

Leaf traits show different relationships with shade tolerance in moist versus dry tropical forests

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Summary

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- Shade tolerance is the central paradigm for understanding forest succession and dynamics, but there is considerable debate as to what the salient features of shade tolerance are, whether adult leaves show similar shade adaptations to seedling leaves, and whether the same leaf adaptations are found in forests under different climatic control.

- Here, adult leaf and metamer traits were measured for 39 tree species from a tropical moist semi-evergreen forest (1580 mm rain yr⁻¹) and 41 species from a dry deciduous forest (1160 mm yr⁻¹) in Bolivia. Twenty-six functional traits were measured and related to species regeneration light requirements.

- Adult leaf traits were clearly associated with shade tolerance. Different, rather than stronger, shade adaptations were found for moist compared with dry forest species. Shade adaptations exclusively found in the evergreen moist forest were related to tough and persistent leaves, and shade adaptations in the dry deciduous forest were related to high light interception and water use.

- These results suggest that, for forests differing in rainfall seasonality, there is a shift in the relative importance of functional leaf traits and performance trade-offs that control light partitioning. In the moist evergreen forest leaf traits underlying the growth–survival trade-off are important, whereas in the seasonally deciduous forest leaf traits underlying the growth trade-off between low and high light might become important.

Introduction

Shade tolerance is considered to be the central paradigm for understanding the succession and dynamics of temperate and tropical forests (Bazzaz, 1979; Pacala *et al.*, 1996). Although the notion of shade tolerance dates back as far as the eighteenth century, there is still considerable debate as to what constitutes the salient features of shade tolerance (Sack & Grubb, 2001; Kitajima & Bolker, 2003; Niinemets, 2006), with two contrasting hypotheses. One hypothesis suggests that shade-tolerant and light-demanding species partition spatial and temporal gradients in irradiance because of a trade-off between survival and growth (Kitajima, 1994; Kobe *et al.*, 1995). The alternative hypothesis suggests that species partition light gradients because of a trade-off in growth performance between low and high light (Shugart, 1984; Givnish, 1988).

The reasoning behind the first hypothesis is that shade-tolerant species regenerate in the shaded forest understory where carbon gain proceeds at low rates. For such species, a high survival rate is thought to be important, if they are eventually to make it to the canopy. Indeed, temperate and tropical seedling studies under controlled conditions have shown that shade-tolerant species are characterized by tough, structurally reinforced leaves with a low specific leaf area (SLA; leaf area per unit leaf mass) (reviewed in Veneklaas & Poorter, 1998; Walters & Reich, 1999). This would allow them to deter potential herbivores (Coley, 1983), pay back the initial construction costs of the leaves (Poorter *et al.*, 2006), reduce leaf turnover (King, 1994) and enhance plant survival (Poorter & Bongers, 2006). For light-demanding species that regenerate in the ephemeral, high-light conditions of gaps, a high growth rate is thought to be important. Seedlings of

light-demanding species have been found to have high SLA, leaf area ratio (LAR; leaf area per unit plant mass) and assimilation rates (Veneklaas & Poorter, 1998; Walters & Reich, 1999). This would allow them to overshadow and outcompete their neighbours, attain a position at the top of the re-growing gap vegetation, and achieve fast growth.

Several authors (Sack & Grubb, 2001; Lusk & Warton, 2007; Valladares & Niinemets, 2008) have argued that most of our knowledge on shade adaptations comes from work on small seedlings, and that the observed patterns may largely be driven by interspecific variation in seed size, as seed size is known to have large effects on seedling morphology (Grubb, 1998). Many light-demanding species have minute seeds with little reserves, and depend on photosynthetic carbon gain for onward autotrophic growth. As a result, they have a high biomass fraction in leaves, and high SLA and LAR. By contrast, many shade-tolerant species have large seeds, and form large seedlings with large leaves that need more structural reinforcement, and therefore have low SLA and LAR. Morphological differences between small-seeded light-demanding species and large-seeded shade-tolerant species are therefore largest just after germination, but may change dramatically over time when the light-demanding species catch up in size with the shade-tolerant species (Grubb *et al.*, 1996; Sack & Grubb, 2001; Poorter & Rose, 2005). Lusk & Warton (2007) showed in a meta analysis that saplings (0.2–5 m tall) of evergreen species still showed a positive relation between SLA and regeneration light requirements, whereas for saplings of temperate winter deciduous species this relationship was reversed compared with seedlings. The winter sets a clear upper limit to the leaf lifespan of temperate deciduous shade-tolerant species, and for them it probably does not pay to structurally reinforce their leaves by having a low SLA, and instead, they make high-SLA leaves to enhance light interception. Large-scale comparative studies on leaf traits in later ontogenetic stages are scant. A study on the adult leaves of 63 tropical evergreen tree species found that light-demanding species had higher SLA compared with shade-tolerant species (Popma *et al.*, 1992), whereas a study on 85 temperate deciduous species (Niinemets & Kull, 1994) found that light-demanding species had a lower SLA, paralleling the findings for saplings. Given the fact that SLA and LAR are strong drivers of interspecific variation in growth, this could have large repercussions for species growth performance along the light gradient for taller plants. Indeed, the second hypothesis suggests that shade-tolerant and light-demanding species may partition the light gradient because of a trade-off in growth performance between low and high light. According to this view, shade-tolerant species realize the fastest growth rates in the shade because of a maximization of light interception and low respiration (Givnish 1988), whereas light-demanding species realize the fastest growth rates in high light because of high photosynthetic carbon gain.

