LEAF TRAITS ARE GOOD PREDICTORS OF PLANT PERFORMANCE ACROSS 53 RAIN FOREST SPECIES

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Abstract. We compared the leaf traits and plant performance of 53 co-occurring tree species in a semi-evergreen tropical moist forest community. The species differed in all leaf traits analyzed: leaf life span varied 11-fold among species, specific leaf area 5-fold, mass-based nitrogen 3-fold, mass-based assimilation rate 13-fold, mass-based respiration rate 15-fold, stomatal conductance 8-fold, and photosynthetic water use efficiency 4-fold. Photosynthetic traits were strongly coordinated, and specific leaf area predicted mass-based rates of assimilation and respiration; leaf life span predicted many other leaf characteristics. Leaf traits were closely associated with growth, survival, and light requirement of the species.

Leaf investment strategies varied on a continuum trading off short-term carbon gain against long-term leaf persistence that, in turn, is linked to variation in whole-plant growth and survival. Leaf traits were good predictors of plant performance, both in gaps and in the forest understory. High growth in gaps is promoted by cheap, short-lived, and physiologically active leaves. High survival in the forest understory is enhanced by the formation of long-lived well protected leaves that reduce biomass loss by herbivory, mechanical disturbance, or leaf turnover. Leaf traits underlay this growth–survival trade-off; species with short-lived, physiologically active leaves have high growth but low survival. This continuum in leaf traits, through its effect on plant performance, in turn gives rise to a continuum in species' light requirements.

Key words: Bolivia; growth; leaf life span; light; light requirements; shade tolerance; niche differentiation; photosynthesis; survival; tropical rain forest.

INTRODUCTION

In a diverse range of plant communities, a recurrent pattern of close coordination among leaf traits has been found (Reich et al. 1992, 1999, Wright et al. 2004). There is a continuum of carbon and nutrient investment strategies in leaves that is associated with key aspects of leaf function. Species with short leaf life span tend to have an efficient deployment of leaf area per unit biomass invested (i.e., a high specific leaf area, SLA). They have high nitrogen content per unit leaf area, and consequently, high assimilation and respiration rates. At the other end of the spectrum, species have a long leaf life span, low SLA, and slow metabolic rates.

Leaf life span and SLA are often considered to be the central traits under selection, as they are inferred to determine the position of the species along this continuum (Lambers and Poorter 1992, Poorter and Garnier 1999, Westoby et al. 2002). Species with a high SLA and short-lived leaves are assumed to gamble on a quick return on leaf investments; by investing in cheap,

short-lived leaves they may grow quickly, pre-empt resources, and outcompete their neighbors. Species with a low SLA and long-lived leaves trade rapid growth for persistence, and put their stakes upon a slow but secure return of investments. These species invest in tough, well-protected leaves with low nutrient contents that can diminish herbivory (Coley 1983) and physical hazards, leading to increased leaf life span and enhanced plant persistence. Although this assumption of correlation between foliar design and life history strategy implicitly underlies many ecophysiological studies, how leaf traits actually scale up to whole-plant performance in the field has rarely been directly tested.

Most studies have evaluated seedling growth only under controlled conditions. They show that interspecific variation in biomass relative growth rate is closely associated with variation in SLA (Walters and Reich 1999, Poorter et al. 2005), and, to a lesser extent, with photosynthetic rates (e.g., Poorter 1999, Shipley 2002). The few studies that have related leaf traits to interspecific variation in plant survival have found that SLA and photosynthetic rates in fact are negatively associated with seedling survival (Kitajima 1994), but the potential growth and survival rate under controlled conditions might not be representative for realized growth and survival rates in the field (Kitajima 1996). Reich et al. (1992) did find that the height growth rate of

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tree saplings was positively related to photosynthetic rate, and negatively related to the leaf life span of the species, but their review combined species from different biomes, so it is not clear that the relation will hold within a community. Comparing the height growth rate of 35 co-existing rain forest species growing in treefall gaps, Coley (1988) found that species with short leaf life spans indeed realized faster height growth rates. Hence, there is limited evidence that "fast" leaf traits may translate into rapid growth rates in the field, but it remains to be tested whether "slow" leaf traits result in a high plant survival.

Is this fast–slow continuum in leaf investment and plant performance also reflected in the regeneration niche of the species? Many studies have compared leaf traits and performance of shade-intolerant pioneers and shade-tolerant understory species (e.g., Popma et al. 1992, Strauss-Debenedetti and Bazzaz 1996), which occupy the extremes of a species continuum in light requirements. Early-successional, light-demanding species with short-lived, productive leaves establish in the high-resource environment of gaps. They realize fast growth rates to compete with their neighbors and maintain a position at the top of regrowing vegetation. Late-successional, shade-tolerant species with long-lived, low-productive leaves establish in the low-resource environment of the forest understory. Investment in leaves is costly as carbon gain is low in this light-limited environment. Leaves should therefore be well protected and long-lived to pay back the initial construction costs of the leaves (Poorter and Garnier 1999, Rijkers 2000). Unfortunately, this convenient dichotomy does not reflect reality; the vast majority of rain forest species falls somewhere in between these two ecological extremes (Poorter et al. 2005). A continuum approach, rather than a dichotomy, is therefore needed if we really want to understand how leaf traits scale with light requirements. Here, we used juvenile crown exposure (cf. Poorter et al. 2005) as a continuous measure to rank species by their light requirements for regeneration. A low juvenile crown exposure indicates that species mainly regenerate in the shaded understory, whereas a high juvenile crown exposure indicates that species mainly regenerate in the bright-light environment of gaps.

In this study we compared the leaf traits and plant performance of 53 co-occurring rain forest species that accounted for 84% of the stems ≥10 cm diameter at breast height in the community. This community-based approach provides insight into the spectrum of trait values among co-existing trees and its implications for plant performance and niche differentiation (Reich et al. 2003). The following questions were addressed: (1) How are leaf traits associated with leaf life span? (2) How do leaf traits scale up to plant performance in terms of growth and survival? (3) Do the continua in leaf traits and plant performance also translate into a continuum in species' light requirements?

