

Are Species Adapted to Their Regeneration Niche, Adult Niche, or Both?

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ABSTRACT: Functional traits are important drivers of successional processes and the assembly of plant communities. It is generally assumed that functional traits are closely linked to the regeneration niche because of the high selection pressures in the seedling stage, but recent studies have challenged this view. In this study, I use cross species and phylogenetic correlation analysis between leaf traits and light environment to evaluate whether species are adapted to the regeneration niche, adult niche, or both. Leaf chemistry, morphology, physiology, and crown exposure were quantified for up to 58 Bolivian tropical moist forest tree species that differ in their regeneration and adult light niche. Multiple regression analysis shows that leaf traits of seedlings, saplings, and trees are most strongly related to the regeneration niche, and once this is taken into account, adult niche does not significantly explain any of the remaining variation in leaf traits. This suggests that, although the regeneration phase is short, it has a long-lasting effect on the form and shape of plant species.

Keywords: adaptation, functional traits, light, maximal size, tropical rain forest, regeneration.

Functional traits are plant attributes that enhance establishment, growth, survival, reproduction, and, ultimately, plant fitness. Functional traits are important drivers of the distribution of species along environmental gradients (Fonseca et al. 2000), successional processes (Bazzaz 1979;

Tilman 1982; Grime 2001), and the assembly of plant communities (Keddy 2001). Functional traits are thought to be closely linked to the regeneration niche of the species. Grubb (1977) defined the regeneration niche as the biotic and abiotic species requirements to replace a mature individual. This concept encompasses most processes in the life cycle, from flowering to establishment and onward growth. The regeneration niche is defined here, in line with common usage, as the environmental conditions in the early phase in the life cycle of a plant (seedling and sapling stage). Seeds may get dispersed to most places and germinate under most environmental conditions (Kyereh et al. 1999; Peña-Claros 2001), but it is the strong early environmental requirements, in combination with a high mortality in the seedling stage, that determine where a species regenerates. The regeneration phase is therefore considered to be the bottleneck for successful species establishment, and many studies have evaluated plant adaptations to the regeneration niche.

Species adaptations to the regeneration niche form the central paradigm necessary to understand forest succession (Finegan 1996; Pacala et al. 1996), and early- and late-successional trees are found to differ predictably in their functional traits (Bazzaz 1979; Grime 2001). However, trees are long-lived organisms, and the seedling stage may present only a brief period in the life span of a tree. In a Guyanan tropical rain forest, for example, species may take 12–126 years to attain 3 m in height, while they may live 66–380 years in the forest canopy (Zagt 1997). The question is whether species are adapted to the light conditions they experience for a relatively brief period as a seedling or for a long period as an adult (Popma et al. 1992; Thomas and Bazzaz 1999; Reich 2000). This question becomes more pressing, as many species experience marked changes in irradiance during the transition from seedling to adult (Oldeman and van Dijk 1991; Poorter et al. 2005). Most shade-tolerant species, for example, establish in the shaded understory but encounter gradually brighter conditions when they grow toward the canopy.

Thomas and Bazzaz (1999) made a strong case for the importance of the adult niche. In a closed-canopy forest

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there is a predictable and strong vertical gradient in irradiance, from 1% at the forest floor to 100% above the canopy. Among species that can regenerate in the shade, the tall species experience on average higher light levels than small species, which should have led to the evolution of important high-light adaptations. In their groundbreaking study, Thomas and Bazzaz (1999) evaluated the evolutionary responses to vertical gradients in irradiance by examining leaf traits of 28 shade-tolerant rain forest species using adult stature (maximal height; H_{\max}) as an indicator of the adult light niche. They found, as expected, that leaf traits of exposed adult trees were positively related to the adult stature of the species. Surprisingly, however, they also found that the leaf traits of shaded understory saplings showed similar strong correlations with adult stature. Combined, these results suggest that species are adapted to the adult light niche. However, it may also be possible that these species already differ in light requirements in the sapling stage, in which case differences in leaf traits could reflect both the regeneration and adult niches (Reich 2000). A real test of the adaptation hypothesis, therefore, requires quantification of both the regeneration and the adult light niches.