Given these recent findings, the question is whether the shade adaptations of tropical dry forest species parallel those

of tropical evergreen species or those of temperate winter deciduous species. The importance of shade tolerance is likely to diminish in dry forests, which experience a more extreme dry season and have a seasonally open canopy (Lebrija-Trejos *et al.*, 2008; Markesteijn *et al.*, 2007). Wet tropical forests with a high leaf area index and an evergreen canopy cast a deep, persistent shade, whereas dry tropical forests with a low leaf area index and a seasonally deciduous canopy cast a lighter shade, which disappears during the dry season. The lighter shade could allow subcanopy trees to maintain a moderately positive carbon balance during the wet season, and the high light pulse could allow evergreens to make large carbon gains during the dry season when they are still physiologically active. It is therefore expected that plant adaptations to shade will be less pronounced in dry forests. Instead, the severe dry season may impose a strong environmental filter. Most species that can successfully survive this dry season will have a deciduous leaf habit, possibly leading to a smaller range of leaf lifespans, and to either a strong convergence of functional traits or to similar shade adaptations as found for saplings of temperate deciduous species. However, no data exist on how leaf traits are related to shade tolerance in dry tropical forest species.

In this study, the functional leaf traits of 39 moist forest species and 41 dry forest species are compared. The focus was on adult leaves, as it is argued that they should show different relationships with shade tolerance compared with seedling leaves (Grubb, 1998; Niinemets, 2006). The selected species represent the majority of stems in each community, thus providing insight into the spectrum of trait values among co-existing trees, and its implication for plant performance and niche differentiation (Reich *et al.*, 2003). A suite of 26 functional traits have been selected that are important for the light capture, carbon gain and defence of leaves, and hence for the growth and survival rates of plants. Leaf traits were related to a continuous index of the regeneration light requirements of the species (Poorter & Kitajima, 2007), as light requirements in the regeneration stage are a better predictor of leaf traits of seedlings, saplings and adults than light requirements in the adult stage (Poorter, 2007). This is probably because the regeneration stage is the major bottleneck in the life cycle of the plant.

The aim of this study was to compare leaf adaptations to shade for moist and dry forest tree species. It was predicted that: (i) moist forest species would show more and stronger shade adaptations than dry forest species; (ii) for moist forest species SLA and associated leaf traits would increase, and leaf lifespan decrease with regeneration light requirements, whereas for dry forest species SLA and leaf lifespan would decrease with regeneration light requirements; and (iii) in the moist forest leaf traits underlying the growth–survival trade-off would be important for light partitioning, whereas in the dry forest leaf traits underlying the trade-off between low and high light growth might become more important.

Materials and Methods

Study sites

Research was carried out in the lowland tropical dry deciduous forest of Inpa (16°1'S, 61°4'W; henceforth referred to as 'dry forest') and the moist semi-evergreen forest of La Chonta (15°47'S, 62°55'W; henceforth referred to as 'moist forest'), Bolivia. The two forests are relatively close to one another (c. 250 km) and occur at similar altitudes (400–500 m) but differ strikingly in abiotic conditions and species composition. The two forests experience a similar temperature (24°C) and differ moderately in annual rainfall (1160 vs 1580 mm yr⁻¹), but the dry forest has a longer dry season in which potential evapotranspiration exceeds precipitation (3 vs 1 month for the moist forest). This leads to substantially lower minimum soil water potential in the dry season as measured at the first 20 cm of soil depth (−5.6 vs −1.8 MPa for the moist forest; L. Markesteijn, unpublished), and a canopy that is nearly fully deciduous in the dry season, whereas in the moist forest only one-third of the tree canopy is deciduous in the dry season. Soils in the dry forest have considerably lower phosphorus (P) concentrations compared with soils in the moist forest (2.6 vs 11.2 cmol kg⁻¹, respectively; M. Peña-Claros *et al.*, unpublished).

The moist forest has a taller canopy (27 vs 20 m) and a similar basal area (19.7 m² ha⁻¹) compared with the dry forest (Peña-Claros *et al.*, 2008) for trees larger than 10 cm diameter at breast height (DBH). The moist forest contains 59 tree species per hectare, the most abundant ones being *Pseudolmedia laevis*, *Ampelocera ruizii* and *Ocotea* spp. The dry forest contains 34 tree species per hectare of which the most abundant are *Acosmium cardenasii*, *Casearia gossypiosperma*, and *Caesalpinia pluviosa*.

Species selection and quantification of light requirements

We selected 41 of the most abundant tree and shrub species in the dry forest (representing 77% of all stems > 10 cm DBH) and 39 tree species in the moist forest (representing 77% of all stems), with nine species common to both sites (Supporting Information Table S1). The selected species differ markedly in shade tolerance, adult stature, and adult leaf habit. Evergreen and deciduous species were found in both forest types: 13 out of 39 species were deciduous in the moist forest, versus 25 out of 41 species in the dry forest. In the dry forest, evergreen species tend to be of smaller stature, and some deciduous canopy species start their lives as evergreen saplings in the understory.

In a separate study, Poorter & Kitajima (2007) provided an independent, objective and continuous measure of the regeneration light requirements of the species by analysing, for each species, the crown exposure (CE) in relation to the height of individual trees. To this end, on average 523 individuals (range 16–9064) per species were measured in both forests

over their whole size range for height and CE (Dawkins & Field, 1978). The CE is scored as 1 if the tree does not receive any direct light, 2 if it receives lateral light, 3 if it receives overhead light on 10–90% of the crown, 4 if it receives full overhead light on > 90% of the crown, and 5 if it has an emergent crown. The CE can be measured repeatedly (mean difference between two independent observers is 0.1 ± 0.01 SE), and there is a good relation between CE and both canopy openness and incident radiation (Clark *et al.*, 1993; Keeling & Phillips, 2007). For each species the CE was related to tree height, using a multinomial regression analysis (cf. Poorter *et al.*, 2005). Using the regression equation, the average population-level crown exposure at a standardized height of 2 m (juvenile CE) was calculated. Similar-sized individuals of the same species can be found under a wide range of CEs, but what counts from an evolutionary point of view is the average population-level CE of the species (Poorter *et al.*, 2005). Regeneration light requirement is the inverse of shade tolerance, and these two expressions will be used interchangeably in this paper. Sapling shade survival is an often-used indicator of shade tolerance, and, for the moist forest, the sapling survival of the species indeed shows a strong negative correlation with the juvenile CE (Poorter & Bongers, 2006).

