

Biomass allocation and leaf life span in relation to light interception by tropical forest plants during the first years of secondary succession

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Summary

1. We related above-ground biomass allocation to light interception by trees and lianas growing in three tropical rain forest stands that were 0.5, 2 and 3-year-old regeneration stages after slash and burn agriculture.
2. Stem height and diameter, leaf angle, the vertical distribution of total above-ground biomass and leaf longevity were measured in individuals of three short-lived pioneers (SLP), four later successional species (LS) and three lianas (L). Daily light capture per individual (Φ_d) was calculated with a canopy model. Mean daily light interception per unit leaf area (Φ_{area}), leaf mass ($\Phi_{\text{leaf mass}}$) and above-ground mass (Φ_{mass}) were used as measures of instantaneous efficiency of biomass use for light capture.
3. With increasing stand age, vegetation height and leaf area index increased while light at the forest floor declined from 34 to 5%. The SLP, *Trema micrantha* and *Ochroma pyramidale*, dominated the canopy early in succession and became three times taller than the other species. SLP had lower leaf mass fractions and leaf area ratios than the other groups and this difference increased with stand age.
4. Over time, the SLP intercepted increasingly more light per unit leaf mass than the other species. Lianas, which in the earliest stage were self-supporting and started climbing later on, gradually became taller at a given mass and diameter than the trees. Yet, they were not more efficient than trees in light interception.
5. SLP had at least three-fold shorter leaf life spans than LS and lianas. Consequently, total light interception calculated over the mean life span of leaves ($\Phi_{\text{leaf mass total}} = \Phi_{\text{area}} \times \text{SLA}_{\text{death leaves}} \times \text{leaf longevity}$) was considerably lower for the SLP than for the other groups.
6. *Synthesis.* We suggest that early dominance in secondary forest is associated with a high rate of leaf turnover which in turn causes inefficient long-term use of biomass for light capture, whereas persistence in the shade is associated with long leaf life spans. This analysis shows how inherent tradeoffs in crown and leaf traits drive long-term competition for light, and it presents a conceptual tool to explain why early dominants are not also the long-term dominants.

Key-words: biomass allocation, Bolivian Amazon, canopy model, leaf longevity, lianas, light interception, pioneers, leaf mass ratio, secondary succession, tropical forest

Introduction

During the fallow period of slash-and-burn agriculture in tropical forests, both herbaceous and woody plant species rapidly colonize the site. Short-lived pioneer trees (SLP)

establish early in succession and dominate the canopy throughout the first 10–20 years. Long-lived pioneer trees and some late successional species are also present from the early stage onwards, initially grow in the shade of the SLP but replace them in the top of the canopy later in succession (Whitmore 1989). Lianas are thought to be more abundant in early successional forest than in old growth forest (Putz 1984;

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De Walt *et al.* 2000). These changes in size probably result, in part, from differences in morphology and biomass investment patterns between species and from inherent differences in growth rates.

In this study, we focus on the effects of differences in the morphology and investment patterns of species during the first 3 years of secondary succession. Vegetation height, leaf area index and basal area increase and light at the forest floor decreases as succession proceeds (Brown & Lugo 1990, Saldarriaga 1994; Peña-Claros 2003). Hence, competitive interactions for light probably play an important role in determining the course of succession (Werger *et al.* 2002). Species that are able to grow tall can deploy their foliage in the upper layers of the canopy and capture the greater part of available photosynthetically active radiation (Hirose & Werger 1995). Investment in height improves access to light but incurs construction and maintenance costs (Givnish 1982).

Much research has focussed on understanding the mechanisms by which tree species differing widely in height coexist in tropical forest. Early studies (Horn 1971; Kohyama 1987; Kohyama & Hotta 1991) focussed on how crown structure influenced light acquisition. It was proposed that shade tolerant species should have shallow broad crowns with minimal leaf overlap thus maximizing light capture. Conversely, sun species should produce narrow crowns investing more of their resources in vertical growth by which they are better able to compete with neighbours and thus secure future light acquisition (Kohyama 1987; Kohyama & Hotta 1991; Sheil *et al.* 2006). Contrary to these predictions, later successional shade tolerant species are often found to have deeper crowns with more layers than pioneer species (e.g. Kitajima *et al.* 2005; Sterck *et al.* 2006). To maintain rapid growth, pioneers may have to shed older leaves and branches and reallocate resources to support new leaf growth in the canopy (Kikuzawa 1995; Kitajima *et al.* 1997, 2002; Hikosaka 2005; Boonman *et al.* 2006; Sterck *et al.* 2006), the result being a relatively shallow crown. For shade tolerant species the production of a broad crown may not only facilitate efficient light capture but may also entail additional costs of producing extra branches (Valladares *et al.* 2002).

A further understanding of how light competition between species shapes succession requires a quantitative analysis relating biomass allocation, crown structure and biomass turnover to light acquisition. Hirose and Werger (1995) used a modelling approach to compare above-ground biomass expenditure to light acquisition for different species coexisting in a temperate grassland. They found that on a daily basis short subordinate species absorbed less light per unit of leaf area (Φ_{area}) than did tall dominant species but equal or more light per unit of above-ground mass (Φ_{mass}) (Hirose & Werger 1995; Anten & Hirose 1999). Similar Φ_{mass} values between short and tall species were also observed in several young secondary tropical forest stands (Selaya *et al.* 2007; van Kuijk *et al.* 2008). However, this similarity in mass-use efficiency for light capture appears to be limited to relatively open stands (with LAI values of less than 2.5 to 3.5) (Anten & Hirose 1999; Werger *et al.* 2002; Aan *et al.* 2006). In such stands,

enough light penetrates to deeper layers of the canopy such that shorter species can compensate for a lower Φ_{area} by having a large leaf area per unit mass (LAR). The question arises how light capture efficiencies will compare between different species as the LAI increases during succession.

Lianas use other plants for support, and thus need to invest less in thickening their stems and branches than do self-supporting species. Consequently, they can achieve greater length per unit of stem biomass and allocate a larger proportion of their resources to production of additional leaves or to reproduction than can self-supporting species (Putz 2005). This suggests that lianas might exhibit greater light capture per unit of mass than trees. Yet only one study (Selaya & Anten 2008) has tested this idea and found that in a 4-year-old successional forest stand, lianas were more efficient than later successional species but not when compared with SLP.

In the studies listed above, light capture relative to mass (Φ_{mass}) was calculated based on the standing biomass at a single point in time. They therefore do not account for costs associated with the continuous production and loss of leaves and branches, the rate of which, as noted above, may differ strongly between species. Consequently, it is important to analyse the long-term biomass-use efficiency for light capture including costs associated with turnover as well as the changing light climate during succession (Niinemets 2006).

