Leaf Traits Determine the Growth-Survival Trade-Off across Rain Forest Tree Species

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ABSTRACT: A dominant hypothesis explaining tree species coexistence in tropical forest is that trade-offs in characters allow species to adapt to different light environments, but tests for this hypothesis are scarce. This study is the first that uses a theoretical plant growth model to link leaf trade-offs to whole-plant performances and to differential performances across species in different light environments. Using data of 50 sympatric tree species from a Bolivian rain forest, we observed that specific leaf area and photosynthetic capacity codetermined interspecific height growth variation in a forest gap; that leaf survival rate determined the variation in plant survival rate under a closed canopy; that predicted height growth and plant survival rate matched field observations; and that fast-growing species had low survival rates for both field and predicted values. These results show how leaf trade-offs influence differential tree performance and tree species' coexistence in a heterogeneous light environment.

Keywords: carbon, economy, growth-survival trade-off, leaf trade-off, rain forest trees, plant growth model.

One way of understanding why plant species can coexist is by assuming that they partition resource gradients in space or time. Plant species from high-resource environments tend to have high resource acquisition rates, high resource turnover rates, and fast growth rates, whereas plant species from low-resource environments have lower

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acquisition and turnover rates and persist for a longer time. This general observation applies to a variety of plant communities, ranging from grasslands to forests. For example, grass species of eutrophic environments have higher nitrogen uptake and loss rates than grass species of oligotrophic environments (Berendse and Elberse 1989), and forest trees of high-light gaps have higher carbon uptake and loss rates than slow-growing trees that survive in the shade (Veneklaas and Poorter 1998; Walters and Reich 1999).

From these observations it has been suggested that in productive environments, plants maximize their growth rates by continuously placing new roots or leaves in favorable patches. The high resource availability allows them to rapidly "pay back" the costs of producing leaves and roots. Conversely, in nonproductive environments, plants pay back the construction costs through slow turnover rates of roots and leaves and long residence times of key resources such as nitrogen and carbon in plant parts. Here, the slow turnover enhances the survival of a plant because otherwise, the species would run out of essential nutrient and carbon resources and die. Such a conservative resource-use strategy, however, comes at the expense of a reduced growth rate (Williams et al. 1989). These interactions between environmental productivity and turnover rates of plant components, carbon, and nutrients can thus explain the trade-off between growth and persistence across species (e.g., Berendse and Elberse 1989; Kitajima 1996; Pacala and Rees 1998; Poorter and Garnier 1999; Loehle 2000; Grime 2001).

In tropical rain forest and other plant communities, a similar fast-slow continuum has been observed in morphological and physiological leaf traits (Reich et al. 1992, 1997; Poorter and Garnier 1999; Wright et al. 2004). Light-demanding species that regenerate in gaps have low leaf survival rates and high specific leaf areas (SLAs) and photosynthetic capacities (maximum assimilation rate per unit leaf mass). These species can pay back their investment in leaves rapidly because of low costs of producing leaf area and high photosynthetic rates. Shade-tolerant species have higher leaf survival rates and lower SLAs and photosynthetic capacities. These species regenerate in the shaded

understory and can only pay back such costs by increasing their leaf survival rates and having low respiration rates (Reich et al. 2003). Such long-lived leaves require additional mechanical and chemical protection against herbivores (Coley 1987, 1988), resulting in a low SLA and low photosynthetic capacity. These observations and ideas suggest that the cross-species-correlated leaf traits contribute to the growth-survival trade-off, as observed for pioneer versus shade-tolerant species (Kitajima 1994; Kobe et al. 1995; Wright et al. 2003). This hypothesis emerges from several ecophysiological and comparative studies, but it has never been explicitly tested.