Because the dry forest has a lower and more open canopy than the moist forest, the dry forest species have, on average, a higher juvenile CE (L. Poorter, unpublished). A direct quantitative comparison of the juvenile CE amongst dry and moist forest species is difficult, because the researcher tends to rescale the CE values to the range of canopy conditions observed in the forest (Zagt, 1997). It allows, however, comparisons of species within the same forest.

Data collection

Five sun-exposed individuals were selected per species (Rozendaal *et al.*, 2006; Markesteijn *et al.*, 2007). Selected individuals were generally between 10 and 20 cm DBH and between 8 and 15 m in height. Eight species attain a maximum height of only 2–7.5 m and for these species the tallest individuals were sampled. Mean estimated canopy openness above the tree crown (dry forest) or part of the crown where the metamers were sampled (moist forest) was 66.5% ± 1.0 (SE). Per individual, five metamers were collected with a pruner on an extension pole from the outer leaf layer midway between the bottom and top of the crown, providing in total 2050 metamers. Young, fully expanded leaves without epiphylls and significant herbivore damage were selected, including the corresponding petioles and internodes (twig section below the leaf, between two nodes).

Metamers (i.e. the internode, and corresponding petiole and leaf) rather than individual leaves were collected. Plants show large ontogenetic changes in their whole-plant biomass fractions in leaves, stem, and branches, because of the different longevities of these components (Körner, 1994). Especially for

large trees it is therefore difficult to estimate how species partition their acquired carbon to different plant functions. By focusing on the growing branch tips only, we obtain a first estimation of how species partition their carbon aboveground (Falster & Westoby, 2005). Evidently, the annual new biomass allocation to stem thickening from base to current metamers may often exceed annual allocation to all metamers, but this is very difficult to measure. Four metamers per individual were divided into leaves, petioles and internodes. Leaf area (LA; in cm^2) was determined by scanning the leaves with a flatbed scanner and analysing the pictures with pixel-counting software (PIXELS!; Van Berloo, 1993 and SIGMA SCAN PRO 5; SPSS Inc., Chicago, IL, USA). Twenty-six species had (palmately) compound leaves (Table S1), and for these whole leaves rather than leaflets were measured. The petiole length (PL; in cm), internode length (IL; in cm), and internode diameter in two directions (IDiam; in mm) were measured with a ruler or calliper. Leaf thickness (LTh; in μm) was measured between the major veins using a micrometer. For the moist forest the chlorophyll content per unit leaf area was estimated with a SPAD meter (Minolta SPAD 502 Chlorophyll Meter, Spectrum Technologies Inc., Plainfield, IL, USA). Leaves were rehydrated overnight in a fridge between wet sheets of paper. Afterwards leaves were superficially dried with a tissue and the leaf fresh mass was determined. The force required to punch leaves (leaf punch force (LPF)) was measured with a penetrometer. The leaves were penetrated between the veins with the head of a nail (with a diameter of 3 mm). 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 punch force (N cm^{-2}). For the fifth collected leaf per tree, a leaf punch was made between the major veins. Leaves, petioles, internodes and leaf punches were oven-dried for at least 48 h at 70°C and weighed. For each species the nitrogen content (N_{mass} ; in % dry mass) and phosphorus content (P_{mass} ; in % dry mass) were determined for a pooled sample of leaves.

From these data the metamer biomass fractions in leaf, petiole and internode (LMF_m , PMF_m and IMF_m , respectively; $100 \times$ dry mass per unit dry metamer mass; in %), the SLA of leaves and punches (the leaf blade area per unit leaf mass; in $\text{cm}^2 \text{g}^{-1}$), the leaf area ratio (LAR_m ; the leaf area per unit metamer mass; in $\text{cm}^2 \text{g}^{-1}$), the specific petiole length (SPL; the petiole length per unit petiole mass; in cm g^{-1}), and the specific internode length (SIL; the IL per unit internode mass; in cm g^{-1}) were calculated. For species with metamers with opposite leaves the leaf, petiole and internode mass fractions and LAR_m were calculated taking both opposite leaves into account. In addition, the leaf dry matter content (LDMC; $100 \times$ leaf dry mass divided by leaf fresh mass; in %), density of leaves and punches (LD; leaf dry mass/(leaf area \times leaf thickness); in g cm^{-3}), internode density (ID; internode mass/(IL \times internode cross-sectional area); in g cm^{-3}), internode cross-sectional area (IA; $0.25 \times \pi \times \text{IDiam}^2$; in mm^2), and internode area to leaf area (IA : LA; in $\text{mm}^2 \text{cm}^{-2}$) were determined. Nitrogen per

unit area (N_{area} ; in mg cm^{-2}) and phosphorus per unit area (P_{area} ; in mg cm^{-2}) were calculated by multiplying the nutrient concentrations by SLA. SPAD values were converted to chlorophyll concentration per unit leaf area (Chl_{area} ; in $\mu\text{mol m}^{-2}$) using an average of the regression equations for six temperate herbaceous species ($\text{Chl}_{\text{area}} = (13.9 \times \text{SPAD}) - 112.9$; Anten & Hirose 1999), and to chlorophyll per unit mass (Chl_{mass} ; in $\mu\text{mol g}^{-1}$) by multiplying Chl_{area} by (SLA/10000). Species were also classified as to whether they have compound leaves (Comp), and whether their adult trees are deciduous during the dry season (Dec). Trait abbreviations are given in Table 1.

Leaf size, IL and PL are important for the spatial positioning of the leaves. IMF_m and PMF_m indicate the biomass investment in biomechanical and hydraulic support, and SIL and SPL reflect the efficiency of biomass investment for foraging. LMF_m , SLA and LAR_m reflect the biomass investment at the metamer level in leaf display and light capture. LDMC, LD, LPF and ID indicate whether plant tissues are biomechanically tough and physically well protected. Mass- and area-based nutrient contents are estimators of the photosynthetic capacity.