We hypothesize that early dominance of species in a regenerating secondary forest is associated with biomass allocation patterns that facilitate a high instantaneous light interception at leaf level. As the vegetation becomes denser and taller during the first years of succession a strong investment of biomass and a high leaf turnover will be necessary to maintain this efficiency. Consequently, we hypothesize that SLP will have a lower long-term efficiency for biomass use of light capture than later successional species (LS). We also expect that once climbing lianas species, given their habit to rely on trees for support, will have higher Φ_{mass} compared to the LS but not compared to the SLP. To test these hypotheses we employ a canopy model based on earlier grasslands models, modified to incorporate specific features of forest trees. This model incorporates the dynamics of the leaf turnover, albeit in a simplified manner, and thus enables us to quantify long-term use of biomass for light capture ($\Phi_{\text{leaf mass total}}$, the amount of light captured during a leaf's life). In combination with field measurements this model enables us to relate interspecific differences in biomass allocation, crown structure, leaf inclination angles, and leaf turnover to light interception.

Methods

MODEL CALCULATIONS OF WHOLE-PLANT LIGHT INTERCEPTION

Model calculations were used to estimate daily light interception of individual plants both in absolute terms and per unit leaf area and mass, and above-ground mass. To this end, we used the model from Selaya *et al.* (2007). A detailed explanation can be found there, and

Table 1. List of most common symbols and abbreviations

Variables	Definition	Units
LAI	Leaf area index	m ² m ⁻²
SLA	Specific leaf area	cm ² g ⁻¹
LMR	Leaf mass ratio	g g ⁻¹
LAR	Leaf area ratio	cm ² g ⁻¹
PPFD	Photosynthetically photon flux density	mol m ⁻² s ⁻¹
Φ_d	Light attained by an individual plant per day	mol plant ⁻¹ day ⁻¹
Φ_{area}	Light per leaf area per day	mol m ⁻² day ⁻¹
$\Phi_{\text{leaf mass}}$	Light per leaf mass per day	mol g ⁻¹ day ⁻¹
Φ_{mass}	Light per total above-ground mass per day	mol g ⁻¹ day ⁻¹
$\Phi_{\text{leaf mass total}}$	Total light per leaf mass per mean leaf longevity	mol g ⁻¹

we only briefly describe it here. The model is very similar to previous two-dimensional canopy models (e.g. Anten 1997; Depury & Farquhar 1997). It considers 9 m² subplots around target plants and thus assumes that within these plots vegetation structure is horizontally homogeneous. Based on light measurements, we found this to be a reasonable assumption for our stands. The model assumes horizontal layers of 0.25 m thickness, and calculates the light interception of target plants within each layer as a function of its leaf area and leaf angle distribution and that of the other plants in the subplot (see eqns 1–8 in Selaya *et al.* (2007)). This calculation takes differences in leaf angle and vertical leaf area distribution between target individuals and surrounding vegetation into account. Whole plant light capture is calculated as the summation of the light attained in every layer (eqn 9 in Selaya *et al.* (2007)). This value was subsequently integrated over the day (Φ_d), taking account of the daily courses of direct and diffuse irradiance above the canopy and the solar inclination as a function of the latitude (11° S 66.1° W) and date following Gates (1980).

Light interception per unit of area Φ_{area} , leaf mass $\Phi_{\text{leaf mass}}$ and total above-ground mass Φ_{mass} were calculated by dividing Φ_d by the leaf area (A), leaf mass (LM) and total above-ground mass (M) (Hirose & Werger 1995; Selaya *et al.* 2007) as:

$$\Phi_{\text{area}} = \frac{\Phi_d}{A} \quad \text{eqn 1}$$

$$\Phi_{\text{leaf mass}} = \frac{\Phi_d}{LM} \quad \text{eqn 2}$$

$$\Phi_{\text{mass}} = \frac{\Phi_d}{M} \quad \text{eqn 3}$$

These parameters were interpreted as instantaneous efficiencies of leaf area or biomass use for light interception (Hirose & Werger 1995). We also estimated total efficiency of biomass use for light interception as the total amount of light intercepted over the mean time that a leaf spends on the plant ($\Phi_{\text{leaf mass total}}$, mol g⁻¹). This efficiency was calculated by multiplying the amount of light per leaf area intercepted daily, with the SLA of death leaves and the mean leaf life spans ($\text{Leaf}_{\text{long}}$).

$$\Phi_{\text{leaf mass total}} = \Phi_{\text{area}} * SLA_{\text{dead leaves}} * \text{Leaf}_{\text{long}} \quad \text{eqn 4}$$

This calculation was done for the seven species for which we had leaf turnover data (*Trema*, *Ochroma*, *Cecropia*, *Couratari*, *Rinereocarpus*, *Brosimum* and *Uncaria*, see full species names below). The Φ_{area} value in this calculation is the combined average for the three stages.

Thus, our calculation represents the first 3 years of succession only. The $SLA_{\text{dead leaves}}$ was introduced in the model to account for the cost in leaf biomass construction. It was determined on fully yellowed, non-withered leaves that were about to drop of the branch. The latter was determined by testing how easily they drop off the plant. Table 1 presents a list of the most common symbols.

STUDY SITE AND PLANT MATERIAL

We studied three secondary forest stands of 0.5, 2 and 3-year-old after field abandonment, growing near Riberaltá, in the Bolivian Amazon (11° S 66.1° W). Mean annual temperature is 26 °C and rainfall 1780 mm with a dry season lasting from May to September (Selaya 2007). The forest has been classified as lowland evergreen forest (Hueck & Sebert 1972).

Many of the results for the youngest stand are taken from Selaya *et al.* (2007) and are used here for comparative purposes only. The stands were all forest regeneration stages in a slash-and-burn cycle and had been cultivated with rice, maize and cassava for about 3 years prior to abandonment. In each stand, plots of 0.75 ha at least 20 m away from the edge were selected to avoid the influence of the surrounding forest. All the stands were surrounded by old growth forest. Because this study includes data from only three successional stands, the generality of the conclusions that can be drawn about these forests is somewhat limited.

In each stand, 10 of the most common species were selected based on an inventory of the species composition in a number of plots of secondary forest stands from 1–25 years and also in mature forest (N.G. Selaya, unpublished data) and on a previous study on species diversity and abundance along a chronosequence (Peña-Claros 2003). *Trema micrantha*, *Ochroma pyramidale* and *Cecropia ficifolia* were found to be present from land abandonment to about 4–25 years and were denoted as short-lived pioneers (SLP). *Couratari guianensis*, *Rinereocarpus ulei*, *Brosimum lactescens* and *Pseudolmedia laevis* were common from land abandonment but showed a peak in abundance between 30–100 years. The latter species was classified as shade tolerant by Peña-Claros (2003). To avoid any confusion in terminology we denote all four species as later successional (LS, i.e. later than the SLP). The lianas (L) *Uncaria guianensis*, *Combretum gracilis*, and *Adenocalymma impressum* showed an occurrence pattern similar to the LS but were treated as a separate group due to their climbing growth habit. Hereafter species are named by their generic name only.