MATERIALS AND METHODS

Research site

Fieldwork was carried out in the semi-evergreen lowland tropical moist forest of La Chonta (15°47′ S, 62°55′ W), Bolivia, a research site of the Instituto Boliviano de Investigación Forestal (IBIF). Annual precipitation in the region is 1520 mm, with a dry season (<100 mm/mo) from April through October. The forest is situated on an extension from the Brazilian shield, at an altitude of 400 m. The forest has an average canopy height of 25 m, stem density of 367 stems/ha, basal area of 19.3 m^2/ha, and species richness of 59 species/ha (all data for trees ≥10 cm dbh; IBIF, unpublished data).

Data collection

Fifty-three of the most common tree species that vary in adult stature and shade tolerance were selected (see Appendix). Light requirements varied gradually and continuously among species. In a separate study (Poorter et al. 2006), we estimated the crown exposure (cf. Dawkins and Field 1978) and height for, on average, 662 individuals per species (range 41–9319). This crown exposure (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 full overhead light on the whole crown, and 5 when it has an emergent crown that receives light from all directions. The crown exposure can be measured repeatedly (difference between two independent observers is 0.1 ± 0.01 [mean $\pm$ SE]), 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 population-level juvenile crown exposure at a standardized height of 2 m (CE_{juv}).

For each species, about 16 saplings (mean 15.7, range 4–22, total 817) with a height between 0.5 m and 2.5 m were selected. Individuals were searched for under closed-canopy conditions, but light-demanding species were also sampled in gaps and along skid trails or roads to assure a sufficient number of individuals. Sapling height was measured vertically from the forest floor to the apex of the plant. The most recently formed leaf was marked along the stem for monopodial species, and along a branch for sympodial species. Plants were monitored for their height and survival at about 2, 4, 9, 13, and 25 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 with a differently colored marker. In total, 11 450 leaves were monitored and, on average, 225 leaves per species (range 35–688). Leaf survival rate of the first four leaf cohorts was analyzed with a survival analysis (Fox 1993, SPSS 2001). Leaf life span of

individual leaves was calculated as the time from the start of monitoring until the census when the leaves were dead. The leaf life span was slightly underestimated because the first leaf cohort was already present at the start of the monitoring period. Leaves that survived until the end of the monitoring period were right-censored. Leaf life tables were calculated based on a Kaplan-Meier approach, which gives the proportion of leaves that survive a certain time. The median expected leaf life span was derived from a quadratic regression of the proportional survival against time.

Annual height growth rate was calculated as the difference in height between the first census and the last census that the plant was alive, divided by the length of the evaluation period (varying between 2 and 25 months), and multiplied by 12. Species-specific height growth rates were calculated based on log-transformed values. All plants with height growth rates less than −5 cm year (13% of the data) had damage due to animals, lianas, or falling debris, and were excluded from the analysis. This did not affect the results to any significant extent; the log(height growth rate) of species based on this reduced data set was strongly correlated with the log(median height growth rate) of species based on the complete data set ($r = 0.86$, $P < 0.001$, $n = 51$), and the correlation between both measures of height growth rate and leaf traits, mortality rate, and juvenile crown exposure was virtually the same. The daily sapling survival rate (SR) was calculated for each species from the regression slope of $\log_{10}$(percentage of surviving saplings) against time (in days). Annual survival rate was then calculated as 10^{365SR}. Species with an SR of -8.55×10^{-5} would have an annual survival rate of 0.93.

Photosynthesis measurements

Photosynthesis was measured in February 2004 for five additional saplings per species (average 4.9, range 3–6). To determine the inherent photosynthetic capacity of the species, measurements were made on saplings growing in high-light conditions (lateral light, or overhead light) in forest gaps, clearings, and along forest roads. Photosynthetic measurements were made between 0800 and 1600 hours with a portable infrared gas exchange system (CIRAS-1, PP system, Hitchin, UK) under ambient temperature, providing a CO_2 concentration of 360 ppm and a relative humidity of 75% in the leaf chamber. A halogen light unit mounted on the leaf chamber provided a saturating irradiance of 1300 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Measurements were done on the youngest fully expanded leaf, and light-saturated photosynthetic rates (A_{area}, in $\mu mol \cdot m^{-2} \cdot s^{-1}$) were recorded after the leaf was fully induced. Leaves were then covered with a dark cloth, and dark respiration rate (R_{area}, in $\mu mol \cdot m^{-2} \cdot s^{-1}$) was recorded when readings stabilized. When all data were combined, photosynthetic rates were highest around noon and slightly lower at the beginning and end of the day (quadratic regression of z scores for each species against time, $P < 0.01$). Time explained

very little of the variation in A_{area} ($r^2 = 0.039$), and measurements of individual species were spread out over the day. The time of measurement has, therefore, little effect on the results. Chlorophyll content was estimated with a SPAD meter (Minolta SPAD-502, Spectrum Technologies, Plainfield, Illinois, USA). The SPAD value was converted to chlorophyll concentration per unit leaf area (in $\mu mol/m^2$) using an average of the regression equations for six temperate herbaceous species ($Chl_{area} = -112.9 + 13.9 \times SPAD$; Anten and Hirose 1999). Subsequently, the leaf was detached, leaf area determined with a flatbed scanner, and one or several punches taken from the leaf blade, excluding the midrib or large veins. Leaf blade and punches were oven-dried for 48 h at 70°C and weighed. The SLA (m^2/kg) was calculated as the leaf blade area divided by the leaf dry mass, and punch area by punch dry mass. Both measures of SLA were closely correlated ($r = 0.95$, $P < 0.001$). Total organic N mass per unit leaf mass (N_{mass}, in %) was determined using Kjeldahl assay, and converted to N per unit leaf area (N_{area}, in g/m^2) using the SLA of the leaf blade area.