It was logistically impossible to measure leaf lifespan for adult trees, and leaf lifespan was therefore measured for saplings instead. About 16 saplings per species (mean 14.7; range 4–22; total 817) with heights between 0.5 and 2.5 m were selected (Poorter & Bongers, 2006; L. Poorter, unpublished). Individuals of all species were sampled under closed canopy conditions, and those of light-demanding species were in principle also sampled under closed canopy conditions, but also sampled in gaps and along skid trails or roads to assure a sufficient number of individuals. The most recently formed leaf was marked. Moist forest plants were monitored at *c.* 2, 4, 9, 13 and 25 months after the start of the study, and dry forest plants at *c.* 1, 3, 5, 8, 14 and 27 months after the start of the study. At each census the remaining leaves of the old leaf cohort(s) were counted, and the leaves of the new leaf cohort were counted and tagged. Median leaf lifespan was estimated using survival analysis.

Data analysis

For each tree the mean leaf trait value was calculated, based on the arithmetic mean of the four leaves. Subsequently for each species mean leaf trait values were calculated, based on the logarithmic₁₀ mean of the five trees. For the current study back-transformed means were mostly used, unless data were not normally distributed. Deciduous species had a slightly higher CE compared with evergreen species, although this difference was not significant (*t*-test on CE: $P = 0.28$ for the dry forest; $P = 0.07$ for the moist forest). Still, the deciduous species may show different relationships between leaf traits and juvenile CE compared to evergreen species. A series of ANCOVAs was therefore carried out for each site, with each of the leaf traits as dependent variable, leaf habit as a factor, and juvenile CE as a covariate. A significant leaf habit \times covariate interaction indicates that relationships between leaf traits and juvenile CE

Table 1 Pearson correlation (r) of leaf traits with juvenile crown exposure (CE) for moist forest species and dry forest species

Trait	Description	Moist forest		Dry forest	
		r	P	r	P
LL	Leaf lifespan	-0.81	0.002	-0.51	0.001
Comp	Compoundness	0.29	0.073	0.30	0.053
Dec	Deciduousness	0.29	0.071	0.17	0.284
LA	Leaf area	0.43	0.007	0.46	0.003
PL	Petiole length	0.43	0.006	0.42	0.006
IL	Internode length	0.21	0.208	0.51	0.001
SPL	Specific petiole length	0.16	0.341	-0.36	0.022
SIL	Specific internode length	-0.19	0.235	-0.42	0.006
LMF _m	Leaf mass fraction of the metamer	-0.47	0.003	-0.35	0.024
PMF _m	Petiole mass fraction of the metamer	0.41	0.009	0.30	0.055
IMF _m	Internode mass fraction of the metamer	0.08	0.645	0.22	0.165
IA	Internode cross-sectional area	0.50	0.001	0.46	0.002
IALA	Internode area to leaf area	0.05	0.759	0.32	0.040
ID	Internode density	-0.52	0.001	-0.43	0.005
LD	Leaf density	-0.25	0.131	-0.12	0.443
LDpu	Leaf density of the punch	-0.53	0.001	-0.17	0.284
LTh	Leaf thickness	-0.05	0.750	0.41	0.008
LPF	Leaf punch force	-0.46	0.004	-0.18	0.279
LDMC	Leaf dry matter content	-0.47	0.003	-0.15	0.339
SLA	Specific leaf area	0.43	0.006	-0.17	0.291
SLApu	Specific leaf area of the punch	0.57	0.000	-0.10	0.559
LAR _m	Leaf area ratio of the metamer	0.35	0.029	-0.33	0.038
N_{mass}	Nitrogen per unit mass	0.45	0.005	0.35	0.026
P_{mass}	Phosphorus per unit mass	0.26	0.110	0.33	0.036
N_{area}	Nitrogen per unit leaf area	0.06	0.711	0.38	0.013
P_{area}	Phosphorus per unit leaf area	0.00	0.986	0.41	0.008
Chl _{area}	Chlorophyll per unit leaf area	0.06	0.734	-	-
Chl _{mass}	Chlorophyll per unit mass	0.37	0.021	-	-
Chl:N	Chlorophyll to nitrogen ratio	-0.06	0.730	-	-

Moist forest species, $n = 39$; dry forest species, $n = 41$.

Significant correlations are given in bold. Leaf lifespan and leaf area were \log_{10} -transformed before analysis.

vary with leaf habit. The confounding effect of leaf habit was only minor, as in only six cases a significant interaction was found (Table S2), the most important interactions being for leaf lifespan and SLA in the moist forest. Leaf traits were, therefore, for subsequent analyses only correlated with juvenile CE at each site, using a Pearson correlation. To examine which traits are the strongest determinants of juvenile CE, a forward multiple regression was carried out for each site, with juvenile CE as the dependent variable, and the other species traits as independent variables. All statistical analyses were carried out using SPSS 12 (SPSS Inc.).

Results

Most of the adult leaf traits evaluated (85%) were significantly correlated with juvenile CE (hereafter CE), at one or both sites (Table 1). More traits were significantly affected by CE in the dry forest than in the moist forest (16 vs 14 traits), but for these traits CE explained less of the variation (r^2 is 0.17 vs 0.25, respectively; t -test on r^2 , $t = 2.4$, $P = 0.024$, $df = 28$). The leaf

traits are discussed in four groups, related to leaf size (Table 1), leaf reinforcement (Fig. 1), leaf display at the metamer level (Fig. 2), and leaf chemistry (Fig. 3).

Relative to shade-tolerant species, light-demanding species (with a high CE) had in both forests a large leaf area (Table 1) and internode cross-sectional area, long petioles, and a large biomass fraction in petioles (although for the PMF_m of the dry forest this was at the edge of significance; $P = 0.055$). Light-demanding species were also characterized by a low internode density (Fig. 3e,f).