In each stand, we selected 10–20 individuals per species of different heights such that they covered the height range with which each species occurred in the stand. We carefully avoided resprouts as these

Table 2. Vegetation height, LAI (leaf area index) and light (PPFD) at the forest floor of secondary forest stands of 0.5, 2 and 3 years old. Different letters denote differences at $P < 0.05$

Year	Vegetation height (cm)			LAI (m ² m ⁻²)			PPFD at forest floor (%)		
	N	Mean	SE	N	Mean	SE	N	Mean	SE
0.6	63	177	5.45a	60	1.66	0.06a	61	34.36	4.40a
2	60	606	17.41b	71	3.54	0.10b	79	5.20	0.39b
3	59	781	18.06c	61	3.68	0.11b	58	4.74	0.30b

may have a different carbon balance than plants growing from seeds. Each sampled individual had germinated within 3 months after field abandonment.

CANOPY STRUCTURE AND LIGHT (PPFD) DISTRIBUTION IN SUBPLOTS

Canopy structure and light distribution were determined during the rainy season following Selaya *et al.* (2007). In each stand about 60 subplots of 9 m² were established (in line with the model assumption, see above) such that they contained at least one of the selected plants (Table 2). Photosynthetic Photon Flux Density (PPFD, 400–700 nm) was measured at vertical increments of 25 cm in each of the subplots with an SF 80 Line Sensor (Decagon devices Ltd., UK). PPFD above the canopy was measured simultaneously with a point Li-190 SA Quantum sensor (LiCor, Lincoln, USA) connected to a data logger LI1000 (LiCor). Average leaf area index (LAI, m² m⁻²) and average leaf angle distribution in each subplot were measured with the LAI-2000 Plant Canopy Analyzer (LiCor). An above canopy measurement followed by four below canopy measurements, viewing from each corner to the centre of the subplot was taken. A view cap of 45° was used to restrict the lens field of view. PPFD and LAI measurements were taken under an overcast sky or at sunset. The vertical distribution of leaves in the canopy was measured using the point method, lifting a scaled pole from the bottom to the top of the canopy and recording the height at which the tip of the pole touched a leaf. The procedure was repeated at the centre of every square meter of each 9 m² subplot, for nine replicates per subplot.

STEM TRAITS, CROWN STRUCTURE AND ABOVE-GROUND BIOMASS ALLOCATION IN INDIVIDUAL PLANTS

Total height, height at the first leaf or branch with leaves, stem diameter at 0.3 and 1.30 m height were measured on all target plants. When individuals did not reach 0.3 m height, the stem diameter was measured at 10 cm. Individuals were stratified in horizontal layers of 0.25 m and the inclination angles of five randomly selected leaves were measured in each layer using a hand-held protractor. The distribution of the above-ground biomass was determined by means of destructive harvesting. Individuals were harvested and clipped every 0.25 m in height. The samples of stems, branches, petioles and leaves of each 0.25 m layer thus obtained were put separately in plastic bags and kept fresh to be processed in the laboratory. Digital photographs of a representative sample of leaves were taken. Leaf area was calculated using the Sigma Scan Pro 5 (SPSS Inc). All samples were then oven dried at 70 °C for about 5 days and weighed to obtain the dry mass values. Thus light capture of individual plants could be calculated as a function of their vertical leaf area distribution relative to the distribution of the total leaf area in the subplot.

For each individual the leaf mass ratio LMR (leaf mass per above-ground mass, in g g⁻¹), specific leaf area SLA (leaf area per leaf mass, in cm² g⁻¹) and leaf area ratio LAR (leaf area per above-ground mass, in cm² g⁻¹) were calculated. Crown depth (fraction of stem length with leaves to total stem length, in %) was also calculated. Stem dry mass density was estimated for segments that ranged between 30 to 100 cm in length. The volume was calculated as $0.25D^2\pi L$, where L is the segment length and D the diameter measured in the middle of the segment.

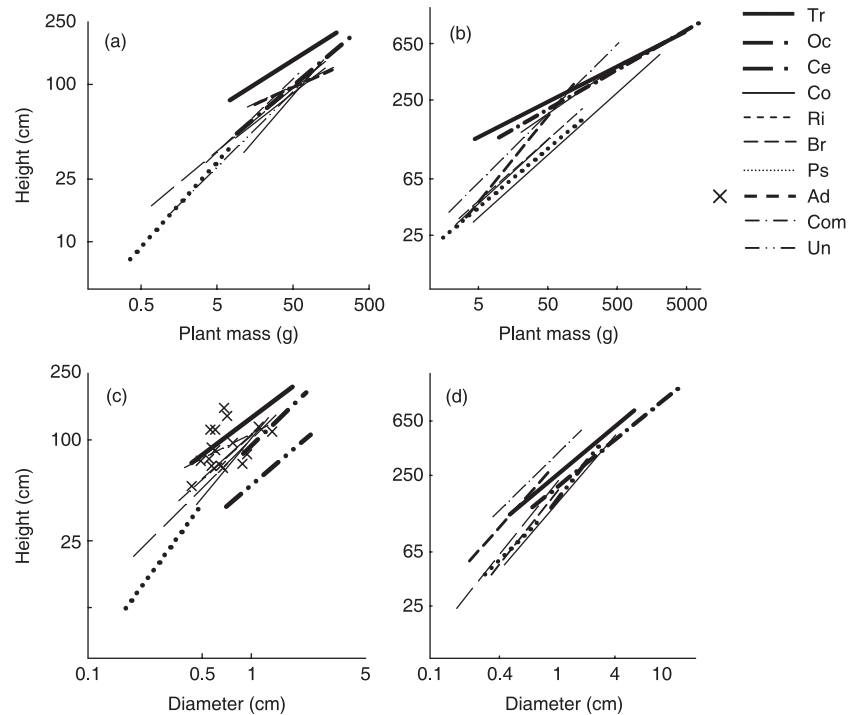
LEAF LONGEVITY

Leaf longevity was measured on twenty individuals of each species. Individuals grew within the 6 months old stand, which was 20 months old at the end of the leaf dynamics measurements. Leaf dynamics were followed on cohorts on each branch of the selected plants. At the first census we counted the leaves on each cohort and marked the newest one. Every 60 days, the number of leaves lost, and newly produced leaves were counted and the youngest expanded leaf was marked. These censuses were repeated every 60 days for a period of 12–14 months. Leaf life span was calculated as the number of leaves on the plant, divided by the average of the leaf production and the leaf death rate (eqn 15 in King 1994). Dead or yellow leaves that were still on the plant were collected and their area and weight was measured. For the tree *Pseudolmedia* and the two lianas *Combretum* and *Adenocalymma*, we did not obtain sufficiently accurate data, and leaf longevity and associated calculations are thus only presented for the other seven species.