The leaf temperature in the cuvette could not be controlled, and the R_{area} was therefore measured at different ambient temperatures (29.3°C ± 2.6°C [mean ± SD]). To control for the temperature sensitivity of respiration, the R_{area} was calculated for an average temperature of 29°C, assuming a Q_{10} (proportional increase of R_{area} with a 10°C increase in temperature) of 2.0 (Atkin and Tjoelker 2003). Mass-based assimilation (A_{mass}, in $nmol \cdot g^{-1} \cdot s^{-1}$) and respiration ($R_{mass}$, in $nmol \cdot g^{-1} \cdot s^{-1}$) rates were calculated by multiplying the area-based rates with the SLA of the leaf punch. The intrinsic photosynthetic water use efficiency (WUE_i, in mmol/mol) was calculated as the A_{area} over the light-saturated stomatal conductance (g_s, in $mmol \cdot m^{-2} \cdot s^{-1}$).

Statistical analysis

Species-specific leaf trait values were calculated using arithmetic means and then $\log_{10}$-transformed prior to statistical analysis. Correlations amongst leaf traits were analyzed with a Pearson's correlation; all reported correlations were significant at a P level of 0.05, unless stated otherwise. Multivariate association of the 14 leaf traits was analyzed with a principal-component analysis, based on a correlation matrix. CE_{juv}, sapling growth, and survival were not included in the PCA analysis, but later correlated with the PCA axes. Again, all variables were $\log_{10}$-transformed prior to analysis. All statistical analyses were carried out using SPSS version 11.0 (SPSS 2001).

RESULTS

Leaf traits vs. leaf life span

The 53 co-occurring species differed significantly in all their leaf traits (one-way ANOVA for species, $F_{52,205} > 3.14$, $P < 0.001$ in all cases, r^2 ranged from 0.42 to 0.76). Leaf life span varied 11-fold among species (2.7–31 mo),
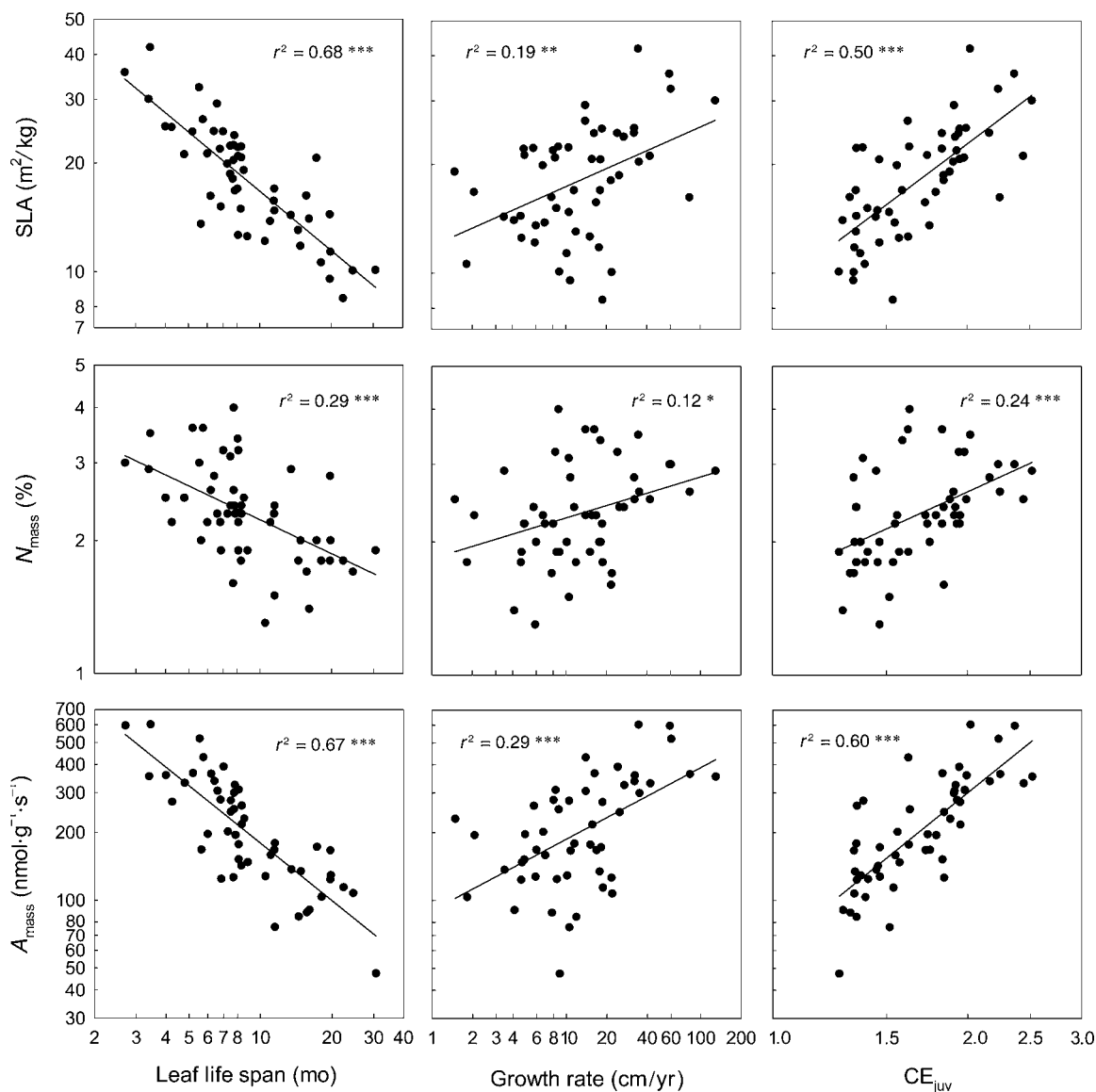
FIG. 1. Relationships between leaf traits and leaf life span (left panels), sapling height growth rate (middle panels), and juvenile crown exposure (CE_{juv}; right panels) of 53 rain forest tree species. Measurements from top to bottom are: specific leaf area (SLA), nitrogen per unit mass (N_{mass}), mass-based photosynthesis (A_{mass}), mass-based dark respiration (R_{mass}), stomatal conductance (g_s), and photosynthetic water use efficiency (WUE). Continuous lines indicate significant regressions; the broken line indicates a nonsignificant regression. Coefficients of determination and significance levels are given: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS, $P > 0.05$. Note the log–log scales.