Six leaf traits were only correlated with CE in the moist forest, and nearly all these traits were related to leaf toughness and persistence. Shade-tolerant species (with a low CE) had a low SLA at the leaf and lamina level (Fig. 2c), and a high leaf dry matter content, leaf density (Fig. 1a) and leaf punch force (Fig. 1c). Species with a low CE had in both forests a long leaf lifespan (Fig. 1e,f). In the moist forest there was a significant interaction between leaf habit and CE for leaf longevity and SLA (ANCOVA; Table S2). Log(leaf lifespan) showed stronger relationships with CE for evergreen species ($r = -0.85$,

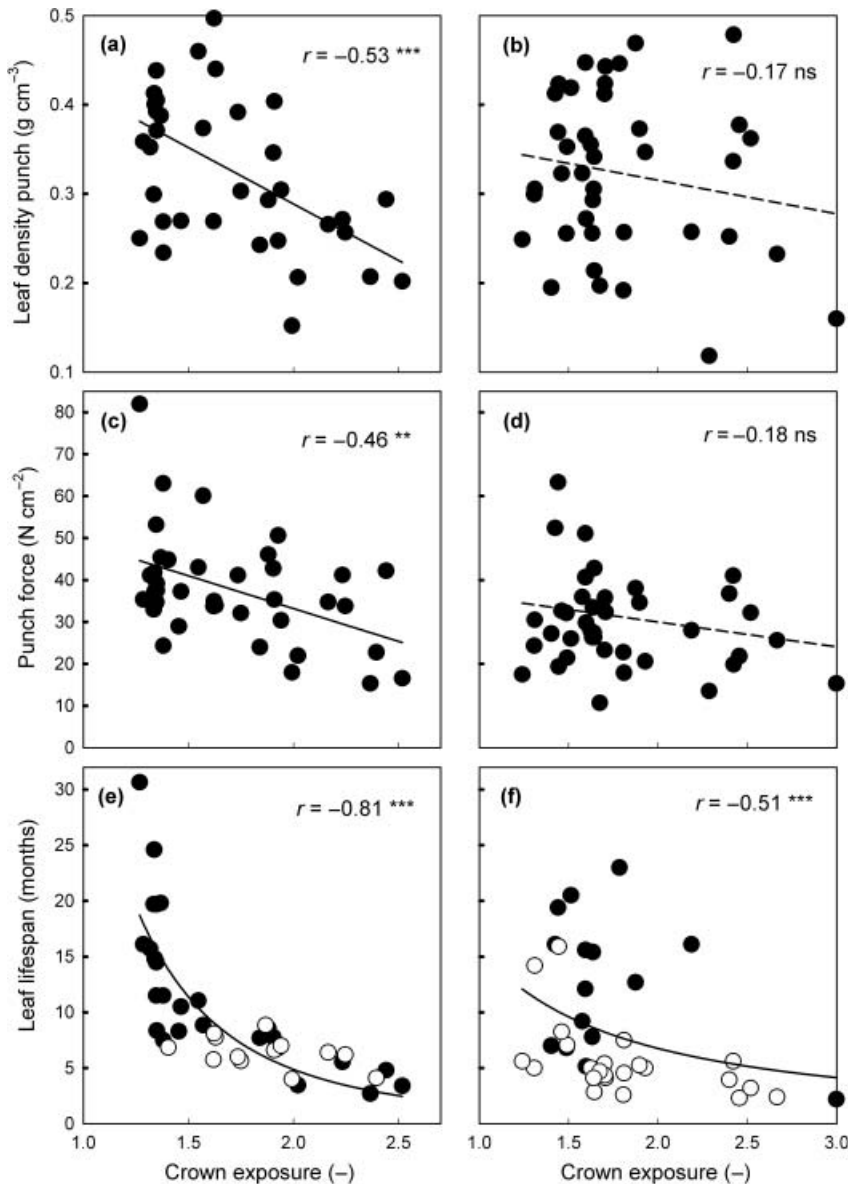


Fig. 1 Relationship between leaf traits and juvenile crown exposure (CE) for moist forest species ($n = 39$, left panels) and dry forest species ($n = 41$, right panels). (a, b) Leaf density of the punch, (c, d) punch force and (e, f) leaf lifespan for saplings. For leaf lifespan the deciduous (open circles) and evergreen species (closed circles) are shown with different symbols, because it was expected that they might show different relationships with CE. Regression lines (continuous lines are significant, and broken lines are not significant), Pearson correlations, and significance levels are given. ns, $P > 0.05$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

$P < 0.001$, $df = 24$) than for deciduous species ($r = -0.48$, $P = 0.09$, $df = 11$), and the same applied for SLA at the leaf level ($r_{\text{evergreen}} = 0.63$, $P < 0.001$; $r_{\text{deciduous}} = -0.13$, $P = 0.67$).

Light-demanding species invested, in both forests, a low fraction of their biomass in leaves (LMF_m ; Fig. 2a,b). Light-demanding species in the moist forest compensated for this low LMF_m by making leaves with a high SLA (Fig. 2c) and had, as a consequence, a high leaf area per unit metamer mass (LAR_m ; Fig. 2e). By contrast, light-demanding species in the dry forest did not compensate for a low LMF_m with their SLA (Fig. 2d), and they had, therefore, a low LAR_m (Fig. 2f).

Light-demanding species in the dry forest had high mass- and area-based N and P contents (Fig. 3b,d), whereas light-demanding species in the moist forest had only a high N_{mass} (Fig. 3a,c). Chlorophyll was only measured for the moist for-

est species. Chl_{mass} was positively correlated with CE, whereas Chl_{area} was not correlated with CE (Table 1).

Nine leaf traits were correlated with CE only in the dry forest; light-demanding species had, amongst others, long internodes, thick leaves, and a high internode area to leaf area ratio.

To evaluate which leaf traits are the best predictors of CE, a multiple forward regression analysis was performed, including all measured 26 leaf traits (Table 2). In the moist forest, four traits explained 78% of the variation in CE. Leaf lifespan was first included in the analysis, and explained most (66%) of the variation. CE was negatively related to leaf lifespan, and positively related to internode cross-sectional area, SPL, and leaf mass fraction. In the dry forest four traits explained 67% of the variation in CE. CE was positively related to internode length, and negatively related to leaf lifespan, LAR_m , and deciduousness.