STATISTICS

Differences in vegetation height, LAI and PPFD at the forest floor between stands were tested with an ANOVA. Pair-wise *post hoc* Bonferroni tests were used to test differences among stand pairs. Within each stand the effect of species on height, biomass, diameter, crown depth, Φ_d , Φ_{area} , $\Phi_{leaf\ mass}$, Φ_{mass} and $\Phi_{leaf\ mass\ total}$ were tested with a mixed general linear model ANOVA. As individuals sampled within each subplot (see above) were not statistically independent, subplot was entered as a random factor. Variables were log transformed to meet the assumptions of homogeneity of variances of the Levene's test. Species effects on leaf longevity were tested with a one-way ANOVA as plants used for this measurement were not selected in subplots. Pair-wise *post hoc* Sidak tests were used to test differences among species. A second-order polynomial regression was done to test the linearity of the relationships between height, biomass, and diameter. ANCOVA was applied with height as the dependent variable and diameter and above-ground biomass as covariates, as well as an ANCOVA with LMR, LAR, SLA, Φ_d , and Φ_{area} as the dependent variables and either height or mass as covariates with species as a fixed factor and subplot as a random factor.

Fig. 1. Relationship between height and above-ground mass (a, b) and between height and diameter (c, d) for trees and lianas in a 6-month-old (a, c) and a 3-year-old (b, d) secondary forest stand. *Tr* denotes *Trema micrantha*, *Oc* *Ochroma pyramidale*, *Ce* *Cecropia ficifolia* all short-lived pioneers (SLP). *Co* denotes *Couratari guianensis*, *Ri* *Rinereocarpus ulei*, *Br* *Brosimum lactescens*, *Ps* *Pseudolmedia laevis* all later successional species (LS). *Ad* denotes *Adenocalymma impressum*, *Com* *Combretum gracilis* and *Un* *Uncaria guianensis* all liana species. Lines denote significant regressions and symbols per plant values where linear regression was not significant. Panels (a) and (c) redrawn from Selaya *et al.* (2007).



In the regression analyses the choice of independent vs. dependent variable was based on causal relationships assumed in the model. Height and light interception were analysed as dependent variables against mass or diameter (in the case of height) as independent variables, to indicate how efficiently a given amount of mass is converted into height or used for light interception. SLA, LMR and LAR ($\text{LAR} = \text{SLA} \times \text{LMR}$) were analysed against height, because we assumed that due to biomechanical constraints, as plants grow taller, they have to invest disproportionately in support at the expense of leaves (LMR) and because height is strongly correlated with light availability (SLA).

Results

CANOPY STRUCTURE AND LIGHT VERTICAL DISTRIBUTION

The stands differed in canopy height, LAI (leaf area index) and percentage of light at the forest floor (ANOVA at $P < 0.05$, Table 2). Canopy height increased with the time after field abandonment from 1.8 m at 6 months to 7.8 m at 3 years succession. The mean leaf area index (LAI) increased from 1.7 to 3.7 and light (PPFD) at the forest floor decreased from 34% at 6 months to 4.5% at 3 years. The LAI and light at the forest floor differed significantly in the stand of 6 months compared with the stands of 2 and 3 years old but not between the two older stands.

ALLOMETRY AND BIOMASS ALLOCATION

The species differed in height, stem diameter and above-ground mass in all the three stands (ANOVA at $P < 0.05$, Table 3). The SLP *Trema* and *Ochroma*, which were the most

frequent species across all stands, were the tallest and the ones with the greatest above-ground mass. Differences in height between these two species and the others, including the other SLP *Cecropia*, gradually increased with stand age. *Pseudolmedia* was the shortest species and its individuals had the lowest mass in all stands except in the 3-year-old one where *Rinereocarpus* showed the lowest mass values. Plant height differed considerably within species. For the tallest species *Ochroma* the height range was 0.5–2.2 m and 1.0–9.9 m and for the shortest species *Pseudolmedia* it was 0.1–0.6 m and 0.4–1.9 m in the 0.5 and 3 y/o stands respectively. The dominant species *Trema* and *Ochroma* had shallower crowns than LS and liana species (data not shown).

Height was positively related with mass and diameter (Fig. 1 only the 6-month and 3-year-old stand shown). The analysis of covariance (ANCOVA) showed heterogeneity of slopes among species in the relationship between height and mass in the 3-year-old stand and difference in intercept between species for the height to mass relationship in the other two stands. In all three stands there was a species effect on the intercept of the height vs. diameter relationship (Table 4).

In the 0.5-years-old stand, the individuals of SLP *Trema* were taller relative to their mass than the other species (Fig. 1a), but this was not the case in the 2 and 3-year-old stands (Fig. 1b). In the 3-year-old stand the lianas *Combretum* and *Adenocalymma*, showed a steeper increase in height with biomass than other species (Fig. 1b). *Combretum* was also taller relative to its diameter (Fig. 1d).

LMR (leaf mass ratio) and LAR (leaf area ratio) were negatively related with height in all three stands. The SLP had lower LMR at a given height than the species of the other

Table 3. Mean height, above-ground mass, stem diameter, leaf mass ratio (LMR), specific leaf area (SLA), leaf area ratio (LAR) and whole-plant daily light interception (Φ_d) of three short-lived pioneer species (SLP), four later successional species (LS) and three lianas (L) in stands of 0.5, 2 and 3 years old. Different letters denote differences between species within a successional stage at $P < 0.05$ after Sidak or Games Howell (G-H) tests