We present field data on leaf traits and sapling performance for 50 co-occurring Bolivian moist-forest tree species. Species-specific leaf parameters were included in a theoretical plant growth model that integrates the carbon economies of leaves to the whole-plant level (Sterck et al. 2005). For each species, we model leaf and whole-plant performance in a high-light environment (a canopy gap) and a low-light environment (a closed canopy). The model predictions for height growth and survival are compared with actual rates under field conditions. This study is, as far as we know, the first one that uses a theoretical plant growth model to scale up correlated leaf traits to whole-plant performance and to show how leaf traits influence differential sapling performance and tree species coexistence in a heterogeneous light environment.

Methods

Data Collection

Fieldwork was carried out in the lowland tropical moist forest of La Chonta, Bolivia (15°47′S, 62°55′W). Annual precipitation in the region is 1,520 mm, with a dry season (<100 mm month^{-1}) from April to October. The forest has an average canopy height of 20–30 m, stem density of 367 ha^{-1}, and species richness of 59 ha^{-1} (all data for trees >10 cm diameter at breast height [DBH]; Instituto Boliviano de Investigación Forestal, unpublished data).

Fifty of the most common tree species were selected. These species differ widely in adult stature and shade tolerance and represent 84% of the stems >10 cm DBH in the forest. Data on sapling growth, survival, and leaf traits come from L. Poorter and F. Bongers (unpublished). For each species, 15 saplings between 0.5 and 2.5 m in height were tagged. These saplings experienced low- to intermediate-light conditions, and their height and survival were remeasured five times during a 2-year period in about the second, fourth, ninth, thirteenth, and twenty-fifth months 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 different-colored marker. In total, approximately 11,500 leaves were monitored, on average 225 leaves per species (range 35–688) and 15 leaves per individual. Leaf survival rate of the first four cohorts was analyzed with a survival analysis (Scheiner and Gurevitch 1993). The life span of each leaf was calculated from the start of monitoring until the leaf died. Leaves that survived the monitoring period were right censored. The Kaplan-Meier approach provided leaf life tables, that is, the percentages P of the leaves that survived until a moment in time T (days). The probability that a leaf dies during a day is calculated as the slope b from the regression

$$\ln P = 100 - bT.$$

The leaf survival rate (probability to survive 1 day) was then calculated as $1 - b/100$.

Photosynthesis was measured in February 2004 for five additional saplings per species. These saplings occurred at high-light conditions (crown position index ≥ 2.5, a lot of lateral and/or overhead light) in forest gaps, in clearings, and along forest roads. Photosynthetic measurements were made on the youngest fully expanded leaf, using a portable infrared gas-exchange system (CIRAS-1 PP system, Hitchin, UK). Light-saturated photosynthetic rates (A_{max}, in μmol m^{-2} s^{-1}) were recorded after the leaf was fully induced. Subsequently, leaves were detached, their areas were determined with a flatbed scanner, and they were oven-dried for 48 h at 70°C and then weighed. The SLA (m^2 kg^{-1}) was calculated as the leaf blade area divided by the leaf mass. A forthcoming article by L. Poorter and F. Bongers will provide further details on the leaf and plant measurements.

Plant traits were not measured under equal conditions. Leaf survival rate and plant survival rate were measured at low or intermediate light levels, where leaf survival rate is expected to be most important for plant survival. SLA and photosynthetic capacity were determined at high irradiance, where they were expected to be most important for height growth rates. Height growth rate was, however, measured at low or intermediate irradiance. Because growth rates in gaps correlate positively and strongly with growth rate in the shade (Kitajima 1994; Poorter 1999), field data on height growth rates were used as proxies for the height growth rates under optimal resource conditions. As a consequence, the model predictions cannot provide realistic quantitative predictions of growth and survival, but they do provide good predictions about the ranking in the performance of the different species.

A Carbon-Based Plant Growth Model

To analyze the consequence of leaf traits for whole-plant performance, we used a carbon-based plant growth model (Sterck et al. 2005). The model consists of a three-dimensional tree growing in a three-dimensional light environment. Carbon gain (photosynthesis) and loss (respiration, leaf shedding) are scaled to the whole-plant level. Net carbon gain is invested in growth, and no carbon is stored. The plant may die eventually when carbon losses exceed gains.