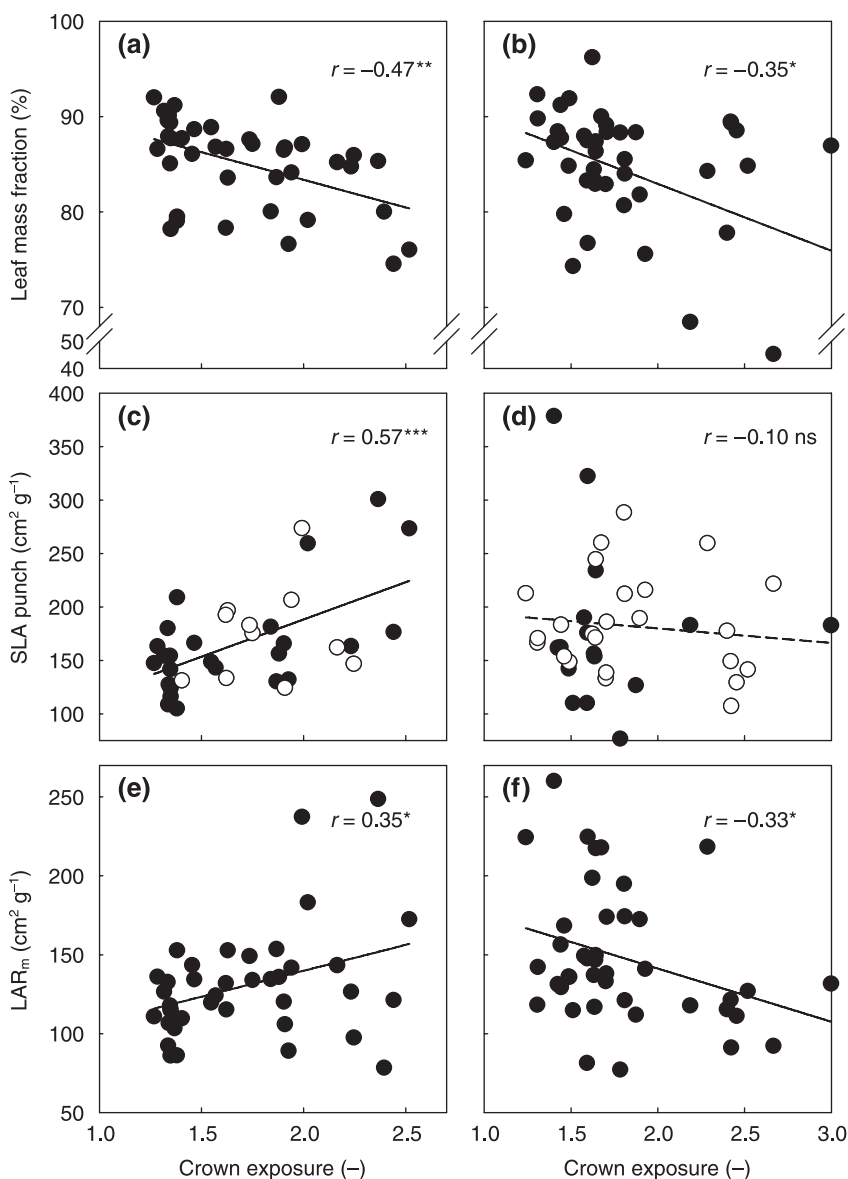


Fig. 2 Relationship between leaf traits and juvenile crown exposure (CE) for moist forest species ($n = 39$, left panels) and dry forest species ($n = 41$, right panels). (a, b) Leaf mass fraction of the metamer, (c, d) specific leaf area (SLA) of the punch, and (e, f) leaf area ratio of the metamer (LAR_m). For SLA the deciduous (open circles) and evergreen species (closed circles) are shown with different symbols, because it was expected that they might show different relationships with CE. Regression lines (continuous lines are significant, and broken lines are not significant), Pearson correlations, and significance levels are given. ns, $P > 0.05$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

Table 2 Results of a forward multiple regression of 26 traits on the juvenile crown exposure of moist forest species and dry forest species

	Moist		Dry	
	<i>b</i>	<i>r</i> ²	<i>b</i>	<i>r</i> ²
Constant	0.234		3.206	
LL	-0.969	0.66	0.104	0.29
IA	0.448	0.04	-1.021	0.17
SPL	0.003	0.04	LAR_m	0.15
LMF_m	0.019	0.03	Dec	0.06
Total		0.78		0.67

Moist forest species, $n = 36$; dry forest species, $n = 38$. The regression coefficient (*b*) and partial r^2 (r^2) are shown. LL, leaf lifespan; IA, internode cross-sectional area; SPL, specific petiole length; LMF_m , leaf mass fraction; IL, internode length; LAR_m , leaf area ratio; Dec, deciduousness. Total indicates the total explained variation of the model.

Discussion

General plant adaptations to shade

Adult leaf traits were clearly associated with the regeneration light requirements of the species, but at a given shade tolerance there was a wide scatter in trait values (Figs 1–3), indicating that there are many different ways to be a pioneer or a shade-tolerant species. Here I focus on the general trends. If the same trait correlations with regeneration light requirements are found in both forests, then it might be concluded that these traits are generally important for shade tolerance. Only eight leaf traits showed significant correlations with CE at both sites (Table 1). Light-demanding species often grow in a dense gap vegetation, characterized by strong vertical light gradients. Light-demanding species in both forests tend to have long