	Stand age	<i>Trema</i> (SLP)		<i>Ochroma</i> (SLP)		<i>Cecropia</i> (SLP)		<i>Couratari</i> (SLP)		<i>Rinereocarpus</i> (LS)	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Height (cm)	0.5	140.13	12.22a	129.22	12.56a	73.71	7.31abc	96.59	8.18ab	86.27	9.37abc
	2	344.93	39.31a	307.71	43.53ab	228.86	29.69abc	172.78	16.35b	138.41	15.08cd
	3	477.11	42.40a	524.65	64.47a	252.22	22.69ab	165.15	24.77bcd	69.94	8.14d
Mass (g)	0.5	63.50	14.63abc	115.76	20.68a	38.07	9.02abc	67.83	9.53ab	27.35	4.03bc
	2	447.54	171.47a	576.24	200.34a	138.63	35.50ab	170.53	32.53ab	132.73	41.57ab
	3	1163.59	300.96a	2443.41	807.92a	137.40	38.76b	337.69	136.03b	16.39	3.49c
Diameter (cm)	0.5	1.00	0.10bc	1.40	0.11a	1.39	0.09ab	0.88	0.07cd	0.67	0.05cde
	2	2.13	0.30ab	3.01	0.50ab	1.81	0.21ab	1.35	0.10abc	0.95	0.11cd
	3	3.07	0.34a	5.19	0.99a	1.82	0.12ab	1.50	0.24bc	0.53	0.05e
LMR	0.5	0.36	0.02d	0.39	0.02d	0.37	0.02d	0.61	0.02ab	0.47	0.03cd
	2	0.11	0.01g	0.21	0.02f	0.26	0.03ef	0.50	0.02ab	0.36	0.03cd
	3	0.09	0.01e	0.14	0.01d	0.21	0.01c	0.50	0.02a	0.52	0.03a
SLA (cm ² g)	0.5	188.19	5.42abc	151.29	2.79c	153.41	2.36c	121.12	2.29de	227.67	6.17a
	2	197.40	9.46ab	171.50	6.47bc	205.71	12.59ab	128.28	4.04d	247.56	6.44a
	3	187.42	10.75bcd	172.18	11.36bcd	217.00	7.28b	138.05	5.14e	291.24	11.57a
LAR (cm ² g)	0.5	68.24	4.96cd	58.65	3.18d	57.15	3.50d	73.76	2.52bcd	106.38	7.62ab
	2	20.57	1.85e	35.41	4.08d	55.58	7.84cd	64.79	4.00bc	91.05	7.33ab
	3	15.36	1.03f	23.69	2.96f	44.49	2.79e	69.55	4.73cd	155.79	12.39a
Φ_d (mol day ⁻¹)	0.5	9.83	2.15ab	18.11	4.01a	4.30	1.21bc	9.04	1.52ab	4.36	0.75bc
	2	14.62	6.30ab	24.57	10.00a	3.88	1.34abc	4.20	0.95ab	4.89	1.25ab
	3	38.67	11.92ab	94.40	31.35a	3.97	1.18bc	6.17	2.53bc	0.34	0.05c

	Stand age	<i>Brosimum</i> (LS)		<i>Pseudolmedia</i> (LS)		<i>Adenocalymma</i> (L)		<i>Combretum</i> (L)		<i>Uncaria</i> (L)	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Height (cm)	0.5	64.53	9.41b	22.38	3.27d	95.84	6.82ab	97.13	6.01ab	60.13	10.24c
	2	146.00	23.24cd	74.20	8.57e	139.80	26.18de	216.61	24.94abc	196.27	35.75bcd
	3	88.74	13.59cd	80.21	11.71cd	175.45	27.22bc	289.37	29.72ab		
Mass (g)	0.5	29.60	10.05c	3.05	0.76d	52.10	8.96ab	56.85	10.89ab	32.47	9.87c
	2	89.46	33.02bc	15.57	3.40c	51.11	10.67bc	89.61	20.47ab	131.19	34.53ab
	3	35.58	12.23bc	32.70	10.75bc	48.25	8.16bc	123.74	28.81bc		
Diameter (cm)	0.5	0.63	0.09e	0.30	0.03f	0.71	0.06cde	0.78	0.06cde	0.79	0.08de
	2	0.67	0.09d	0.41	0.05e	0.66	0.06d	0.75	0.07d	1.06	0.14bcd
	3	0.55	0.08e	0.63	0.08de	0.64	0.06d	0.96	0.10cd		
LMR	0.5	0.58	0.02abc	0.72	0.02a	0.53	0.02bc	0.49	0.02bc	0.61	0.03ab
	2	0.38	0.03bcd	0.58	0.03ab	0.46	0.02abc	0.34	0.03de	0.36	0.02bcd
	3	0.49	0.03a	0.61	0.02a	0.47	0.01a	0.31	0.02b		
SLA (cm ² g)	0.5	145.27	5.29cd	173.62	5.20b	117.32	3.21e	124.73	3.16de	172.75	9.65bc
	2	170.80	6.12bc	187.38	7.80bc	133.33	5.73d	148.76	8.23cd	214.60	13.05ab
	3	190.95	6.18bc	187.64	7.16bcd	145.71	3.45d	180.00	13.13cde		
LAR (cm ² g)	0.5	84.51	5.23bc	125.65	6.09a	61.44	2.22cd	61.58	3.41cd	107.31	9.69a
	2	64.68	5.52bc	111.90	7.85a	62.42	4.47bc	49.19	4.55cd	77.70	6.38ab
	3	92.34	5.47bc	115.27	7.47ab	69.21	2.65cd	47.69	3.83de		
Φ_d (mol day ⁻¹)	0.5	2.87	0.85c	0.32	0.07d	5.15	0.82abc	7.28	1.78ab	3.66	1.09bc
	2	1.65	0.57bcd	0.44	0.13d	0.95	0.42cd	1.09	0.28bcd	2.54	0.76bcd
	3	0.61	0.18c	0.94	0.43c	0.61	0.13c	3.08	0.9bc		

groups (Fig. 2a,b). In the 6-month-old stand LAR was also lower at a given height for the SLP *Ochroma* and *Cecropia*, and this difference increased over time (Fig. 2c,d). Generally ANCOVA showed species differences in the intercepts of the relationship LMR vs. height and LAR vs. height (Table 4). There was a negative correlation between the mean SLA of a plant and its height. There was a species effect on the intercept

of this relationship in the 0.5 and 2 y/o stands and on the slope in the 3 y/o stand (Table 4). Overall the LS *Rinereocarpus* had the highest SLA (Table 3).

The SLP *Trema*, *Ochroma* and *Cecropia* had at least three-fold lower leaf life spans than the other species measured (Fig. 3a). We were unable to obtain reliable data for *Pseudolmedia*, *Combretum* and *Adenocalymma*, though there was an

Table 4. Results of analysis of covariance (ANCOVA) of plant height, LMR (leaf mass ratio), LAR (leaf area ratio), SLA (specific leaf area), Φ_d (whole-plant light capture) and Φ_{area} (light per leaf area per day) as dependent variables with either plant above-ground mass, height, or diameter as covariates and species as discrete factor

Dependent	Covariate	Stand age	Slope effect (<i>P</i>)	Intercept
Height	Mass	0.5	ns	< 0.001
		2	ns	< 0.001
		3	0.004	na
Height	Diameter	0.5	ns	< 0.001
		2	ns	< 0.001
		3	ns	< 0.001
LMR	Height	0.5	ns	< 0.001
		2	ns	< 0.001
		3	ns	< 0.001
LAR	Height	0.5	ns	< 0.001
		2	ns	< 0.001
		3	< 0.001	na
SLA	Height	0.5	ns	< 0.001
		2	ns	< 0.001
		3	< 0.001	na
Φ_d	Mass	0.5	ns	0.014
		2	ns	ns
		3	ns	ns
Φ_{area}	Height	0.5	ns	0.045
		2	< 0.001	na
		3	< 0.001	na

indication that their leaf longevity was also considerably greater than that of the SLP. Mean leaf longevity was not correlated with the mean specific leaf area of species of the pooled data among all individuals of all three stands (Fig. 3b), but positively related with leaf mass ratio (Fig. 3c).