In the model, a tree is defined at the metamer level (a segment [internode plus distal node], leaf, and appending apical and axillary meristem), whereby a pipe runs from the leaf blade basis through the petiole, through the segments between the petiole and the tree root. For the presented simulations, metamer dimensions were set to constant values (segment length, 5 cm; leaf length, 5 cm; leaf width, 2.5 cm) that fall within the range of observed leaf areas observed for these species. Metamer component orientations were also fixed (phyllotaxis [137°], local elevation [45°], and leaf plane lie in the horizontal plane; see also table 1).

In the model, a plant may produce new metamers and drop metamers or leaves at every time step (set to 10 days). With each new metamer, the plant produces a new pipe that runs from leaf blade to tree root and thus results in radial growth of the segments between leaf and tree root. A fixed proportion was set aside for the roots, but roots were not explicitly modeled in three dimensions. With the set parameter values, trees grew with height: basal stem diameter ratios were close to 100, which is typical for juvenile trees (Hallé et al. 1978). The simulated plants thus grow in three dimensions according to a fixed-branch algorithm, with fixed local branch angles and phyllotaxis (Sterck et al. 2005).

The carbon gain depends on the leaf properties and on the light environment. For each leaf, the gross photosynthesis is the integral of the instantaneous photosynthetic rate over the time interval between sunrise and sunset, calculated with the nonrectangular hyperbola (Johnson and Thornley 1984; Pearcy and Yang 1996; Sterck et al. 2005).

The irradiance on each leaf can be calculated at any time on the basis of solar position (defined by latitude, day, and time) and light interception by the surrounding canopy and the tree crown itself (self-shading; Sterck et al. 2005). By integrating the instantaneous photosynthetic rates at the leaf center in response to light for the hours between sunrise and sunset, we calculated the gross photosynthesis per leaf. By following the same procedure for all the leaves in a tree, we calculated the gross photosynthesis rate per day for the whole tree and the net acquired carbon per time step. The acquired carbon equals the growth and maintenance costs and is the major "engine" of tree growth in the model.

Because some tree growth parameters (e.g., wood respiration, root allocation) are estimated with considerable uncertainty, one should be careful with the results in an absolute sense. However, in this article, the model will be used only to compare the performances of simulated trees in different light environments. These simulated trees are equivalent in all plant traits (table 1) except photosynthetic capacity, SLA, and leaf turnover rate. For each of the 50 species, we simulated growing trees with the measured species-specific values for each of these latter three leaf parameters. We did not evaluate the effects of geometrical traits (e.g., leaf angle, leaf size; Falster and Westoby 2003) and environmental traits (e.g., falling debris, herbivory, pathogens) that can have significant effects on the carbon economy. We here focus exclusively on the effects of pho-

Table 1: Parameters set as constants in presented model runs

Parameter	Value	References
Morphology:		
Phyllotaxis (°)	137	This article (see "Methods")
Local elevation of branch (°)	45	This article (see "Methods")
Surface area of leaf (cm^2)	40	This article (see "Methods")
Density of pipe (kg m^{-3})	600	Reyes et al. 1992; Niklas 1994
Density of leaf (kg m^{-3})	300	Bongers and Popma 1990
Cross-sectional area of pipe (mm^2)	.25	Sterck et al. 2005
Carbon economy:		
Carbon mass to biomass ratio	.45	Poorter 1989
Pipe maintenance costs (nmol C mol C^{-1} s^{-1})	60	Penning de Vries 1975; Veneklaas and Poorter 1998
Leaf maintenance costs (% photosynthetic capacity)	5	Pons and Anten 2004
Construction cost (mol C mol C^{-1})	1.45	Poorter and Villar 1997
Adsorption coefficient	.86	Poorter et al. 2000
Quantum yield (mol CO$_2$ mol photon^{-1})	.06	Lambers et al. 1998

tosynthetic capacity, SLA, and leaf survival on interspecific performance differences in productive (gap) versus non-productive (closed canopy) environments.