SLA 5-fold (8–52 m^2/kg), N_{mass} 3-fold (1.3–4.0%), A_{mass} 13-fold (27–603 nmol·g^{-1}·s^{-1}), R_{mass} 15-fold (5–71 nmol·g^{-1}·s^{-1}), g_s 8-fold (69–570 mmol·m^{-2}·s^{-1}), and WUE$_i$ 4-fold (14–62 mmol/mol) (see Appendix). We used the leaf life span as a major descriptor of the resource investment strategy of the species. Species with long-lived leaves had a low SLA, and were metabolically less active, having a low N_{mass}, A_{mass}, R_{mass}, and g_s (Fig. 1, Table 1). The photosynthetic WUE$_i$ was positively correlated with leaf life span. In general, correlations with leaf life span were stronger when the metabolic leaf traits were expressed on a mass basis rather than an area

basis (Table 1). For example, the correlation between leaf life span and A_{mass} was −0.82, compared to −0.57 for A_{area}, and the correlation with R_{mass} was −0.75 compared to −0.45 for R_{area}.

Coordination of photosynthetic traits and water relations

Photosynthetic leaf traits were strongly coordinated. Both A_{mass} and R_{mass} were positively correlated with N_{mass} (Fig. 2a, b) and SLA (Table 1). Multiple regression shows that mass-based photosynthetic rates were more determined by SLA (standardized regression coefficient $b = 0.57$, $P < 0.001$) than by N_{mass} ($b = 0.42$,
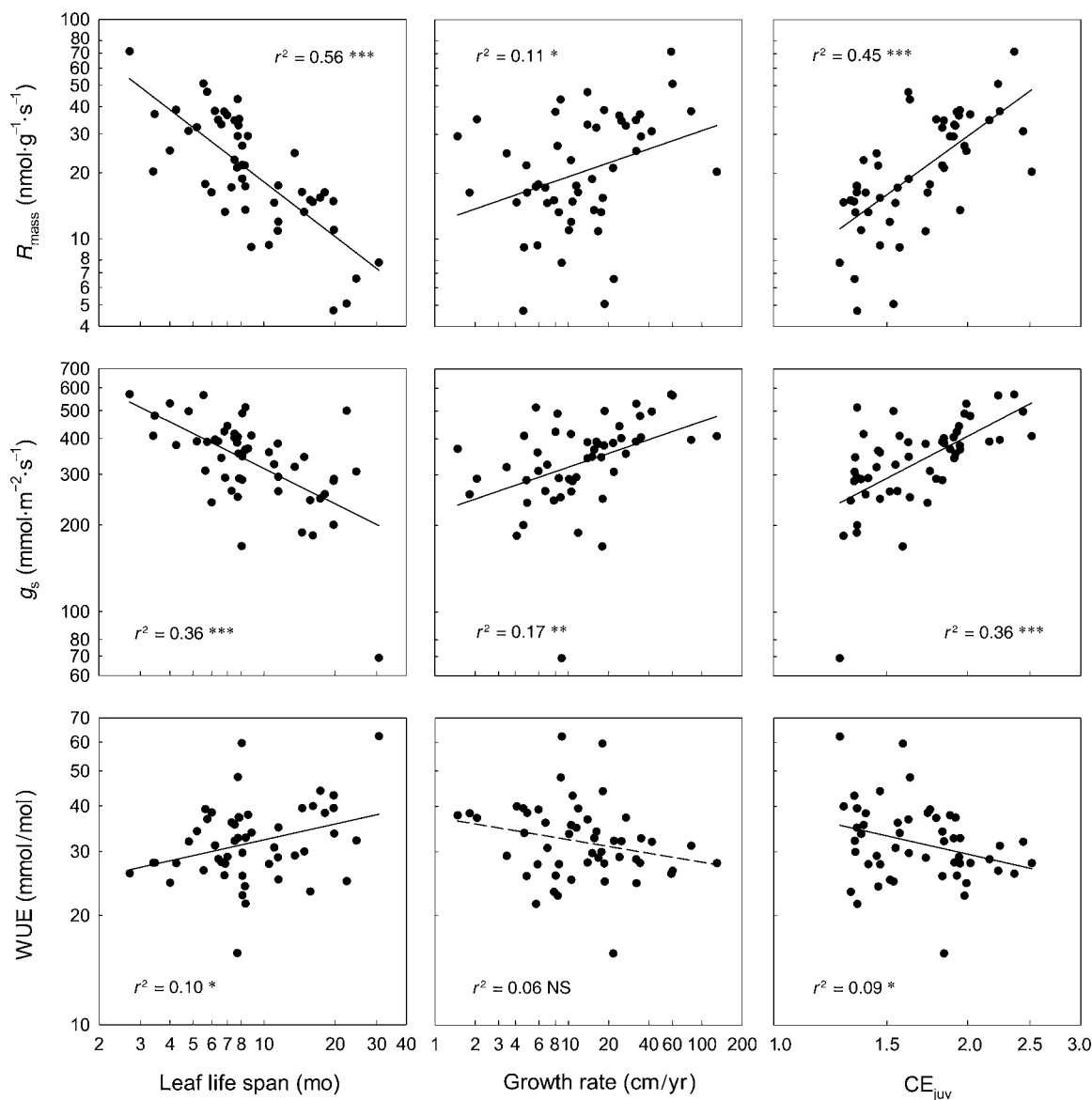
FIG. 1. Continued.

$P < 0.001$). The same applied for the R_{mass} ($b = 0.56$, $P < 0.001$ for SLA; $b = 0.32$, $P < 0.01$ for N_{mass}). The relationship between assimilation rates and nitrogen content disappear when expressed on an area basis (A_{area} vs. N_{area}, $r = -0.03$, NS; R_{area} vs. N_{area}, $r = -0.03$, NS), whereas the relationship between area-based assimilation rates and SLA were maintained, although being much weaker compared to the mass-based relation (correlation between SLA and A_{mass} was 0.84 compared to 0.43 for A_{area}; correlation with R_{mass} was 0.77 compared to 0.33 for R_{area}). Species with a high A_{mass} also had a high R_{mass} (Fig. 2c).