Trait associations with H_{\max} are also of interest in themselves. H_{\max} is considered to be one of the important plant axes of variation, capturing a large part of functional trait variation found among species (Westoby 1998; Westoby et al. 2002). Light is a unidirectional resource, and competition for light is highly asymmetric. Early in succession, small, light-demanding species are gradually replaced by taller shade-tolerant ones that overtop the smaller species and outshade them (Huston and Smith 1987; Finegan 1996). For early-successional species, there may be a negative relationship between light demand and H_{\max} , whereas for late-successional species that regenerate under closed-canopy conditions, there may be a positive relationship (Thomas and Bazzaz 1999; Falster and Westoby 2005). This may also explain why different relationships are found between functional traits and H_{\max} for early- and late-successional species (Falster and Westoby 2005; van Gelder et al. 2006).

In this study I provide a first test of whether plant traits reflect adaptation to the regeneration niche, adult niche, or both. To this end I quantified leaf traits and light environments of up to 58 rain forest tree species that differ in their regeneration and adult light niches. I focus on three functional traits related to leaf morphology (specific leaf area; SLA), physiology (light-saturated photosynthetic rate on a mass basis; A_{mass}), and chemistry (nitrogen content per unit mass; N_{mass}). The SLA indicates the efficiency of biomass investment for light capture and is closely associated with the leaf life span and leaf economics spectrum of the species (Wright et al. 2004). The N_{mass} is an

important component of the photosynthetic machinery (Rubisco) and the light harvesting complex, and the A_{mass} indicates the species' capacity for carbon gain. Leaf traits have been measured for sun leaves of seedlings, saplings, and adult trees, and they have been related to H_{\max} and the crown exposure of species in the regeneration and adult stage.

Methods

Research Site

Research was carried out in part in the semievergreen lowland tropical moist forest of La Chonta (15°47'S, 62°55'W), Bolivia. Annual precipitation in the region is 1,520 mm, with a dry season (<100 mm month⁻¹) from April to October. The forest is situated on an extension of the Brazilian shield at an altitude of 400 m. Over 150 tree species are found in the area. The forest has an average canopy height of 25 m, stem density of 368 ha⁻¹, basal area of 19.7 m² ha⁻¹, species richness of 59 ha⁻¹ (all data for trees ≥10 cm diameter at breast height [DBH]; Instituto Boliviano de Investigación Forestal [IBIF], permanent sample plot data). The IBIF monitors trees in a large set of permanent sample plots, according to a nested design (trees ≥40 cm DBH in 320 ha; trees ≥20 cm DBH in 160 ha; trees ≥10 cm DBH in 48 ha).

Species Selection and Crown Exposure

Fifty-eight of the most common species that differed in adult stature and shade tolerance have been selected (see the appendix in the online edition of the *American Naturalist*). Maximum adult stature (H_{\max}) was calculated for each species using the diameter for the third-thickest tree in the permanent sample plot (IBIF, unpublished data) and species-specific height-diameter relationships (Poorter et al. 2006). The H_{\max} values presented here are slightly higher than those in Poorter et al. (2006) because the latter were based on the thickest tree in a subsample. Adult stature varied from 5 m for *Erythrochiton fallax* to 46 m for *Ficus boliviana* (table A1 in the online edition of the *American Naturalist*). Based on field observations, the species were classified as pioneers (combining both short- and long-lived pioneers) if they needed high light for successful establishment (Justiniano et al. 2004; J. Justiniano and L. Poorter, personal observation) and as shade tolerants if they could establish and survive in the shade. Yet, light demand varied gradually and continuously among species. In a separate study, I provided an objective, quantitative measure of the light demand by analyzing the height-light trajectories for each species. These height-light trajectories give a population-level description of how the

crown exposure varies with the height of the species. To this end, all individuals ≥ 10 cm DBH of a species occurring in the permanent sample plots in La Chonta were selected. In addition, for each species we searched for an additional 30 plants between 20 cm height and 10 cm DBH. For individuals up to 5 m, we measured height directly with a measuring pole, and for taller individuals, we estimated height from DBH, using species-specific regression curves (Poorter et al. 2006). For each individual, we estimated the crown exposure (CE; cf. Dawkins and Field 1978). This crown exposure has been given the following values: 1 if the tree does not receive any direct light, 2 if it receives lateral light, 3 if it receives overhead light on part of the crown, 4 if it receives full overhead light on the whole crown, and 5 if it has an emergent crown that receives light from all directions. The crown exposure can be measured repeatably (average difference between two independent observers is 0.1 ± 0.01 SE), and there is a good relation between CE and both canopy openness (Davies et al. 1998) and incident radiation (Clark et al. 1993). The average number of individuals per species was 662 (range 41–9,319). For each species, we related the CE to tree height using a multinomial regression analysis (Poorter et al. 2006; cf. Poorter et al. 2005). Using the regression equation, the average population-level crown exposure at a standardized height of 2 m (CE_{reg} ; regeneration niche) and at maximal species height (CE_{adult} ; adult niche) was calculated. Similar-sized individuals of the same species can be found under a wide range of crown exposures, but what counts from an evolutionary point of view is the average population-level crown exposure of the species (Poorter et al. 2005).