LIGHT (PPFD) INTERCEPTION

Trema and *Ochroma* plants intercepted more light both on a whole-plant basis (Φ_d , Table 3) and per unit leaf area (Φ_{area} , Fig. 4a) in all the three stands, though more apparently so in the oldest stand. The Φ_{area} values were significantly positively related with height. The slopes of the relationship between Φ_{area} and height differed between species in the two oldest stands but not in the 0.5 y/o one where the intercept was different between species (Table 4).

In all the three stands *Trema* and *Ochroma* differed in $\Phi_{leaf\ mass}$ ($\Phi_{area} \times SLA$) from the other species and the differences increased with stand age (Fig. 4b). Within each stand there was no significant difference in light intercepted per above-ground mass unit (Φ_{mass}) among the SLP, LS and lianas (Fig. 4c).

The $\Phi_{leaf\ mass}$ values were negatively correlated with leaf longevity (Fig. 5a) and in the regression after log transformation of both axes the slope was greater than -1 (-0.46), suggesting that leaf longevity increased more than proportionally with a reduction in $\Phi_{leaf\ mass}$. We calculated the total amount of light intercepted by individuals over their mean leaf life spans $\Phi_{leaf\ mass\ total}$ as the product of the daily Φ_{area} , the SLA of dead leaves and the leaf longevity (eqn 4). LS and lianas had higher $\Phi_{leaf\ mass\ total}$ values than the SLP (Fig. 5b).

Discussion

BIOMASS ALLOCATION AND INSTANTANEOUS EFFICIENCY OF LIGHT CAPTURE

Our first hypothesis that early dominance of short-lived pioneers (SLP) is associated with high instantaneous light interception per unit of standing leaf mass ($\Phi_{leaf\ mass}$) was

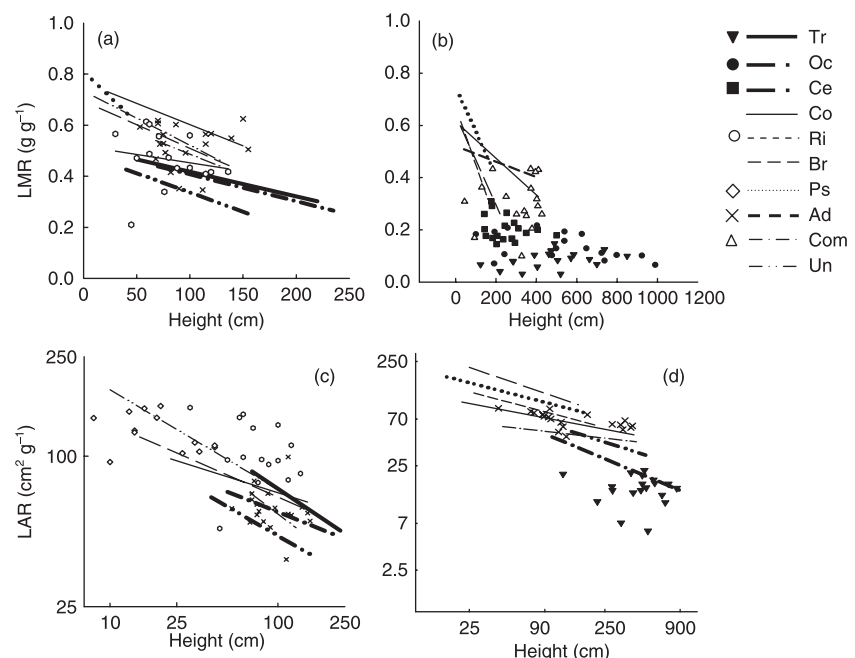


Fig. 2. Relationship between leaf mass ratio (LMR) and height (a, b) and between the leaf area ratio (LAR) and height (c, d) for trees and lianas in a stand of 6 months old (a, c) and a 3-year-old (b, d) secondary forest stand. Species abbreviations as in Fig. 1. Lines denote significant regressions and symbols per plant values where linear regression was not significant. Panels a and c redrawn from Selaya *et al.* (2007).

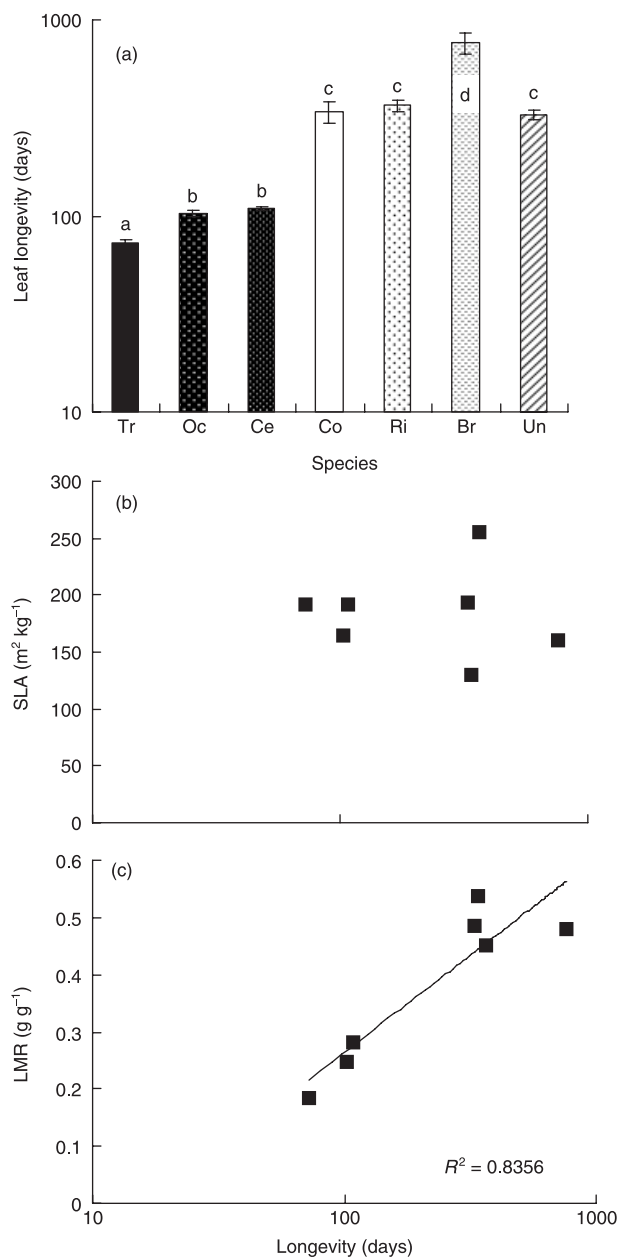


Fig. 3. (a) Mean leaf longevity of seven species. Different letters denote significant differences between species at $P < 0.05$. Bars denote Standard Error. (b) Leaf longevity vs. SLA (specific leaf area) (c) Leaf longevity vs. LMR (leaf mass ratio). Each point denotes the species mean for the three stands and the lines regressions. Species abbreviations are given in Fig. 1.