The photosynthetic WUE_i of the species, defined as the area-based photosynthesis over the g_s, ranged from 14 to 62 mmol/mol. Multiple regression shows that

WUE was more determined by g_s (standardized regression coefficient $b = -1.51$, $P < 0.001$) than by the A_{area} ($b = 1.1$, $P < 0.001$).

From leaf traits to plant growth and survival

There was a clear fast–slow continuum of leaf investments in short-term carbon gain vs. long-term leaf persistence. How does this investment strategy translate into whole-plant growth and survival? Height growth rate was positively correlated with the SLA, N_{mass}, A_{mass}, R_{mass}, and g_s of the species (Fig. 1, Table 1). Species with fast growth rates were characterized by a high SLA and nitrogen concentration, and were physiologically more active by having high photosynthesis, respiration, and conductance rates. Height

TABLE 1. Pearson's correlation (r) between leaf traits and juvenile crown exposure of 53 rain-forest tree species in La Chonta, Bolivia.

							Trait									
Trait	LL	SLA	N_{area}	N_{mass}	A_{area}	A_{mass}	R_{area}	R_{mass}	g_s	WUE_i	C_i	Chl_{area}	Chl_{mass}	PNUE	GR	SR
SLA	−0.82															
N_{area}	0.56	−0.70														
N_{mass}	−0.54	0.63	0.11													
A_{area}	−0.57	0.43	−0.03	0.58												
A_{mass}	−0.82	0.84	−0.38	0.79	0.81											
R_{area}	−0.45	0.33	−0.03	0.43	0.39	0.44										
R_{mass}	−0.75	0.77	−0.38	0.68	0.50	0.79	0.83									
g_s	−0.60	0.48	−0.30	0.34	0.77	0.74	0.25	0.47								
WUE_i	0.32	−0.22	0.43	0.17	−0.07	−0.18	0.07	−0.12	−0.65							
C_i	−0.14	0.07	−0.41	−0.35	−0.14	−0.06	−0.17	−0.03	0.47	−0.94						
Chl_{area}	0.57	−0.54	0.56	−0.14	−0.01	−0.37	−0.02	−0.35	−0.37	0.48	−0.42					
Chl_{mass}	−0.55	0.82	−0.48	0.63	0.46	0.73	0.23	0.59	0.41	0.11	−0.28	−0.03				
PNUE	−0.82	0.78	−0.58	0.49	0.77	0.92	0.36	0.69	0.78	−0.31	0.10	−0.44	0.63			
Growth rate	−0.44	0.43	−0.24	0.34	0.37	0.53	0.07	0.33	0.41	−0.24	0.07	−0.49	0.32	0.55		
Survival rate	0.56	−0.51	0.41	−0.27	−0.32	−0.47	0.01	−0.27	−0.35	0.21	−0.10	0.56	−0.29	−0.49	−0.57	
CE_{juv}	−0.71	0.64	−0.27	0.59	0.52	0.74	0.17	0.51	0.49	−0.16	0.00	−0.57	0.38	0.67	0.56	−0.65

Notes: All variables were log_{10}-transformed prior to analysis; n varies from 47 to 53 species for the bivariate comparisons. Correlations with a P level < 0.05 are shown in italics, $P < 0.01$ in boldface and italics, $P < 0.001$ in boldface. Of the 136 correlations, 99 are significant ($P < 0.05$), whereas 6.8 correlations would be expected to turn out significant by chance alone. Abbreviations are as follows: leaf life span, LL; specific leaf area, SLA; nitrogen per unit area, N_{area}; nitrogen per unit mass, N_{mass}; area-based photosynthesis, A_{area}; mass-based photosynthesis, A_{mass}; area-based dark respiration, R_{area}; mass-based dark respiration, R_{mass}; stomatal conductance, g_s; intrinsic photosynthetic water use efficiency, WUE_i; internal CO_2 concentration, C_i; chlorophyll concentration per unit leaf area, Chl_{area}; chlorophyll concentration per unit leaf mass, Chl_{mass}; photosynthetic nitrogen use efficiency, PNUE; growth rate, GR; survival rate, SR; and juvenile crown exposure, CE_{juv}.

growth rate was not correlated with the WUE_i of the species. The growth rate was best correlated with the PNUE ($r = 0.55$, $P < 0.001$) and A_{mass} ($r = 0.53$, $P < 0.001$) of the species.

Height growth rate and plant survival rate were negatively related ($r = -0.57$, $P < 0.001$; Fig. 3c), indicating that species that grow fast die fast as well. Survival rate was significantly negatively correlated to the SLA ($r = -0.51$), A_{mass} ($r = -0.47$), and g_s ($r = -0.35$), but not to the N_{mass} ($r = -0.27$, $P = 0.069$) and R_{mass} ($r = -0.27$, $P = 0.066$) of the species (Table 1). Survival rate was most tightly correlated with the leaf life span ($r = 0.56$, $P < 0.001$) and chlorophyll content per unit area ($r = 0.56$, $P < 0.001$). In general, the correlations with survival were less tight than those with growth, probably because many species did not show any mortality during the two-year monitoring period (Fig. 3c). Leaf life span may contribute to the growth–survival trade-off, as species with long-lived leaves had slow growth rates, and high survival rates (Fig. 3a, b).

Leaf traits vs. juvenile crown exposure

We used the juvenile crown exposure to rank the species based on their light requirements for regeneration. Light-demanding species were characterized by a high SLA, and were metabolically more active, having a high N_{mass}, A_{mass}, R_{mass}, and g_s, but a lower WUE_i compared to shade-tolerant species (Fig. 1, Table 1).