Data Collection

For the description of the leaf traits, we used different subsets of these 58 species, capitalizing on already existing data sets (Slot 2004; Poorter and Bongers 2006; Rozendaal et al. 2006; L. Poorter, unpublished data). Leaf traits were measured under “optimal” resource conditions (intermediate to high light). Leaf traits may differ between sun and shade leaves, but this light-dependent variation in leaf traits is rather small (average partial r^2 for 16 leaf traits = 0.08) compared with the large variation found among species (average partial r^2 = 0.76; Rozendaal et al. 2006). The measured leaf traits are therefore a good reflection of the inherent leaf characteristics of the species.

Leaf traits of saplings were made in situ in February 2004 for 53 species, five saplings per species (Poorter and Bongers 2006). To determine the inherent photosynthetic capacity of the species, measurements were made on 0.5–3.5-m-tall saplings occurring in high-light conditions (lateral direct light, or overhead light) in forest gaps, clearings,

and along forest roads. Measurements using a CIRAS-1 portable infrared gas analyzer (PP Systems, Amesbury, MA) were done on the youngest fully expanded leaf. The CO_2 concentration was kept at 360 ppm, and light-saturated photosynthetic rates (A_{area} in $\mu mol m^{-2} s^{-1}$) were measured after full induction at a saturating photosynthetic photon flux density of $1,300 \mu mol m^{-2} s^{-1}$. The leaf was thereafter detached, and the leaf area was determined with a flatbed scanner, after which one or several leaf punches were taken from the leaf blade, excluding the midrib or large veins. Leaf blade and punches were oven-dried for 48 h at $70^\circ C$ and weighed. The SLA (in $m^2 kg^{-1}$) was calculated as the leaf blade area divided by the leaf dry mass and the punch area divided by the punch dry mass. Both measures of SLA were closely correlated ($r = 0.95$, $P < .001$). Mass-based assimilation rate (A_{mass} , in $nmol g^{-1} s^{-1}$) was calculated by multiplying the area-based rates by the SLA of the leaf punch. Total organic N was determined using the Kjeldahl assay.

Leaf traits of adult trees were measured for 39 species from November 2004 to February 2005 (Rozendaal et al. 2006). Five sun trees were selected per species, with their leaves exposed to direct sunlight for at least part of the day. Trees were between 10 and 20 cm DBH and 8–15 m tall (except for two species that attained smaller maximal sizes—for these two species, leaves were collected for the tallest individuals). For each tree, four fully expanded leaves were sampled from the outer leaf layer, in the middle of the crown. SLA was measured as indicated above, and N_{mass} was determined per species by pooling all leaves. Unfortunately, no taller trees could be sampled because of limited canopy access. Canopy leaves of tall trees experience more water stress because of increased water transport path length and gravity effects, and they have a reduced SLA and A_{mass} (Koch et al. 2004). Slightly different correlations between adult leaf traits and H_{max} might have been found if leaves had been sampled at the maximal height of the species.

Leaf traits of 5–25-cm-tall seedlings were measured under experimental conditions in two replicated greenhouses in Santa Cruz, Bolivia ($18^\circ 49' S$, $63^\circ 12' W$; Slot 2004; L. Poorter, unpublished research). Seeds were germinated under intermediate light conditions in a shade house and transplanted to 200-mL pots with half river sand and half topsoil from the forest. Five seedlings per species were transferred to each of two shade houses providing 10% of full sunlight. Seedlings of 13 species were measured after 2 months for their photosynthesis after full induction at a saturating photosynthetic photon flux density of $850 \mu mol m^{-2} s^{-1}$ and at a CO_2 concentration between 360 and 380 ppm. The leaf used for the photosynthesis measurement was detached and measured for the SLA following the above procedure. This SLA was used for calculating

the mass-based photosynthetic rate. Also, the SLA at the whole-plant level was measured for 22 species, which will be used for comparisons of leaf morphology