The closed canopy and the canopy surrounding the gap were 30 m tall and had spherically homogeneous leaf distributions and a leaf area index of 3. This leaf area index is low compared to values in real forest, but in combination with homogeneously distributed leaves, it resulted in forest-floor light levels of 2%–4% in the closed canopy and ∼40% (of open-sky light) in the gap center (Sterck et al. 2005), which is typical of tropical forests (e.g., van der Meer 1995; Sterck 1999).

Tree growth was simulated for each species in both environments, and height growth rates in gap and survival rates in closed canopy are presented. The modeled survival is expressed as the number of days that trees survived over 5 years, divided by the total number of days. To test our predictions, we compared the modeled height growth rates in the gap and survival rates in the closed canopy with the measured height growth rates and survival rates in the Bolivian forest. Ultimately, the modeled height growth rate in the gap was correlated with the modeled survival rate in the closed canopy.

Results and Discussion

Plant Trait Correlations

Leaf traits varied strongly among saplings of the 50 sympatric tree species of a Bolivian rain forest. SLA varied by a factor of ∼4, photosynthetic capacity by ∼5, and leaf life span by ∼10 (2.7–31.1 months; L. Poorter and F. Bongers, unpublished data). These factors for interspecific leaf trait differences typically exceed the reported factor of ∼2 for intraspecific differences (Veneklaas and Poorter 1998; Reich et al. 2003) and suggest that interspecific leaf trait variation strongly contributes to interspecific differences in carbon economy and plant performance. This study neglects plastic light responses in plant traits and exclusively focuses on the effects of measured (average) specific leaf trait values on performance differences across species.

The leaf traits were strongly correlated: SLA and photosynthetic capacity decreased with increasing leaf survival rate (SLA = 1,311 − 1,300(leaf survival rate), $r^2 = 0.67$, $P < .001$; light-saturated mass-based photosynthetic rate = 21,201 − 21,136(leaf survival rate), $r^2 = 0.66$, $P < .001$; fig. 1A, 1B). Height growth rate decreased linearly with sapling survival rate (height growth rate = 1.77 − 1.67(sapling survival rate), $r^2 = 0.57$, $P < .001$; fig. 1C). Similar results have been shown for other tree communities worldwide (for leaf traits, e.g., Reich et al. 1992, 1997; Wright et al. 2004; for growth vs. survival, Kitajima 1994; Wright et al. 2003). In this study, the results were
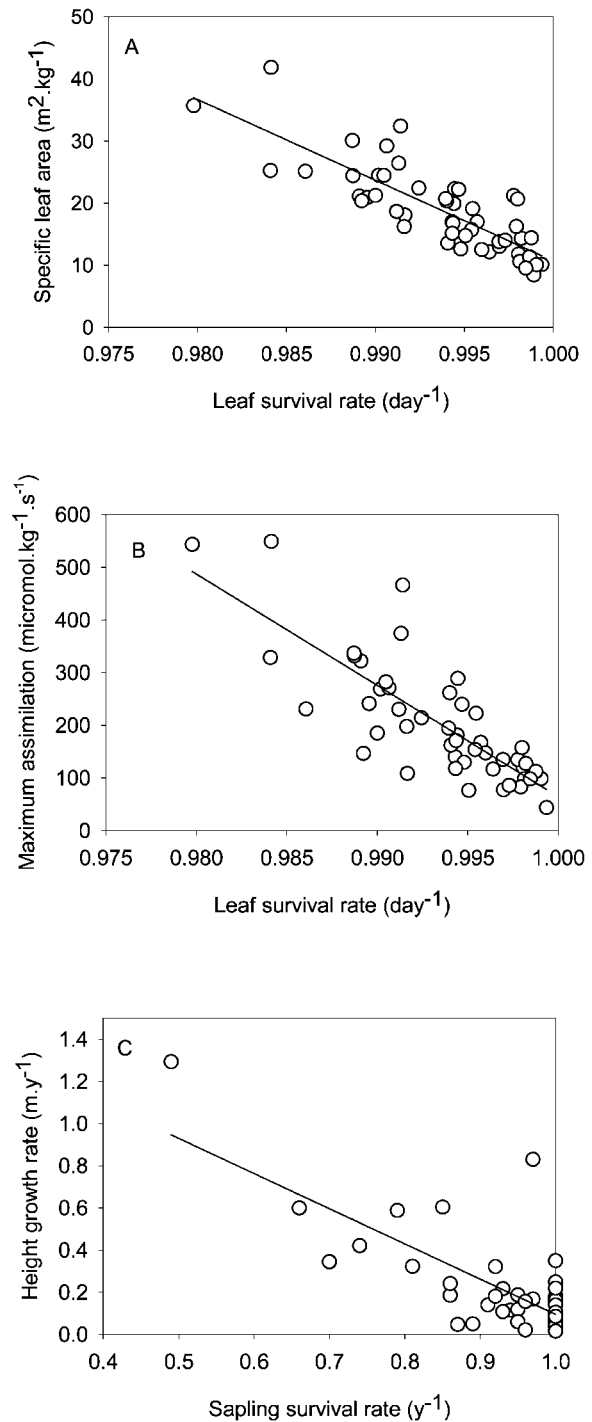