Association of leaf and plant traits

The association of leaf and plant traits was analyzed with a principal-component analysis (Fig. 4a). The first axis of the PCA explained 52% of the variation in leaf traits, and reflects the fast–slow continuum in growth vs. persistence. The positive side of the axis reflects the light-demanding species (Fig. 4b) with a high CE_{juv} and high growth rate (Figs. 3e, 4a). They were characterized by a high SLA, high area- and mass-based assimilation, and respiration rates, a high PNUE, N_{mass}, and g_s. The negative side of the axis indicates shade-tolerant species with a high survival rate (Fig. 3d), a high leaf life span (Fig. 3f), a high N_{area}, and a high chlorophyll content per unit area. The second axis of the PCA explained 18% of the variation in leaf traits, with species with a high N_{area} and WUE_i at the top. Photosynthetic traits were, to some extent, phylogenetically conserved, as congeners such as *Ocotea* spp., *Pouteria* spp., *Aspidosperma* spp., and *Cariniana* spp. were relatively closely together in the multivariate leaf trait space (Fig. 4b).

DISCUSSION

Within a rain forest community, the coexisting tree species indeed differed to a large extent in their leaf traits. We asked whether leaf traits were coordinated and closely associated with leaf life span, whether this was associated with plant performance in terms of growth and survival, and whether the continua in leaf traits and plant performance were linked to the species' light requirements. Here we discuss our main results that leaf traits are well coordinated, that the slow–fast continuum at the leaf level closely parallels the slow–fast continuum at the plant level, and that this strongly affects the variety of species light requirements.

Leaf trait coordination and life span

All leaf traits were closely correlated with leaf life span (Fig. 1). Both leaf life span and SLA are thought to capture one of the major axes of ecological variation among species (Westoby et al. 2002). Long-lived, dense leaves with a low SLA are expensive to build, but have higher leaf toughness and are better able to withstand physical damage and deter generalist herbivores (Coley 1983, Wright and Cannon 2001, Díaz et al. 2004). Dense leaves are the result of more densely packed cells, leading to CO_2 diffusion limitation within the leaf and lower mass-based photosynthetic rates (Niinemets 1999). Short-lived leaves on the other hand, can be cheaply built if nutrients are readily available, but do not withstand biotic and abiotic pressures. Such leaves have a high SLA with a high nitrogen concentration per unit mass, leading to a large light-capturing surface per unit biomass invested. SLA plays a strong modifying role in leaf physiology: mass-based assimilation and respiration rates are more determined by SLA than by the N_{mass}. The rates scaled positively with SLA, indicating that minimizing diffusive resistance is more important than maximizing the photosynthetic compounds per unit area (cf. Niinemets 1999, Wright et al. 2003).

The 14 leaf traits were closely associated, with the first PCA axis (Fig. 4) representing a slow–fast continuum of returns in leaf investment. The leaf life span is a good indicator of these different carbon investment strategies. One extreme reflects species with long-lived, well-protected leaves, with high initial construction cost (per unit leaf area) and a long payback time, whereas the other extreme indicates species with cheap, short-lived leaves. High assimilation rates allow for a rapid payback of initial construction costs, making these leaves net carbon exporters in due time (Kikuzuwa 1991, Poorter et al. 2006). Remarkably similar patterns have been observed for a diverse range of plant communities, both at the global (Reich et al. 1999, Wright et al. 2004) and local scale (Reich et al. 1991, Poorter and Garnier 1999).

Orthogonal to this slow–fast axis is an axis of efficiency of water use, with species having high WUE_i and N_{area} having high loadings on the second axis. Species with a high N_{area} invest heavily in Rubisco. Such species may effectively draw down C_i, thus creating a strong CO_2 diffusion gradient within the leaf. This causes a stronger CO_2 influx for the same stomatal aperture and water efflux, thus enhancing the WUE_i. Wright et al. (2001) found a similar water conservation strategy for Australian shrub species from arid sites compared to species from wetter sites. The current study shows that a similar range of strategies exists within a single tropical forest community.

Congeners had similar photosynthetic characteristics (Fig. 4b), suggesting that photosynthetic leaf traits are partly phylogenetically conserved. A phylogenetic analysis is not likely to change the observed trait relationships to a large extent, as species were sampled from a wide range of families, and studies that do both standard
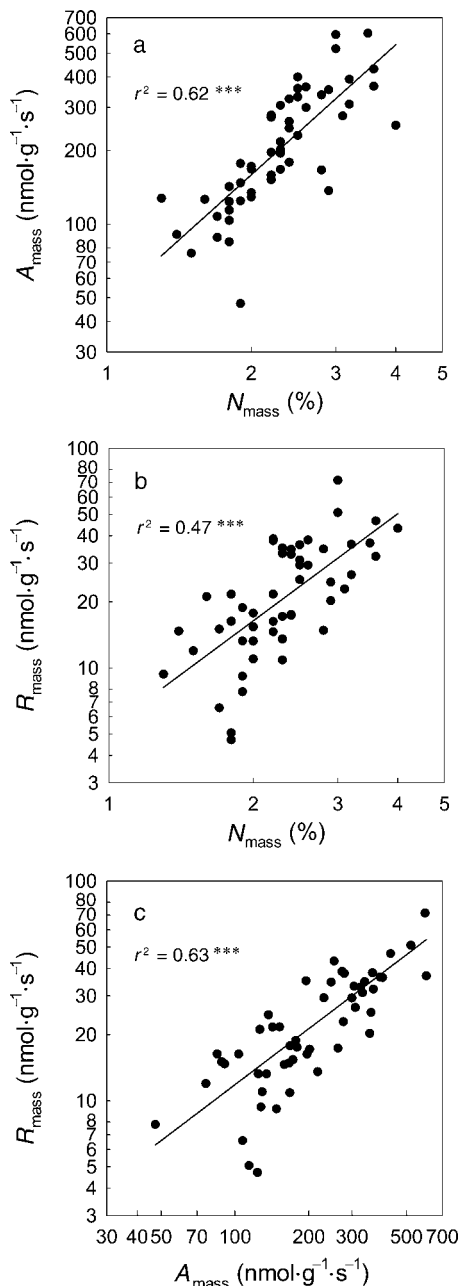

FIG. 2. Coordination of photosynthetic traits among 53 rain forest tree species: (a) mass-based light-saturated photosynthetic rate (A_{mass}) vs. nitrogen per unit mass (N_{mass}), (b) mass-based dark respiration rate (R_{mass}) vs. nitrogen per unit mass, and (c) mass-based dark respiration rate vs. assimilation rate. Regression lines, coefficients of determination, and significance levels are given (see Fig. 1 for *P* levels). Note the log–log scales.

and phylogenetically independent correlations obtain similar results (e.g., Wright et al. 2002).