Data Analysis

Species-specific leaf traits measured in the seedling, sapling, and adult stages were correlated to the crown exposure of 2-m-tall plants (the regeneration niche), the crown exposure at maximal height (the adult niche), and H_{\max} . This was done for all species combined and shade tolerants and pioneers separately. Both cross-species and evolutionary divergence correlation analyses were carried out. In the latter phylogenetic analysis, each branching divergence in the phylogenetic tree represents one data point. A conservative phylogenetic tree was made using the program Phylomatic (Webb and Donoghue 2005). The phylogenies used for this study were based on the conservative angiosperm phylogeny (C20040402). Phylomatic starts with a family-level tree of the angiosperms. For the list of the species in this study, the appropriate families are selected, and the remainder is pruned from the tree. Phylomatic considers genera as polytomies within families and species as polytomies within genera. Phylogenetic correlations were calculated using the "Analysis of Traits" module in Phylocom version 3.34b (Webb et al. 2006). Phylogenetic independent contrasts (PICs) were calculated as the difference in mean trait values for the two nodes (or two species) descending from a node. Following Pagel (1992), phylogenetic branch lengths were set to 1, and polytomies were resolved to provide one contrast. For polytomies, daughter nodes were ranked by trait value and split at the median in two groups (high and low). If there was an odd number of daughter nodes, the median daughter node value was assigned to the lower group if its value was lower than the mean across all daughter nodes or to the upper group if its value was higher than the mean (Wright et al., forthcoming). A correlation coefficient was then calculated between the set of PICs for each pair of traits. Significance tests in these analyses use $n-1$ degrees of freedom, where n is the number of internal nodes providing contrasts. Contrasts were adequately standardized, as they followed a normal distribution (Kruskal-Wallis test, $P > .05$ in all cases). For further details, see Wright et al. (forthcoming).

For each leaf trait, an ANCOVA was carried out with the leaf trait as dependent variable, guild (pioneer or non-pioneer) as a factor, height as a covariate, and a guild-height interaction. A significant interaction term indicates that the relationship between the leaf trait and H_{\max} differs for pioneer and nonpioneer species. A multiple forward regression of leaf traits against CE_{reg} , CE_{adult} , and H_{\max} was done to evaluate whether leaf traits were mainly deter-

mined by CE in the regeneration stage, CE in the adult stage, adult stature, or a combination of these. Because crown exposure and adult stature were used as predictors for functional traits, a normal model I regression was used. A similar multiple regression of leaf traits against CE_{reg} , CE_{adult} , and H_{\max} was carried out using phylogenetic contrasts. In this case the regression was forced through the origin. All statistical analyses were carried out using the software package SPSS 11 (SPSS, Chicago, IL).

Results

Is H_{\max} a Good Predictor of Regeneration and Adult Crown Exposure?

Crown exposure of 2-m-tall saplings varied from 1.27 for the shade-tolerant understory treelet *Erythrochiton fallax* to 2.52 for the short-lived pioneer *Trema micrantha* (fig. 1). Crown exposure in the adult stage varied from 1.10 for *Pricramnia sellowi* to 4.96 for *Ficus boliviana*. There was a significant increase in CE from sapling to adult stage ($\Delta CE = 2.1$, paired t -test, $t = 17.9$, $P < .001$, $n = 58$) indicating that species experience marked shifts in CE over their lifetime. Regeneration and adult crown exposure were positively correlated (Pearson's $r = 0.51$, $P < .001$, $n = 58$). When all species were combined, the CE_{adult} showed a strong positive correlation with H_{\max} ($r = 0.89$, $P < .001$, $n = 58$), whereas the CE_{reg} showed a weaker