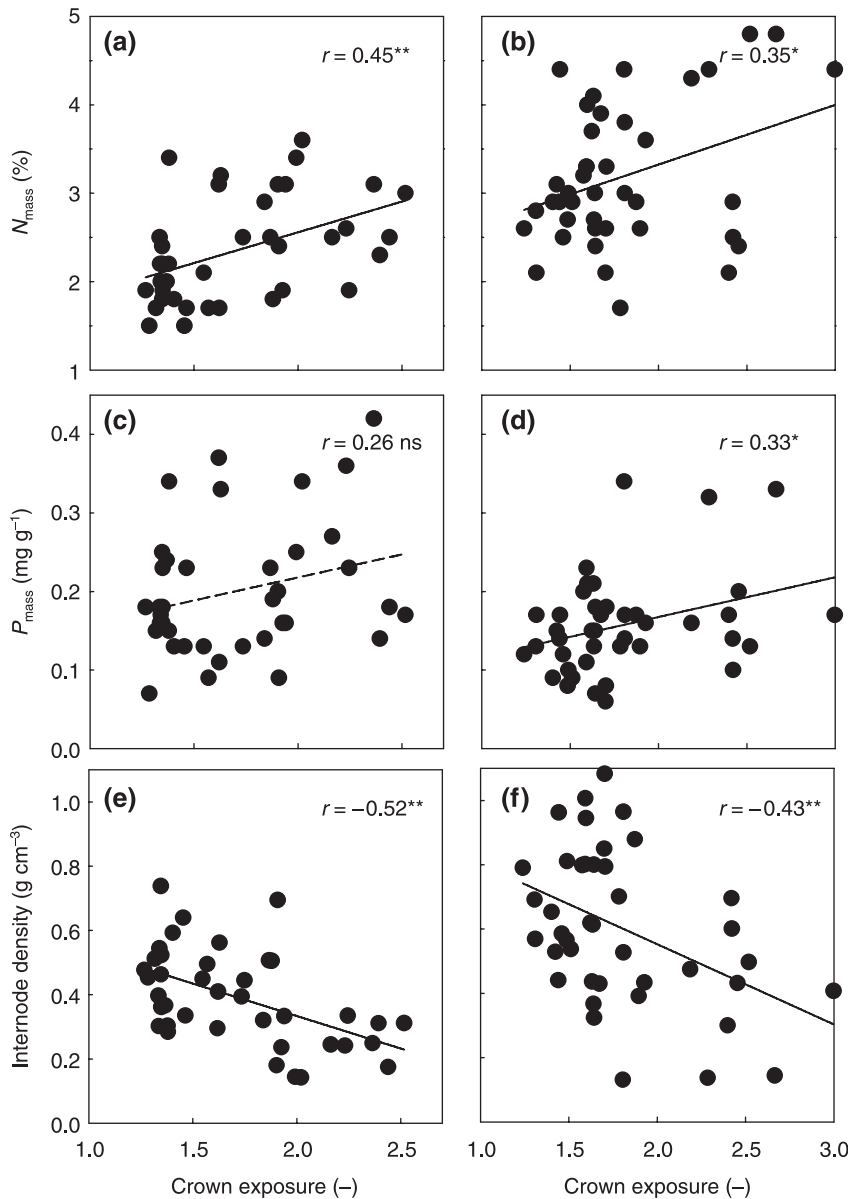


Fig. 3 Relationship between leaf traits and juvenile crown exposure (CE) for moist forest species ($n = 39$, left panels) and dry forest species ($n = 41$, right panels). (a, b) Nitrogen per unit mass (N_{mass}), (c, d) phosphorus per unit mass (P_{mass}), and (e, f) internode density. Regression lines (continuous lines are significant, and broken lines are not significant), Pearson correlations, and significance levels are given. ns, $P > 0.05$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

petioles and large leaves (Table 1), which allows them to position their leaves in the top of the gap vegetation and outshade their neighbours (Horn, 1971; King, 1998). Large leaves require a disproportional amount of structural support (Niinemets *et al.*, 2007), and light-demanding species therefore invest a large proportion of their metamer mass fraction in petioles (Table 1), to support and space their leaves. The high radiation load in gaps, in combination with the large leaf size, may enhance the transpirational demand of light-demanding species dramatically. Both a large cross-sectional internode area (Table 1) and a low internode density (Fig. 3c,d) increase the hydraulic conductance to the leaf, leading to enhanced photosynthetic rates (Santiago *et al.*, 2004). High photosynthetic rates are also enabled by a high N_{mass} (Fig. 3a,b). Shade-tolerant species have the opposite suite of traits. By investing less in

petioles they can invest a larger biomass fraction of their metamers in leaves (Fig. 2a,b). Shade-tolerant species have a high internode (i.e. wood) density, which helps them to withstand pathogens and falling debris (Augsburger & Kelly, 1984; Van Gelder *et al.*, 2006), both of which are common mortality agents in the shaded and moist forest understory. Shade-tolerant species also have low N concentrations which reduce respiration and carbon loss in the shaded forest understory (Lusk & Reich, 2000; Baltzer & Thomas, 2007a,b).

Are plant adaptations to shade stronger in the moist than in the dry forest?

It was predicted that trait correlations with CE would be strongest in the moist forest because its dense evergreen canopy

casts a deep, persistent shade, and weakest in the dry forest, because there the canopy is (seasonally) more open. A lower number of significant trait correlations was found in the moist forest compared with the dry forest, in contrast to the first prediction. Interestingly, the CE is related to different suites of traits in each forest (of all significant traits, 63% were exclusively found in one of the forest types only), suggesting that plant adaptations to shade might be fundamentally different for moist and dry forest species.