From leaf traits to plant performance

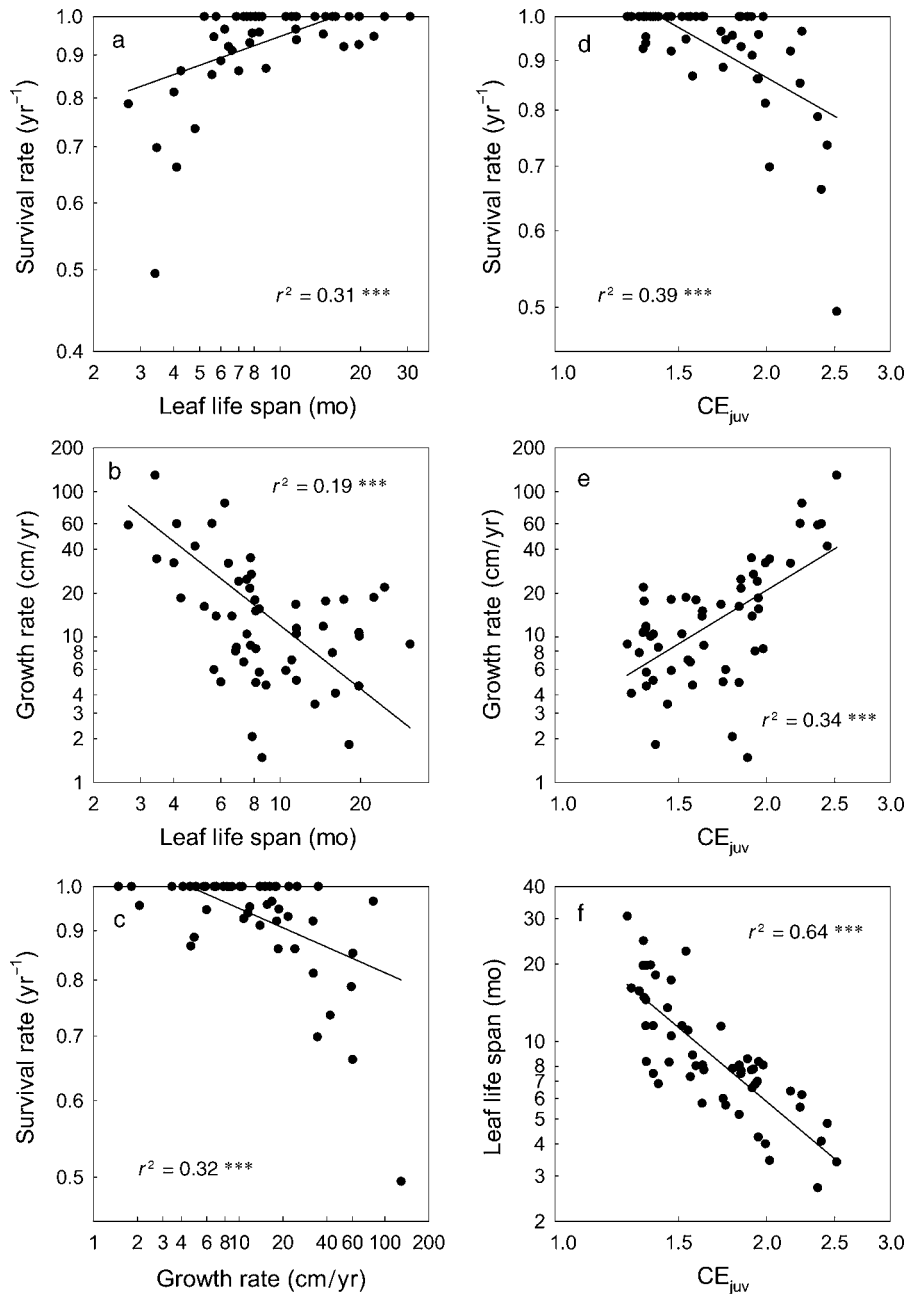Leaf traits were measured in high light under "optimal" resource conditions, thus reflecting the

FIG. 3. Relationships between survival rate, height growth rate, leaf life span, and juvenile crown exposure of 53 rain forest tree species. Regression lines, coefficients of determination, and significance levels are given (see Fig. 1 for P levels). Note the log–log scale.

inherent potential of the plant. Growth, survival, and leaf life span were measured in low to intermediate light, thus reflecting plant performance in the most common forest environment: the understory. Although most species show an increase in growth and survival with irradiance, the rank performance of the species is maintained (Welden et al. 1991, Kitajima 1994, Poorter 1999), suggesting that we can link "inherent leaf traits" to low-light plant performance.

Leaf traits are good predictors of plant performance. Fast-growing species tend to have short-lived leaves with a high SLA. A high SLA enables them to maximize light capture and forage opportunistically for light. Short-lived leaves enable them to track resources over time (Ackerly 1997), shed overshaded unproductive leaves in the bottom of the crown, and replace them with new, productive leaves in the top of the crown (Ackerly and Bazzaz 1995). High conductance and high N_{mass}

facilitate high assimilation rates, fuelling onward growth. Fast-growing species were also characterized by a high PNUE. Similar results were found by Poorter and Evans (1998). They found that fast-growing, high SLA species allocated a larger proportion of their leaf nitrogen into Rubisco instead of chlorophyll. These species enhanced their photosynthetic capacity and PNUE, rather than their light capture. Other studies have shown that sapling growth of rain forest species was negatively related to leaf life span (Coley 1988, Reich et al. 1992) and positively related to A_{mass} (Reich et al. 1992, Ellis et al. 2000), but they did not evaluate the relative importance of the leaf components.