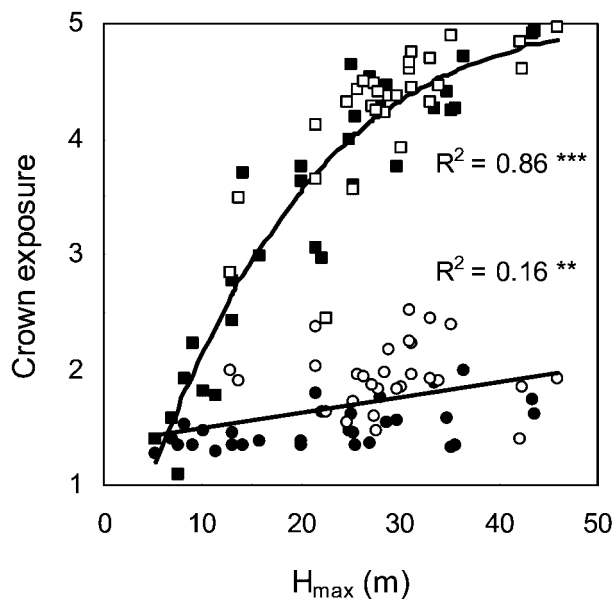


Figure 1: Crown exposure of saplings (circles) and adults (squares) in relation to H_{\max} for pioneer species (open symbols) and shade-tolerant species (closed symbols). Two asterisks, $P < .01$; three asterisks, $P < .001$.

positive relationship ($r = 0.41$, $P = .002$, $n = 58$; fig. 1). Relationships between CE and H_{\max} were stronger for shade tolerants (CE_{adult} : $r = 0.92$, $P < .001$; CE_{reg} : $r = 0.56$, $P < .001$; $n = 31$) than for pioneers (CE_{adult} : $r = 0.74$, $P < .001$; CE_{reg} : $r = -0.01$, $P = 1.00$; $n = 27$).

Relationships between Leaf Traits, Crown Exposure, and H_{\max}

Specific leaf area of seedlings, saplings, and adult trees was positively related to species' crown exposure in the regeneration stage (fig. A1 in the online edition of the *American Naturalist*). The strength of the relationship diminished, or disappeared, when the SLA was related to adult crown exposure or H_{\max} . Relationships between SLA and crown exposure were strongest for seedlings, intermediate for saplings, and weakest for adult trees.

Data on N_{mass} were only available for saplings and adults. The N_{mass} of saplings and adults was positively related to the crown exposure in the regeneration stage (fig. A2 in the online edition of the *American Naturalist*) but not related to the adult crown exposure or H_{\max} . Crown exposures explained similar proportions of the variance for saplings and adults.

Data on A_{mass} were only available for seedlings and saplings. The A_{mass} of seedlings was not related to crown exposure in any stage of the life cycle of the species. The A_{mass} of saplings was strongly positively correlated to the regeneration CE, moderately correlated to the adult CE, and not related to H_{\max} .

Similar correlations between leaf traits, crown exposure, and H_{\max} were obtained when the phylogenetic relatedness of the species was taken into account (table 1). These phylogenetic correlations were slightly weaker and sometimes less significant (SLA_{sapling} , SLA_{adult} , $N_{\text{mass sapling}}$), probably because of the lower N .

The ANCOVA showed that seedlings of shade tolerants and pioneers have similar relationships between leaf traits and H_{\max} (no significant guild- H_{\max} interaction, $F = 0.3$ – 0.9 ; data not shown), whereas saplings and trees of shade tolerants and pioneers have significantly different relationships between leaf traits and H_{\max} (guild- H_{\max} interaction, $F = 5.4$ – 13.1 , $P < .05$ in all cases; data not shown).

Are Leaf Traits Related to the Regeneration or Adult Crown Exposure?

A multiple regression analysis was done to analyze whether leaf traits were mainly determined by crown exposure in the regeneration stage, the adult stage, H_{\max} , or a combination of these (table 2). Forward and backward regression yielded the same results. Leaf characteristics of

seedlings (only SLA), saplings, and adults were only significantly related to crown exposure in the regeneration stage (table 2). This pattern was also confirmed by the phylogenetic regression analyses based on phylogenetic contrasts (table 2). When the regular regression analysis was done for shade tolerants and pioneers separately, some different results emerged. For shade-tolerant species, the regeneration CE was significant in only one case (adult SLA) and H_{\max} in two cases (sapling SLA and A_{mass}). For pioneer species, regeneration CE was significant in three cases. Adult CE had, against expectations, a significant negative effect on adult SLA, and H_{\max} had a negative effect on adult N_{mass} (table 2). If the regression analysis was repeated without H_{\max} , then the adult CE became significant in the three cases where H_{\max} had been significant before.

Discussion

Is H_{\max} a Good Predictor of Regeneration and Adult Crown Exposure?