Figure 1: Trait relationships for 50 tree species in a Bolivian rain forest community. *A*, Specific leaf area versus leaf survival rate ($y = 1,311 − 1,300x$, $r^2 = 0.67$, $P < .001$); *B*, light-saturated mass-based photosynthetic rates versus leaf survival rate ($y = 21,201 − 21,136x$, $r^2 = 0.66$, $P < .001$); *C*, height growth rate versus sapling survival rate ($y = 1.77 − 1.67x$, $r^2 = 0.57$, $P < .001$). The data are from L. Poorter and F. Bongers (unpublished).
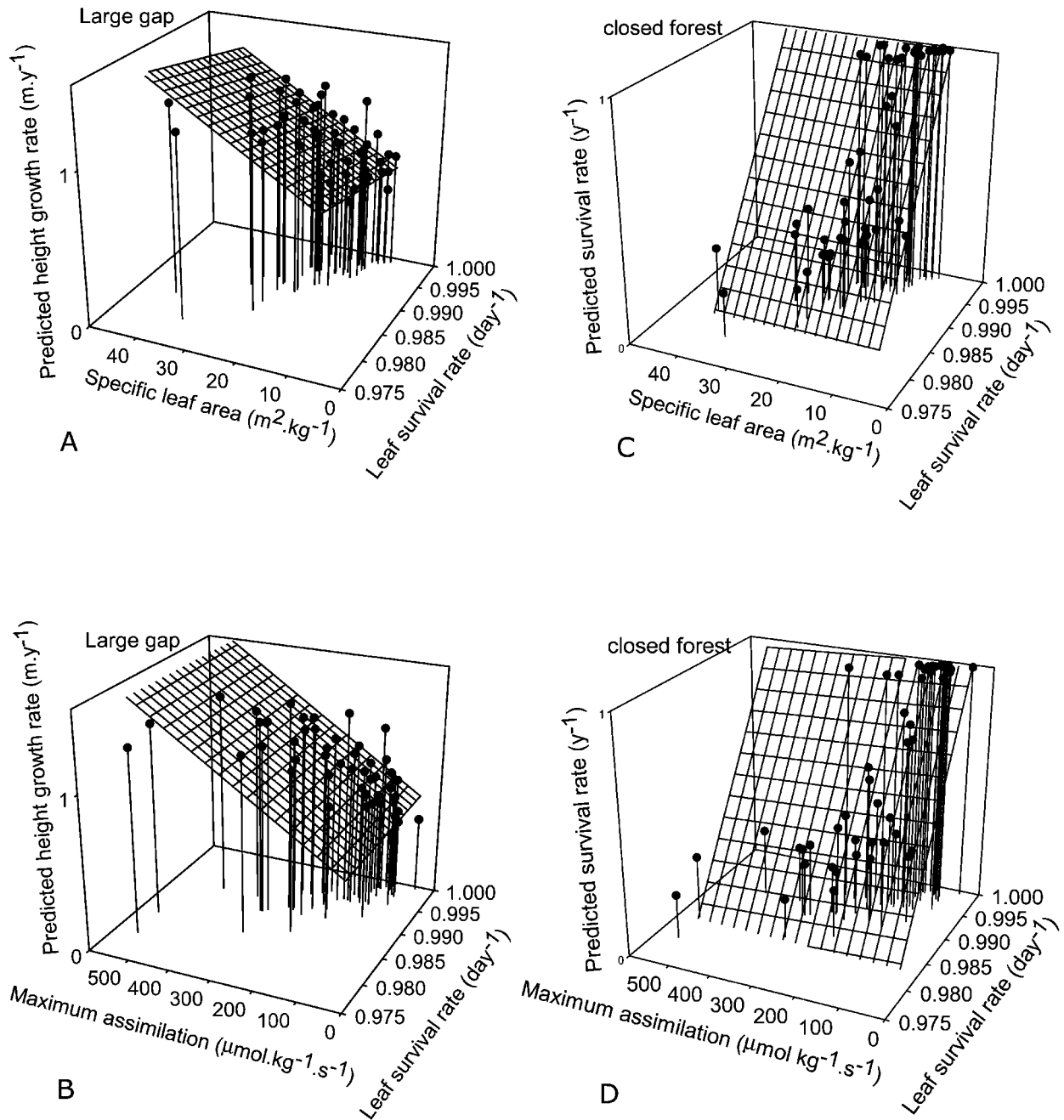
Figure 2: Effects of leaf traits on modeled plant performance. Each dot represents one species, and lines connect each dot with its corresponding parameter value in leaf-trait space. *A, B,* Effects of leaf traits on annual height growth rate in a gap; *C, D,* effects of leaf traits on survival rate in a closed forest. Survival was simulated over a 5-year period and calculated as the period of survival (in years) per 5 years.