Species with a high survival rate are species with long-lived leaves, a low SLA, and a conservative resource use (low assimilation, respiration, and conductance rates). Tough, well-defended leaves makes species less prone to herbivore or fungal attack (Gilbert 2005), which are important agents of mortality in a humid rain forest environment. A slow turnover of leaves and slow respiration reduces the carbon drain, and allows the plant to maintain a positive carbon balance, enhancing plant survival (King 1994, Veneklaas and Poorter 1998, Lusk 2002). The down-regulation of respiration is probably realized through a reduction of photosynthetic enzymes with a high metabolic turnover, and has as inevitable consequence that assimilation rates are reduced as well.

Leaf life span turned out to be the best predictor of plant survival, suggesting that, at the whole-plant level, the shedding of leaves is a much more important carbon drain than maintenance respiration (cf. Veneklaas and Poorter 1998). Species with high survival rates also had a high Chl_{area} (Table 1). This is probably a reflection of the regeneration strategy of the species, as shade-tolerant species had a high survival rate (Fig. 3d). Shade-tolerant species have to maximize light capture in the shaded forest understory, and they may do so by having a high Chl_{area}. In general, the correlations with survival were less tight than those with growth. Survival is, unlike growth, a slow process (many species did not show any mortality during the two-year monitoring period), and interspecific differences are difficult to detect using small sample sizes. Mortality in the field is also a highly stochastic process, because physical damage due to falling debris, herbivory, or pathogens, varies from place to place, obscuring interspecific differences.

Our results show that the growth of a species trades off against its survival (Fig. 3c): Species can be ranked along a continuum of slow growth and long persistence, to fast growth and an ephemeral life (cf. Kitajima 1994, 1996, Wright et al. 2003). The slow–fast continuum at the leaf level thus closely parallels the slow–fast continuum at the plant level. In a modeling study, Sterck et al. (2006) combined the observed leaf trait data for the Bolivian tree community with a whole-plant carbon model. They convincingly showed that leaf traits
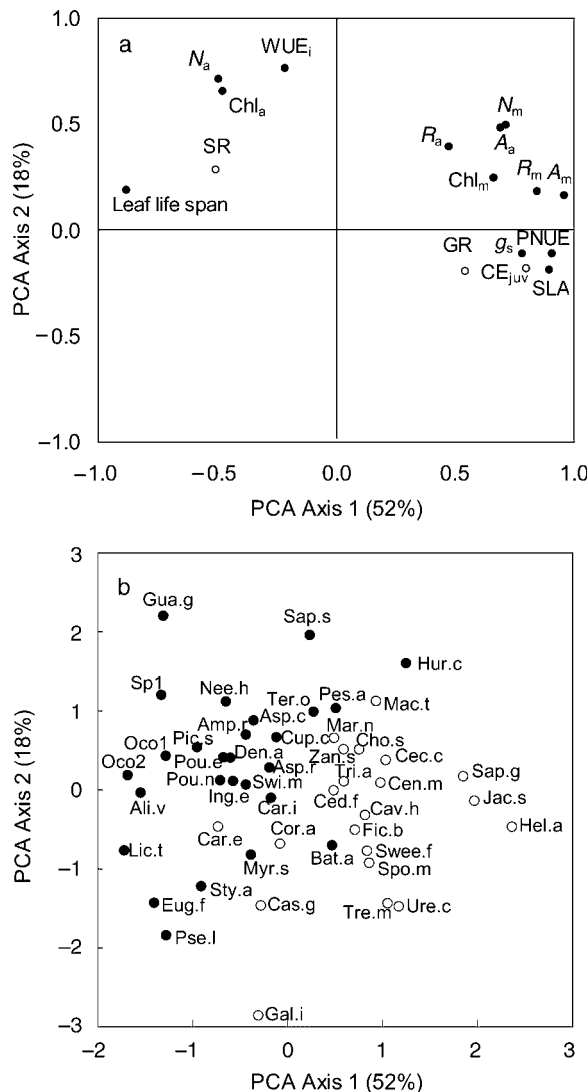

FIG. 4. Principal-component analysis of 13 leaf traits of 48 rain forest tree species. (a) Loading plots for the first axis (explained variation is 52%) and second axis (explained variation is 18%). Juvenile crown exposure (CE_{juv}), growth rate (GR), and mortality rate (MR) were not included in the PCA analysis but later were correlated with the PCA axes (indicated by open symbols). Absolute axis loadings larger than 0.28 are significant ($P < 0.05$). (b) Species loadings on the first and second axes. Trait abbreviations are found in Table 1. Species abbreviations are given in the Appendix. Total and partial shade-tolerant species are indicated by solid symbols; short- and long-lived pioneers by open symbols.

alone can partly explain the growth-survival trade-off observed among species.

Leaf traits, plant performance, and light requirements

Leaf traits varied gradually and continuously with the light requirements of the species (Figs. 1, 4). Species that require more light (higher juvenile CE) grow faster (Fig. 3e) to outcompete their neighbors and attain or maintain a canopy position in a regrowing canopy

gap. They do so by making cheaper, shorter-lived, and physiologically more active leaves (Fig. 1, Table 1; cf. Reich et al. 1995, Poorter et al. 2004). For species that are more shade tolerant (lower juvenile CE), survival, rather than growth, is important. Potentially high growth rates cannot be attained because of the low resource availability (low CE) in the forest understory. Species that are more shade-tolerant survive better (Fig. 3d) and may grow slowly towards the forest canopy, or persist longer until eventually a gap is formed (Lieberman et al. 1985, Clark and Clark 2001). Leaf traits are crucial in this respect: Longer-lived (Fig. 3e), better-protected leaves with lower nutrient concentration, lead to reduced biomass loss by herbivory, mechanical disturbance, or leaf turnover (Coley 1983, King 1994), and higher plant persistence. The continuum in leaf traits, through its effect on plant performance, gives rise to a continuum in species' light requirements.

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APPENDIX

A list of the 53 tree species included in the study with their juvenile light requirements and leaf traits (*Ecological Archives* E087-101-A1).