A good predictor of adult crown exposure turns out to be H_{\max} . The relationship between CE_{adult} and H_{\max} initially increases sharply and then starts to level off at 25 m when species attain the forest canopy (fig. 1). There is a strong vertical light gradient in the forest canopy, and a small increase in adult height pays off in terms of an increased access to light. The relationship between CE_{adult} and H_{\max} is therefore especially tight for shade-tolerant species that establish in the shaded understory (cf. Thomas and Bazzaz 1999), but surprisingly, it is also quite strong for pioneer species that establish in gaps. The reason is that many canopy gaps are wedge or cylinder shaped, and also, in gaps there is a modest increase in irradiance going from the gap floor to the forest canopy (Sterck et al. 2005).

Thomas and Bazzaz (1999) predicted that species that are light demanding in the adult stage are also light demanding in the regeneration stage. Indeed, there was a positive correlation between the adult and regeneration crown exposure ($r = 0.51$), and consequently, there was also a positive relationship between CE_{reg} and H_{\max} (fig. 1). The CE_{reg} - H_{\max} relationship was stronger when only shade-tolerant species were considered. For pioneer species it was hypothesized that the CE_{reg} - H_{\max} relationship would be negative, as during succession, small light-demanding species are replaced by taller, more shade-tolerant species (Finegan 1996). Maybe such a relationship was not found because I did not include small herbs, shrubs, and woody pioneers in the study, which typically are encountered in the very early stages of succession (Peña-Claros 2003; Toledo and Salick 2006).

Table 1: Correlation between leaf traits and regeneration crown exposure (CE_{reg}), adult crown exposure (CE_{adult}), and adult stature (H_{max}) of moist forest tree species

Leaf trait	All species								Shade tolerants								Pioneers							
	Cross				Phylogenetic				Cross				Phylogenetic				Cross				Phylogenetic			
	CE_{reg}	CE_{adult}	H_{max}	n	CE_{reg}	CE_{adult}	H_{max}	n	CE_{reg}	CE_{adult}	H_{max}	n	CE_{reg}	CE_{adult}	H_{max}	n	CE_{reg}	CE_{adult}	H_{max}	n	CE_{reg}	CE_{adult}	H_{max}	n
SLA seedling	.79	.27	.22	22	.74	.04	.06	16	.54	.17	.38	7	-.50	-.26	.13	7	.69	-.03	-.05	15	.63	.15	.03	11
SLA sapling	.69	.40	.33	52	.60	.43	.28	37	.39	.46	.57	28	.43	.60	.60	23	.58	-.16	-.21	24	.50	-.16	-.27	18
SLA adult	.44	-.00	-.09	39	.30	-.09	-.20	30	.42	.08	.26	23	.10	.22	.33	20	.24	-.61	-.60	16	.08	-.63	-.56	11
N_{mass} sapling	.44	.27	.17	52	.27	.22	.06	37	.29	.24	.28	28	.22	.37	.40	23	.33	-.17	-.38	24	.22	-.31	-.55	18
N_{mass} adult	.44	.14	.01	39	.36	.15	.03	30	.30	.19	.20	23	.42	.45	.47	20	.18	-.73	-.73	16	.21	-.75	-.73	16
A_{mass} seedling	-.04	-.06	-.19	13	-.39	-.15	-.53	10	-.96	.04	-.26	4	.30	.20	.12	4	.03	-.40	-.17	9	.03	-.33	-.28	7
A_{mass} sapling	.75	.40	.27	51	.71	.50	.33	37	.46	.50	.56	28	.47	.63	.60	23	.66	-.21	-.35	23	.60	-.18	-.39	18

Note: Species and phylogenetic Pearson correlations are shown for all species combined and shade-tolerant and pioneer species only. The n refers in the latter case to the number of nodes in the phylogenetic tree included in the comparison. The number of polytomies is the difference between the n of the cross-species correlation and the n of the phylogenetic correlation, minus 1. Correlations in bold are significant at $P < .05$; correlations in bold and italic are significant at $P < .01$.