used to test the hypothesis that leaf trait effects on the plant's carbon economy actually contribute to the growth-survival trade-off among sympatric tree species in productive (gap) versus nonproductive (closed canopy) environments.

Scaling Up from Leaf Traits to Whole-Plant Performance

To test this hypothesis, a plant growth model was used to simulate the growth of the 50 tree species in a gap center and a closed forest. In the simulated trees, the model pa-

rameters were set to equal values, except for the leaf traits that were set to species-specific values. Because of a strong correlation between SLA and photosynthetic capacity ($r = 0.91$, $P < .001$), both leaf traits showed similar patterns with leaf survival rate and tree performance (fig. 2). The strong correlation between SLA and photosynthetic capacity violates the statistical assumption of independent predictor variables. To avoid this problem, we ran the same model but with either SLA or photosynthetic capacity kept constant at the mean value for all species pooled (SLA = 19.0 m² kg⁻¹, photosynthetic capacity = 193 μmol CO_2 kg⁻¹ s⁻¹) and thus tested for the independent contributions of each leaf trait to tree performance (regression models 2 and 3 in table 2). These regressions show that both SLA and photosynthetic capacity contributed to cross-species variation in height growth rate in the gap, and the standardized regressions suggest that they did so by the same order of magnitude. Leaf survival rate showed only a relatively weak effect on height growth in one of the three regression models, suggesting that the role of leaf survival is inferior in this respect. Although height growth rates were much lower in the closed canopy, these rates also increased with SLA and photosynthetic capacity (data not shown). In the nonproductive environment, leaf survival contributed most strongly to the interspecific variation in survival in the low irradiance of a closed canopy, and SLA and photosynthetic capacity had no significant effect at all. For the large gap, the simulations predicted 100% survival chance for all species.