Trait correlations exclusively found in the moist forest were those related to tough and persistent leaves for shade-tolerant species, and high potential growth rates for light-demanding species. Shade-tolerant species had a low SLA, and a high leaf density, leaf dry matter content and leaf punch force (Figs 1a,c, 2c), consistent with the second prediction. This implies that leaves of shade-tolerant species are better protected against physical hazards and generalist herbivores than light-demanders (Coley, 1983; Poorter *et al.*, 2004), which may contribute to an enhanced leaf lifespan (Fig. 1e; cf. Wright & Westoby, 2002). Interestingly, leaf density and SLA showed stronger correlations with shade tolerance when measured at the punch level than at the whole-leaf level (Table 1). This suggests that physical protection of the leaf blade is more important for leaf survival than structural enforcement of the whole leaf through thick and strong veins, probably because herbivores feed preferentially on the leaf blade, rather than the veins. A comparable result was obtained by Alvarez-Clare & Kitajima (2007) who found that lamina toughness was a better predictor of seedling survival in the shade than mid-vein toughness. Empirical and modelling studies show that in the forest understory replacement of naturally shed or lost leaves is costly, and that a long leaf lifespan allows plants to maintain a positive net carbon balance and survive well, thus enhancing their shade tolerance (King, 1994; Sterck *et al.*, 2006; Baltzer & Thomas, 2007b). The importance of a long leaf lifespan in a shaded moist forest environment is underscored by the fact that it is the best predictor of species shade tolerance (Table 2) and abundance (L. Poorter *et al.*, unpublished). Light-demanding moist forest species were characterized by high SLA and LAR_m . Both traits are found to be important drivers of interspecific variation in growth (Veneklaas & Poorter, 1998; Walters & Reich, 1999), as they allow the species to intercept a lot of light, thus fuelling onward growth (Sterck *et al.*, 2006), and to outcompete their neighbours through pre-emption of resources (Schieving & Poorter, 1999). It should be noted that for these large trees only the LAR at the metamer level was evaluated. LAR at the whole-plant level is also determined by biomass investments in stems and roots, and the longevity of these components (Veneklaas & Poorter, 1998; Lusk, 2004).

Trait correlations exclusively found in the dry forest were related to crown expansion, photosynthetic carbon gain, and water relations. Light-demanding species had longer internodes, probably in order to expand their crown more rapidly

and outshade their neighbours. It is not clear why internode length is the best predictor of CE in the dry forest (Table 2). Light-demanding species had higher mass- and area-based P concentrations in the dry forest only (Table 1), probably because the dry forest soils had a low P availability, and P is known to be an important determinant of photosynthetic capacity in P-deficient soils (Raaimekers *et al.*, 1995). Light-demanding species in the dry forest had a low LAR_m , probably to reduce transpiration and water loss in a gap environment where radiation loads are high and in a macroclimate where the vapour pressure deficit is high and the water availability is low. They also had a high cross-sectional internode area per leaf area (IALA; Table 1), which implies that they had a higher transport capacity per unit leaf area, to assure sufficient water supply to the leaves.

What confers shade tolerance; maximization of low-light growth or low-light survival?

There is considerable debate as to whether species partitioning of the light gradient is mediated by a trade-off between survival and growth (Kitajima, 1996; Baraloto *et al.*, 2005; Seiwa, 2007) or by a trade-off between growth in low and high light (Popma & Bongers, 1988; Niinemets, 2006). According to the first hypothesis, shade tolerance should be enhanced by traits related to storage and defence (Kitajima, 1996; Kitajima & Poorter, 2008), and according to the second hypothesis, shade tolerance should be enhanced by traits that maximize light interception and minimize respiration in low light (Givnish, 1988). It has also been suggested that the second trade-off becomes more important when plants increase in size (Grubb, 1998; Sack & Grubb, 2001; Lusk, 2004).

The current study shows that, in moist forest, shade-tolerant species invest their biomass in tough and durable tissues (high internode and leaf density), which may result in enhanced survival. The consequence of these investments is low light interception at the leaf (low SLA) and metamer (low LAR_m) levels, thus compromising the potential growth rate. Similar results have been found for seedlings and saplings growing under controlled conditions or in the field (Kitajima, 1994; Poorter *et al.*, 2004; Poorter & Bongers, 2006; Alvarez-Clare & Kitajima, 2007), thus lending strong support to the importance of the growth–survival trade-off for light partitioning (the third prediction made in the Introduction).

The strong differences in opinion about whether light gradient partitioning is driven by a trade-off between growth and survival or by a trade-off between low and high light growth might also be caused by the different study systems used (Valladares & Niinemets, 2008). In evergreen tropical rain forests that experience little seasonality, species may differ tremendously in their leaf lifespan (from a few months to several years). However, in temperate winter-deciduous forests the leaf lifespan of nearly all broad-leafed species is constrained to 5–7 months (Kikuzawa, 1983). For deciduous shade-tolerant

species it would make little sense to make expensive, tough, and well-protected leaves. Under those conditions a positive relationship between SLA and shade tolerance is found (Janse-ten Klooster *et al.*, 2007; Lusk & Warton, 2007), which suggests that a trade-off between low and high light growth might play a role in such systems. A similar argument could be applied to tropical dry deciduous forests. However, in this forest community, the shorter leaf lifespan of adult leaves led to a lack of a relationship between SLA and shade tolerance in the dry forest (Fig. 1d), in contrast to the prediction. Interestingly, LAR_m was positively correlated with CE in the moist forest, and negatively correlated with CE in the dry forest (Fig. 2e,f). Light-demanding species in the moist forest had a high LAR_m to fuel growth, whereas light-demanding species in the dry forest had a low LAR_m , probably to reduce transpiration and water loss. The fact that in the dry forest shade-tolerant species possessed larger LAR_m suggests that a trade-off between low and high light growth may play a role in forests that are under stronger climatic control (e.g. drought-deciduous and winter-deciduous forests; cf. Niinemets, 2006).

Conclusions

Adult leaf traits were clearly associated with shade tolerance, although the correlations were weaker than reported for seedling leaf traits. Leaf traits varied continuously with shade tolerance, thus potentially contributing to fine-tuned light partitioning. Rather than stronger shade adaptations in the moist forest, I found different shade adaptations in the moist and dry forest species. Shade adaptations exclusively found in the moist semi-evergreen forest were related to tough and persistent leaves, and shade adaptations in the dry deciduous forest were related to high light interception and water use. This suggests that, along the climatic gradient, there is a shift in the relative importance of the mechanisms that control light partitioning; in moist evergreen forest the growth-survival trade-off governs light partitioning, whereas in seasonally deciduous forest the low-high light growth trade-off might become important.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Table S1 List of the 39 moist forest species and 41 dry forest species included in this study

Table S2 Results of an analysis of covariance (ANCOVA), with leaf traits as dependent variable, leaf habit (deciduous/evergreen) as factor, juvenile crown exposure (CE) as covariate, and the interaction between leaf habit and CE

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