Table 2: Forward multiple regression of leaf traits of moist forest tree species on crown exposure in the regeneration (CE_{reg}) and adult stage (CE_{adult}) and maximum adult stature (H_{max})

Leaf trait	All species				All species phylogenetic				Shade tolerants				Pioneers			
	CE_{reg}	CE_{adult}	H_{max}	r^2	CE_{reg}	CE_{adult}	H_{max}	r^2	CE_{reg}	CE_{adult}	H_{max}	r^2	CE_{reg}	CE_{adult}	H_{max}	r^2
SLA seedling	27.063	24.855	28.748
SLA sapling	14.848	11.33623	.33	15.433
SLA adult	5.019	5.518	...	-6.238
N_{mass} sapling	.8319
N_{mass} adult	.7019	.5813	-.04	.54
A_{mass} seedling
A_{mass} sapling	29657	24251	3.8	.31	33743

Note: Regression results are shown for all species combined, shade-tolerant species, and pioneer species only. A multiple regression based on the phylogenetic contrasts is given for all species combined as well. The regression coefficient and coefficient of determination (r^2) are shown. Regression coefficients in bold are significant at $P < .05$; regression coefficients in bold and italic are significant at $P < .01$. All variables not significant and not included in the regression are indicated by ellipsis dots (...). For the species number, see table 1. For the shade-tolerant species, no regression of A_{mass} of seedlings was carried out because of the low species number ($n = 4$).

Leaf Traits versus Light Demand

All leaf traits showed adaptations to the crown exposure or light demand of the species (figs. A1–A3 in the online edition of the *American Naturalist*). SLA, N_{mass} , and A_{mass} increased with the light demand of the species (cf. Popma et al. 1992; Reich et al. 1995; Strauss-Debenedetti and Bazzaz 1996; Ellis et al. 2000; Poorter et al. 2004). Light-demanding species are early-successional species that are the first ones to establish during primary succession along meandering rivers (Salo et al. 1986), during secondary succession on areas cleared by shifting cultivation (Peña-Claros 2003), and during cyclic succession when a treefall creates a gap in the forest canopy (Brokaw 1985). Light availability is enhanced just after disturbance and declines over time when the regrowing vegetation develops (Saldarriaga 1994; Van der Meer and Bongers 1996). Light-demanding species realize a fast height growth to attain or maintain a position in the canopy of the regrowing gap vegetation. They are able to do so by forming leaves with a high specific leaf area that require a minimum biomass investment to intercept a certain amount of light. The inexpensive construction costs of the leaves allow them to forage opportunistically for light, shed shaded leaves in the bottom of the crown, and replace them with well-lit leaves in the top of the crown (Ackerly 1999). The high nitrogen concentration allows for a high investment in photosynthetic enzymes (Poorter and Evans 1998) and a high photosynthetic capacity, leading to a high carbon gain and growth (Ellis et al. 2000; Poorter and Bongers 2006). Conversely, shade-tolerant late-successional species have to persist under shaded conditions until eventually a gap is formed. They do so by making well-protected leaves with a low SLA, thus deterring potential herbivores and increasing leaf life span (Coley 1988) and eventually plant survival (Poorter and Bongers 2006; Sterck et al. 2006). Shade-tolerant species cannot benefit from a high pho-

tosynthetic capacity because of the low irradiance in the understory. Consequently, they invest little nitrogen in Rubisco and photosynthetic capacity in order to keep the maintenance respiration low (Reich et al. 1998).

Are Leaf Traits Related to the Regeneration or Adult Niche?

All three leaf traits evaluated showed the strongest correlation with crown exposure in the regeneration stage, and this correlation gradually diminished or disappeared with the crown exposure in the adult stage (figs. A1–A3). These results show that the tree species are more strongly adapted to the regeneration niche than to the adult niche. The same, consistent patterns were found, whether leaf traits were measured for seedlings, saplings, or adult trees. The only variable that did not show a relation with regeneration crown exposure was seedling A_{mass} , probably because of the low number of species included (13). The results of the cross-species analysis were largely confirmed by the phylogenetic correlation analysis (table 1). This strongly suggests that the observed patterns reflect genetic adaptations and have occurred repeatedly throughout evolutionary history. These phylogenetic correlations were slightly weaker and sometimes less significant than the regular cross-species correlations, probably because a relatively crude phylogenetic tree was used (mostly resolved at the family level only), which resulted in comparisons with lower N .

SLA and A_{mass} decreased from seedlings to adults (figs. A1–A3; cf. Thomas and Winner 2002). Trees show a similar response to an increase in irradiance (cf. Oberbauer and Strain 1986), which suggests that tree species do show acclimation responses to the vertical height gradient in the forest canopy. However, there are limitations to the acclimation potential; species turn out to be mainly adapted

to the light environment in the regeneration stage. These results were confirmed by the multiple regression analysis, which showed that, when all species were combined, the leaf traits of saplings and adults were only related to the regeneration niche (table 2) and that the adult niche was not important for any of the traits.

