44$, $P < 0.01$), CE_{change} ($r = 0.41$, $P < 0.05$; Fig. 1a) and H_{max} ($r = 0.45$, $P < 0.01$; Fig. 1b). The plasticity in SLA was negatively correlated to $CE_{juvenile}$ ($r = -0.40$, $P < 0.05$), indicating a decreasing plasticity in SLA with increasing juvenile light demand of the species (Fig. 1c). The plasticity in leaf length was negatively correlated to H_{max} ($r = -0.34$, $P < 0.05$); plasticity in P_{area} was positively correlated to CE_{change} ($r = 0.33$, $P < 0.05$; Fig. 1d).

Plasticity in SLA, leaf thickness, N_{area} and Chl : N was significantly different across functional groups differing in shade tolerance (Table 3). Plasticity in leaf thickness was low for SLP and ST, intermediate for PST, and high for LLP species. SLP species had low plasticity in Chl : N, LLP species had the highest plasticity in Chl : N, whereas ST and PST species showed intermediate values. Plasticity in SLA, N_{area} and total plasticity in leaf traits was low for short-lived pioneer species and high for the other three functional groups (Table 3).

Discussion

SUN AND SHADE LEAVES

Sun and shade leaves differed in most traits. The species showed, surprisingly, a similar proportional response to the light environment, despite large differences in their shade tolerance. Consequently, there was a high correlation between species leaf traits in sun and shade, indicating that the species ranking in trait performance is largely maintained in different light environments.

Sun leaves differed from shade leaves in many leaf traits, and most findings are consistent with other studies. Sun leaves were smaller and thicker, possibly to prevent overheating (Bongers & Popma 1988), which agrees with model simulations using boundary-layer thickness (Parkhurst & Loucks 1972). Sun leaves had higher nutrient concentrations per unit leaf area (Björkman 1981; Gulmon & Chu 1981), indicating a higher photosynthetic capacity as photosynthetic capacity and N_{area} are positively correlated (Field & Mooney 1986; Wright *et al*. 2005; but cf. Coste *et al*. 2005). Differences in N content on a mass basis were not found, but in other studies a higher N content on a mass basis has been reported for shade leaves (Bongers & Popma 1988; Givnish 1988; Poorter *et al*. 2000). Sun leaves were not more slender than shade leaves, indicating that leaf shape is not altered by the light environment across a wide range of species (cf. Bongers & Popma 1988). Apparently species prevent overheating by altering their leaf size rather than their leaf shape. Sun leaves may be tougher to prevent mechanical damage, as wind speeds are higher in the canopy (Chiariello 1984). A side effect might be that exposed leaves are also better protected against the higher herbivore densities in sunny environments (Sterck, van der Meer & Bongers 1992; but cf. Coley & Barone 1996). The cross-sectional internode area in proportion to leaf area was higher in sun leaves, which indicates that sun leaves have a higher water supply to the leaves to compensate for the high transpiration.

The moist conditions in the understorey allow for a high leaf water content and therefore maintenance of turgor, which is a 'cheap' way to enhance leaf display for light capture. Shade leaves enhanced their light capture through high SLA and Chl_{mass} (Chazdon *et al*. 1996), leading to a similar Chl_{area} compared with sun leaves (cf. Poorter, Oberbauer & Clark 1995). In this way, shade leaves maximize their efficiency in light capture per unit leaf mass, as plants in the understorey have to spend the little C they sequestered carefully (Poorter *et al*. 1995; Poorter *et al*. 2000). A higher leaf-level investment in light capture was confirmed by the higher Chl : N in shade leaves, indicating that a greater proportion of leaf N was invested in chlorophyll for light capture at the expense of investment in Rubisco (Hikosaka & Terashima 1995; Poorter & Evans 1998; Poorter *et al*. 2000).

PLASTICITY IN LEAF TRAITS

The magnitude of the plastic response to light differed among leaf traits. Leaf traits with higher plasticity could be more critical for leaf functioning in different light environments (Bongers & Popma 1988). This suggests that ILAR, SLA, N_{area}, P_{area} and Chl : N are most important for light acclimation. The first variable is closely related to water transport, the latter four to the regulation of photosynthetic capacity in different light environments. Bongers & Popma (1988) also found high plasticity for SLA and N_{area} for 61 Mexican rainforest tree species. Phenotypic plasticity should optimize plant functioning in a given environment. This means that sun-acclimated plants should function better in high-light environments, whereas shade-acclimated individuals should perform better in low light (Rice & Bazzaz 1989). The importance of the above-mentioned traits is underscored by the meta-analysis of Poorter & Nagel (2000), who showed that an increase in growth with irradiance is caused by an increase in whole-plant net assimilation rate (NAR). Such an increase in NAR can be attributed partly to the higher photosynthetic rates, and partly to a higher photosynthetic capacity through a lower SLA and higher N_{area}. Similarly, in a simulation study Sims *et al*. (1994) showed that growth is highly dependent on adjustments in SLA to low and high irradiance, whereas growth is mostly dependent on photosynthetic capacity (and hence N_{area}) at high irradiance. Leaf P is essential for the regulation of photosynthetic capacity (ATP, RuBP regeneration). This is especially so for rainforest tree species, as they tend to grow on P-deficient soils (Raaimakers *et al*. 1995). The Chl : N ratio is important in regulating the balance between the light and dark reactions of photosynthesis. In shaded conditions a large proportion of N is invested in chlorophyll for light capture, leading to a high Chl : N, whereas in sunny conditions a large proportion of N is invested in Rubisco for C fixation, leading to a low Chl : N (Poorter *et al*. 2000).