Both modeled height growth rate and survival rate correlated positively with field measurements (fig. 3*A*, 3*B*), and predicted height growth rate correlated negatively with predicted survival rate (fig. 3*C*). The considerable noise in these relationships probably results from the strong assumptions on plant geometry, the interspecific differences in the nonproductive plant components (e.g., wood density) and other carbon sinks (e.g., storage), and the exclusion of ecological factors such as damage by pathogens, herbivores, and fallen debris in the model. Despite these confounding factors, the patterns are in support of our major hypothesis and emphasize a significant role of leaf trait variation in interspecific performance differences among saplings of different rain forest tree species.

Westoby et al. (2000) showed that species that increase in SLA, photosynthetic capacity, and light capture per dry mass by an order of 2 reduce leaf life by more than an order of 2. This means that the area deployed multiplied by the time over which it is deployed tends to be greater for low-SLA leaves (Westoby et al. 2000). Westoby et al. addressed the question of why species with higher SLA did not tend to evolve toward lower values, and they suggested that high-SLA species have a higher growth rate in the more productive environment because of the time-discounting effect. They mention four possible reasons for such a time-discounting effect: first, reduced revenue from older leaves, second, an increase in overshading, third, the risk of death before the long-term benefit, and finally, the resulting compound-interest effect. Our results suggest

Table 2: Effects of leaf traits on height growth and survival in different light environments, using multiple linear regressions

Model and predictor	Height growth in gap (m year⁻¹)	Survival in closed forest (year⁻¹)
Model 1:		
Leaf survival rate (day⁻¹)	NS	.81**
Maximum assimilation (μmol kg⁻¹ s⁻¹)	.79**	NS
Specific leaf area (m² kg⁻¹)	NS	NS
R^2	.63**	.66**
Model 2:		
Leaf survival rate (day⁻¹)	NS	.84**
Specific leaf area (m² kg⁻¹)	.74**	NS
R^2	.53**	.71**
Model 3:		
Leaf survival rate (day⁻¹)	.49*	.86**
Maximum assimilation (μmol kg⁻¹ s⁻¹)	.87**	NS
R^2	.31**	.74**