Grubb (1977) suggested that the regeneration niche of a species may differ strikingly from its adult niche and that species differ in their adaptations to those niches. Thomas and Bazzaz (1999) made a plea for the importance of the adult niche. They found that leaf traits of saplings and adult trees were closely correlated with the adult stature of the species, suggesting that the long time that trees spend as adults has led to important evolutionary adaptations. This led Reich (2000) to conclude that the evolution of leaf traits is probably sensitive to all stages of the life history. The present study shows that although significant correlations with the adult niche may be found (e.g., for sapling SLA and A_{mass}), these relationships disappear when the regeneration niche is also included in the analysis (table 2). This is partly explained by the ontogenetic consistency in crown exposure between the regeneration and adult stage; leaf traits are correlated with the adult niche, because the adult niche is, to some extent, a reflection of the regeneration niche ($r^2 = 0.26$). It would have been very enlightening if Thomas and Bazzaz had also quantified the regeneration niche of their species.

What matters for adaptation is not so much how long a plant spends in a particular life-history stage but more the strength of the selection pressures and associated mortality (Stearns 1992). Mortality is highest in the seedling stage, suggesting that species should be adapted to the regeneration niche. Demographic studies (Zuidema 2000), on the other hand, show that population growth is most sensitive to mortality in the adult stage, suggesting that species should be adapted to the adult niche. Ideally, species are adapted to both niches, but developmental and morphological constraints set an upper limit to the magnitude of ontogenetic plasticity.

Thomas and Bazzaz (1999) found stronger relationships with H_{max} than in this study, which is partly explained by their species selection. Thomas and Bazzaz focused on late-successional species differing in adult stature, thus minimizing the range in regeneration crown exposure and maximizing the range in adult crown exposure. For late-successional species, leaf traits and the plasticity therein might be determined by adult crown exposure (cf. Cai et al. 2005; Martínez-Garza and Howe 2005). In our case the H_{max} predicted leaf traits of late-successionals even better than adult crown exposure itself, especially when phylogeny was taken into account (tables 1, 2). Probably this is because H_{max} closely reflects the average crown exposure at the population level (Poorter et al. 2005) or

because H_{max} is an intrinsic species trait that reflects the position of the species along the r - K continuum (Pianka 1970).

For pioneer species, most leaf traits were best correlated with the regeneration crown exposure and some with the adult crown exposure (table 1). Seedling and sapling SLA were positively related to CE_{reg} , in line with the prediction. It was peculiar that the adult SLA of pioneers was negatively related with the CE_{adult} . I do not have a clear functional explanation for this intriguing relationship other than that different correlations may arise because of smaller and different subsets of species.

The ANCOVA indicated that leaf traits of pioneers and shade tolerants showed different relationships with H_{max} (see also different correlations in table 1). Similarly, Falster and Westoby (2005) found that in an Australian rain forest pioneers and shade tolerants had different relationships between SLA and N_{mass} on the one hand and H_{max} on the other hand. H_{max} may therefore be an important strategic axis of variation (cf. Westoby 1998), as it is closely related to the adult light niche (fig. 1). However, it means something different for pioneers and shade tolerants, because H_{max} is positively related with the regeneration light niche of shade tolerants and negatively related with the regeneration niche of pioneers (fig. 1; cf. Falster and Westoby 2005).

Conclusions

At the community level it appears that the regeneration niche is the only niche that rules, whereas for different functional groups (especially shade tolerants, and to a lesser extent pioneers) the adult niche and H_{max} may be important as well (tables 1, 2). The same results as those found here for the light niche may apply to adaptations to other resource niches (water, nutrients). Although differences between the regeneration and adult niche may be most pronounced for tall and long-lived organisms such as trees, marked niche shifts during ontogeny are also found for shorter-lived herbaceous plants (cf. Bazzaz 1996). Quantifying both functional traits and environmental niches in different phases of the life cycle of the plant may give us important insights into whether species are shaped by their regeneration or adult niche and in the factors that drive the evolutionary ecology of plants (Cavender-Bares et al. 2004). The results of this study indicate that although the regeneration phase is short, it has a long-lasting effect on the form and shape of plant species.

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