In this study, no difference was found in plasticity between physiological and morphological leaf traits. In contrast, physiological plasticity was found to be higher than morphological plasticity for 16 *Psychotria* species from Panama (Valladares *et al*. 2000). These differences could be attributed to the traits included and the ontogenetic stage of the plants, as Valladares *et al*. worked with whole seedlings instead of leaves from trees.

IS PLASTICITY RELATED TO THE ADULT STATURE AND LIGHT DEMAND OF THE SPECIES?

Among species, high plasticity was expected for species with a large ontogenetic change in light availability and for species with a high maximum adult stature (cf. Thomas & Bazzaz 1999). For example, in a study with 61 Mexican rainforest species, greater plasticity was found for gap-dependent (our PST and LLP) tree species that experience marked changes in irradiance during their life, compared with species that complete their life cycle in consistently low (ST) or high (SLP) irradiance (Popma *et al*. 1992). Of all leaf traits evaluated, only plasticity in thickness and P_{area} were positively correlated to ontogenetic change in CE, and only plasticity in leaf thickness was positively correlated to maximum adult stature. Studies that found greater

plasticity for taller trees did so for plasticity in leaf traits between different ontogenetic stages (sapling and tree), rather than plasticity in sun and shade leaves measured for trees of the same ontogenetic stage (Thomas & Ickes 1995; Thomas & Bazzaz 1999; Martínez-Garza & Howe 2005). For example, for eight late-successional species Martínez-Garza & Howe (2005) found no relationship between sun–shade plasticity and H_{max}, but there was a relationship between ontogenetic plasticity (sapling–adult) and H_{max}.

Three hypotheses have been put forward to explain the plasticity of tree species. The first states that plasticity is largest for pioneer species, as they occupy early successional habitats with a large variation in irradiance (Strauss-Debenedetti & Bazzaz 1991; Valladares *et al.* 2000). Plasticity in SLA was negatively related to juvenile CE, and short-lived pioneers showed a smaller plasticity than the other functional groups for SLA, leaf thickness, N_{area}, Chl : N, and for all leaf traits combined (Table 3). These results suggest that we can discard the first hypothesis. Most evidence for greater plasticity in pioneers comes from seedlings (Strauss-Debenedetti & Bazzaz 1991; Veneklaas & Poorter 1998). The capacity for a plastic response depends on the C balance of the plant. At the seedling stage, pioneers fix more C and can invest more in acclimatory leaf responses. At the adult stage, all species fix more C and can invest in high leaf plasticity. Yet leaves of large trees of pioneer species do not survive under extremely shaded conditions (cf. Kitajima, Mulkey & Wright 2005), therefore they may show less sun–shade plasticity.

The second hypothesis states that plasticity is greater for tall species that experience a large ontogenetic change in irradiance during their life cycle, and smaller for species that experience consistently low (shade-tolerant) or high (pioneer) light conditions (Popma *et al.* 1992). This hypothesis is partly confirmed by our data: SLP species did have the lowest plasticity, but ST species had plasticity nearly as high as PST and LLP species.

The third hypothesis states that pioneers and shade-tolerant species might have greater plasticity for those leaf traits that are more important for successful functioning in a high- and low-light environment, respectively (Valladares *et al.* 2002). Species adapted to high irradiance have, for example, higher plasticity in leaf traits related to photosynthesis (in our case not reflected in high plasticity in N_{area}), whereas shade-tolerant species have higher plasticity in traits important for light harvesting (in our case reflected in high plasticity in SLA and Chl : N; Valladares *et al.* 2002; Yamashita, Koike & Ishida 2002; but cf. Bazzaz & Wayne 1994). Plasticity is a compromise between many factors and constraints, and probably all of these may explain the observed patterns to some extent.

Summarizing, leaves show acclimatory responses to irradiance that optimize the C, heat and water balance to their growth environment. ILAR, SLA, Chl_{mass}, N_{area}, P_{area} and Chl : N show the largest plasticity to irradiance. Species show substantial variation in plasticity in leaf traits (7–27%; Table 1) but, in contrast to the hypothesis, it is barely related to the ontogenetic change in CE and maximum adult stature of the species. Short-lived pioneer species show a smaller sun–shade plasticity than other species groups, probably because they are found under consistently high light levels.

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