supported by our data. SLP grew taller, overtopping the other species, and were able to intercept a greater amount of light per unit leaf mass ($\Phi_{\text{leaf mass}}$, $\Phi_{\text{area}} \times \text{SLA}$) than the other species, and this difference increased during the first 3 years of succession. A high $\Phi_{\text{leaf mass}}$ can be realized through a tall stature by which plants deploy their leaves high in the canopy, hence realizing a high light interception per unit leaf area Φ_{area} (Hirose & Werger 1995). In our study, differences in Φ_{area} between the tallest species, *Trema* and *Ochroma*, and the others were small in the 6-month-old stand but increased

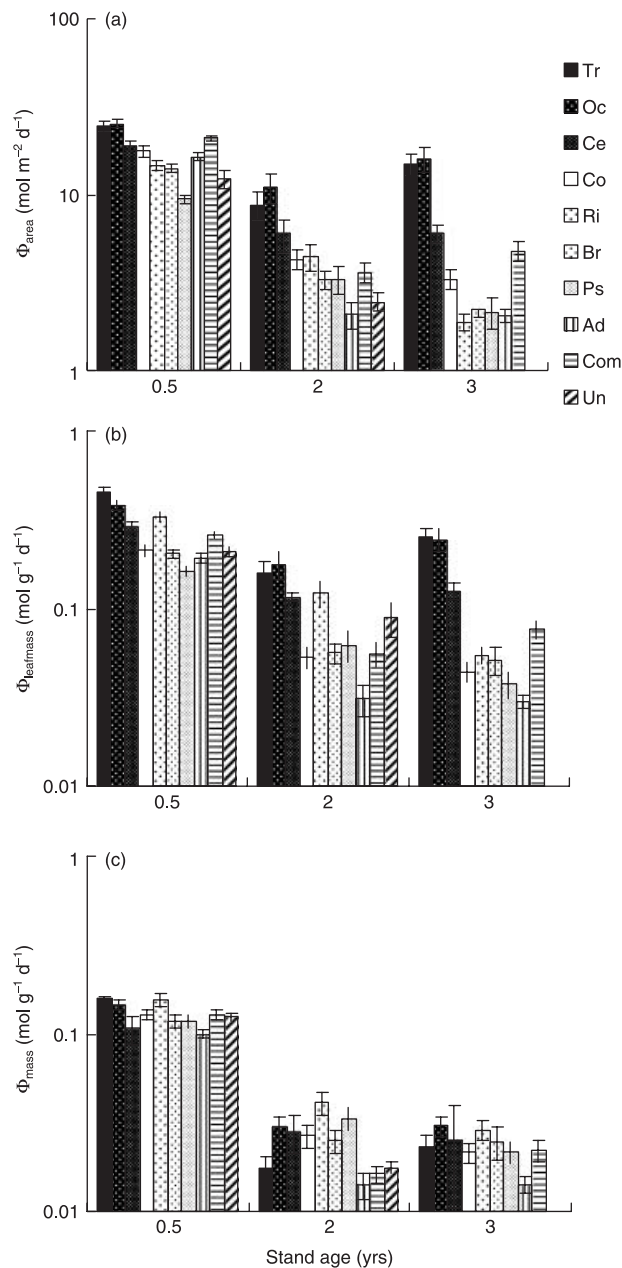


Fig. 4. Mean light interception per unit leaf area (Φ_{area} , a) per unit leaf mass ($\Phi_{\text{leaf mass}}$, b), and per unit above-ground mass per day (Φ_{mass} , c) in secondary forest stands of 6 months, 2 and 3 years old. Bars denote standard errors. Species abbreviations are given in Fig. 1. Values for the 0.5-year-old stand taken from Selaya *et al.* (2007).

about two-fold in the 3-year-old stand. This can largely be explained by the strong increase in LAI and the steepening light gradient in the canopy that occurred during these early years of succession. Similar results were obtained for grasslands (Anten & Hirose 1999; Werger *et al.* 2002; Aan *et al.* 2006).

An advantage in competition for light can be achieved through growing a slender stem, characterized by a low mass investment per unit height. Narrow stems facilitate rapid height growth but also imply a reduced mechanical stability

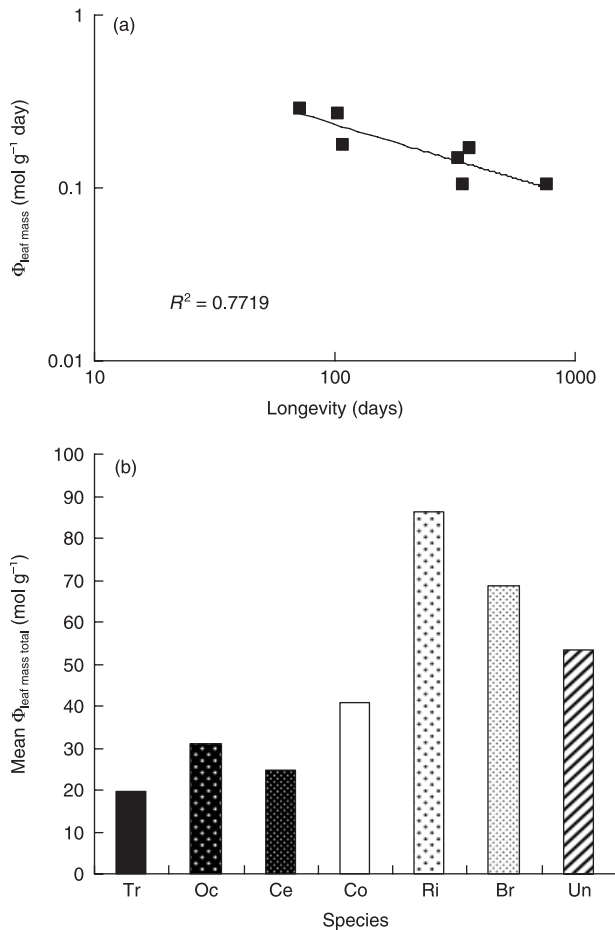


Fig. 5. (a) Relationship between $\Phi_{\text{leaf mass}}$ and leaf longevity. Points represent species means for the three stands and the line the regression. (b) Average of $\Phi_{\text{leaf mass total}}$ over the first 3 years of succession (total PPFD per leaf mass per mean leaf longevity). Species abbreviations are given in Fig. 1.

(Putz 1984; Niklas 1992; Montgomery & Chazdon 2001). *Trema* tended to be taller for a given mass and diameter than the other tree species in all stands, but when *Trema* was compared with lianas at the same diameter, *Trema* was taller only in the 6 months old stand. In the 2 and 3-year-old stands, liana species tended to be taller for a given diameter. Note that liana species were still free-standing in the 6-month-old stand, while most of the individuals in the 3-year-old stand (> 70%) were climbing. In the case of *Trema* having relatively slender stems may not be a major problem because the individuals are short-lived and do not need to grow taller than the height reached by the vegetation within that short time span of a few years. Observations in our study area showed that *Trema* was found in plots up to 4 years old whereas *Ochroma* and *Cecropia* were found even after 25 to 30 years.