Note: NS = not significant. For model 1, all leaf traits were varied according to the species-specific values. Model 2 was similar to model 1, except that the photosynthetic capacity was set to the mean pooled species value (193 μmol kg⁻¹ s⁻¹). Model 3 was similar to model 1, except that specific leaf area was set to the mean pooled species value (19.0 m² kg⁻¹). Standardized regression coefficients and R^2 values are shown for the sake of comparison.
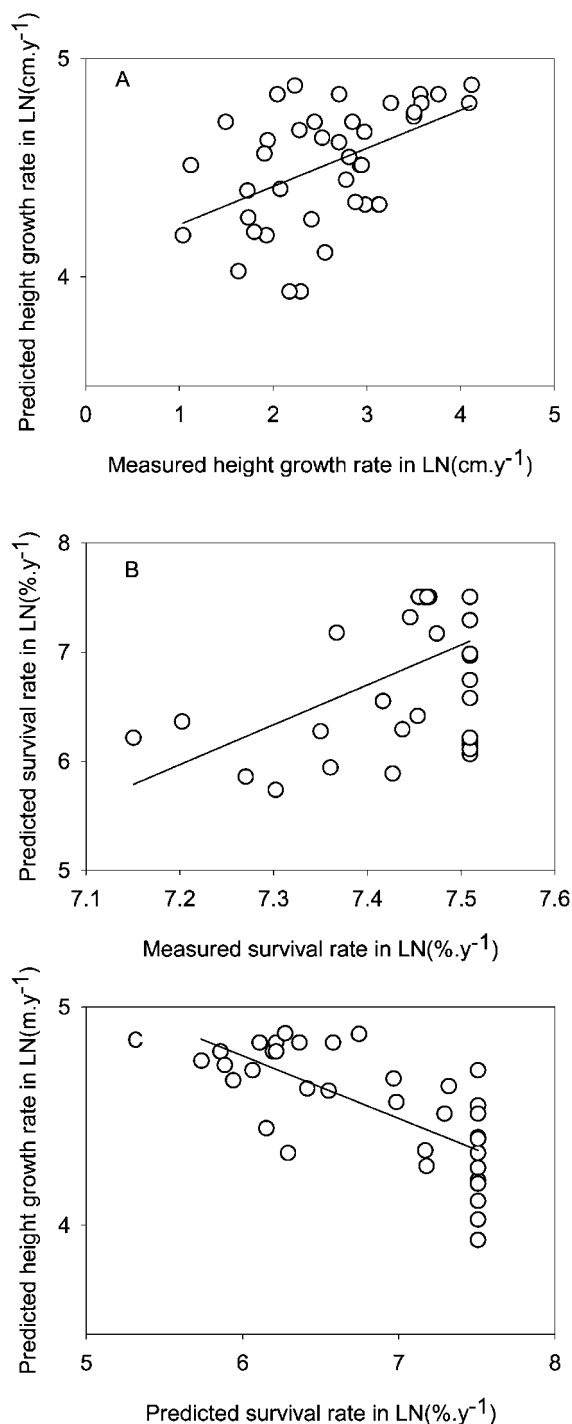
  * $P < .05$.

  ** $P < .001$.

that the compound-interest effect of both a higher SLA and a higher photosynthetic capacity suffices to produce higher growth rates in the gap (see table 2). Such a compound-interest effect is inferior in the shade, as shown by the lack of effects of SLA and photosynthetic capacity on tree survival. Consequently, the leaf survival rate exclusively determined the whole-plant survival in the shade.

Conclusions

A dominant hypothesis explaining species coexistence in tropical forest is that trade-offs in characters allow species to adapt to different environments, but tests for this hypothesis are scarce. Here we tested how the effects of leaf trade-offs on whole-plant carbon economy contribute to differential performances across species in different light environments. This is, as far as we know, the first time that a theoretical plant growth model has been used in combination with a large, multiple-species, comparative data set to test for such leaf trade-off effects. It was observed that SLA and photosynthetic capacity codetermined interspecific height growth variation in a forest gap; that leaf survival rate was the only major factor contributing to the variation in plant survival rate under a closed canopy; and that these leaf traits jointly explain ∼50% of the whole-plant growth-survival trade-off in a high-light versus low-light environment (fig. 3C). This study thus scaled leaf economies to carbon economies of whole growing trees and showed convincingly that leaf trade-offs codetermine the growth-survival trade-off. These trade-offs have important consequences for specialization to different light environments and the coexistence of tree species.

Acknowledgments

Figure 3: Modeled and measured performances in a Bolivian rain forest. *A*, Annual height growth rates in a gap ($\ln y = 4.17 + 0.133 \ln x$, $r^2 = 0.18$, $P = .002$); *B*, survival rates in a closed forest ($\ln y = -621 + 2.25 \ln x$, $r^2 = 0.20$, $P = .002$); *C*, predicted height growth versus predicted survival ($\ln y = 11.19 + 1.60 \ln x$, $r^2 = 0.50$, $P < .001$). The model survival was simulated over a 5-year period and calculated as the period of survival (in years) per 5 years.

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