Ochroma and *Cecropia* tended to have large diameters across all stands and these were associated with a very low wood density (*Ochroma*) or a hollow stem (*Cecropia*) both of which may contribute to an efficient conversion of mass to height. However, low wood density stems tend to be more prone to mechanical failure (Gérard *et al.* 1996) or pathogen

attacks (Coley 1983; Kitajima *et al.* 1997) and is associated with wider xylem vessels that increase the risk of embolisms (Lambers *et al.* 1998).

An advantage in competition for light can also be achieved through allocating a large fraction of mass to leaves (high LMR) or by constructing thinner leaves (high SLA), leading to a high Φ_{mass} ($\Phi_{\text{mass}} = \Phi_{\text{area}} \times \text{LMR} \times \text{SLA}$). We found that the SLP had considerably lower LMR values than the species of the other groups. *Ochroma* and *Trema* grew increasingly taller than the other species. Their lower LMR could therefore partly be explained by the fact that taller plants have to invest disproportionately in support to maintain mechanical stability (Givnish 1982; Anten & Hirose 1998). But even when compared at the same height SLP had still considerably lower LMR values (Fig. 2). A possible explanation might be differences in plasticity. Plants typically respond to the close proximity of neighbours by increasing mass investment to stem growth (Smith 1982), but there are interspecific differences in the degree of this response. Early successional trees tend to show a greater response than late successional ones (Gilbert *et al.* 2001). This greater response can indeed result in lower leaf allocation even when comparing plants at the same height (Anten & Hirose 1998). Another factor causing the low LMR of SLP might be their leaf longevity being much shorter than that of the other species (Claveau *et al.* 2005, and see further below).

It should be noted that our mass ratios are based on above-ground parts excluding roots. It can thus be argued that differences in root mass between SLP and LS may influence Φ_{mass} values, yet Poorter (2005) showed that root mass fraction did not differ between SLP and LS species.

Our hypothesis, that because they climb, lianas need to allocate less biomass for support and can therefore use more resources for leaf production or additional height growth resulting in a higher Φ_{mass} , was not supported by our data. Liana species included in this study were not more efficient than tree species in intercepting light (Φ_{mass} and $\Phi_{\text{leaf mass}}$). This result can be explained by the fact that at our site during the first 3 years of succession lianas gradually moved from a freestanding to a climbing growth habit; in the 0.5-year-old stand almost all lianas were freestanding while by the third year the majority had started climbing. This transition is associated with a number of changes in biomass allocation and wood anatomy including increased xylem vessel diameter and associated reductions in wood density, and an increase in stem slenderness (also observed here) and leaf area to stem diameter ratio (Lambers *et al.* 1998; Gallenmüller *et al.* 2004; Rowe & Speck 2005). It is possible that because lianas were just starting to climb in the third year these changes were not apparent at the whole-plant level. Indeed Selaya & Anten (2008) found in a 4-year-old stand that lianas had higher Φ_{mass} values than trees. It should also be noted that we only included three liana species with an occurrence pattern similar to that of the LS tree species in this study. Many liana species have light requirements similar to SLP (Putz 2005), and especially those species might exhibit different allocation patterns and associated Φ_{mass} values than those reported here.

Growth is not only determined by light acquisition but also by the growth achieved per unit of absorbed light (Schwinning & Weiner 1998), with the latter being strongly related to leaf photosynthetic and respiratory traits. It has been shown that pioneers have higher light saturated rates of photosynthesis than later successional species (Poorter 2005). It is therefore possible that while Φ_{mass} did not differ between the groups, photosynthesis and thus growth per unit mass was higher for the SLP (Anten & Hirose 2003).

LEAF LIFE SPAN AND LONG-TERM EFFICIENCY OF LIGHT CAPTURE

Instantaneous light interception per standing leaf mass ($\Phi_{\text{leaf mass}}$) may help explain how some species attained early dominance. However, in tropical evergreen perennial species leaf and branch production and loss are continuous processes. The short-lived pioneers (SLP) were found to have three-fold lower leaf life spans than the other species (Fig. 3A). There was also a positive relationship between standing leaf mass (LMR) values and leaf longevity (Fig. 3C). This result suggests that the low LMR values of SLP are partly determined by their high leaf turnover rates. Plants may lose their leaves as a response to inherent high light compensation points or as a product of accumulated damage by herbivory (Kikuzawa 1995; Kitajima *et al.* 1997, 2002; Wright *et al.* 2004). A rapid leaf turnover in the SLP however may also be important for light competition. Being shade intolerant the SLP need to continuously produce leaves at the top of the canopy. Leaf area growth tends to be limited by nutrient and particularly nitrogen availability (Lambers *et al.* 1998). It is therefore possible that the SLP cannot obtain all nutrients from the soil to sustain a sufficiently high rate of leaf production and that they therefore drop their leaves to make more resources available by withdrawing them from older leaves (see also Boonman *et al.* 2006).

Leaf mass dynamics may influence light interception but also the competitive ability of the species in the long term. Generally strong negative correlations are found between SLA and leaf longevity with the slope, after log:log transformation, being around -0.5 (see Westoby *et al.* 2000; Wright *et al.* 2004). Thus, a reduction in SLA is associated with a disproportionate increase in leaf longevity. Westoby *et al.* (2000) pointed out that if SLA represents light capture per unit leaf mass; this result implies that long-lived leaves are more efficient in terms of light acquisition. However, as shown here many other traits influence light capture per unit mass which may or may not correlate with SLA. Here we show that mean light capture per unit leaf mass at the whole-plant level ($\Phi_{\text{leaf mass}}$) also correlates strongly and negatively with leaf longevity with the slope also being -0.46 (Fig. 5A). This indicates that in combination, the suite of traits that are associated with a high instantaneous efficiency of light capture, (i.e., high SLA, low wood density, slender stems etc), have a negative trade-off with leaf longevity. It also shows that increasing $\Phi_{\text{leaf mass}}$ results in a disproportionate reduction in leaf longevity.

In accordance with the point above, we found that on average during the first 3 years of succession later successional trees (LS) and lianas, with their greater leaf longevity, captured more light per gram of biomass invested in leaves ($\Phi_{\text{leaf mass total}}$) than SLP (Fig. 5B). It should be noted that this calculation is restricted to the first 3 years of succession. The low $\Phi_{\text{leaf mass total}}$ of SLP compared to the LS and liana species indicates that rapid height growth requires a greater biomass investment to intercept light. The LS appeared to be more efficient in biomass use for light interception, because they had longer lived leaves. These results provide an example of how biomass dynamics influence competition for light in the long run and present a conceptual tool to explain why early dominants are not also the long-term dominants.

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