

ARE FUNCTIONAL TRAITS GOOD PREDICTORS OF DEMOGRAPHIC RATES? EVIDENCE FROM FIVE NEOTROPICAL FORESTS

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Abstract. A central goal of comparative plant ecology is to understand how functional traits vary among species and to what extent this variation has adaptive value. Here we evaluate relationships between four functional traits (seed volume, specific leaf area, wood density, and adult stature) and two demographic attributes (diameter growth and tree mortality) for large trees of 240 tree species from five Neotropical forests. We evaluate how these key functional traits are related to survival and growth and whether similar relationships between traits and demography hold across different tropical forests.

There was a tendency for a trade-off between growth and survival across rain forest tree species. Wood density, seed volume, and adult stature were significant predictors of growth and/or mortality. Both growth and mortality rates declined with an increase in wood density. This is consistent with greater construction costs and greater resistance to stem damage for denser wood. Growth and mortality rates also declined as seed volume increased. This is consistent with an adaptive syndrome in which species tolerant of low resource availability (in this case shade-tolerant species) have large seeds to establish successfully and low inherent growth and mortality rates. Growth increased and mortality decreased with an increase in adult stature, because taller species have a greater access to light and longer life spans. Specific leaf area was, surprisingly, only modestly informative for the performance of large trees and had ambiguous relationships with growth and survival.

Single traits accounted for 9–55% of the interspecific variation in growth and mortality rates at individual sites. Significant correlations with demographic rates tended to be similar across forests and for phylogenetically independent contrasts as well as for cross-species analyses that treated each species as an independent observation. In combination, the morphological traits explained 41% of the variation in growth rate and 54% of the variation in mortality rate, with wood density being the best predictor of growth and mortality. Relationships between functional traits and demographic rates were statistically similar across a wide range of Neotropical forests. The consistency of these results strongly suggests that tropical rain forest species face similar trade-offs in different sites and converge on similar sets of solutions.

Key words: demography; functional ecology; height; life-history theory; seed mass; shade tolerance; species coexistence; specific leaf area; trees; tropical rain forest; wood density.

INTRODUCTION

Functional traits are attributes of species that influence their vital rates (survival, growth, and reproduction) and, ultimately, fitness (Ackerly 2003). A

central goal of plant ecology is to understand how functional traits vary among species and to what extent this variation has adaptive value. The study of interspecific variation in plant traits has generated important insights into the occurrence of trait trade-offs and trait syndromes (Lambers and Poorter 1992, Grime et al. 1997, Reich et al. 2003), the classification of plants into functional groups (Díaz and Cabido 1997, Grime 2001), and the consequences of these trade-offs

Manuscript received 7 February 2007; revised 29 August 2007; accepted 21 September 2007; final version received 7 November 2007. Corresponding Editor: K. T. Killingbeck.

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and functional groups for ecosystem functioning (ter Steege and Hammond 2001, Díaz et al. 2004). Several key traits have been proposed to be universally important for plant performance and to represent relatively independent aspects of plant ecological “strategy.” Among these, seed size, specific leaf area (leaf area per unit leaf mass; SLA), wood density (dry mass per unit fresh volume; WD), and plant height at maturity (H_{\max}) have been shown to play a central role in plant regeneration and functional ecology, and they represent relatively easily measured characteristics that can be obtained for large numbers of species (Westoby 1998, Weiher et al. 1999).

Seed size strongly influences reproduction and establishment (Mazer 1990, Paz et al. 2005). A large seed provides the new germinant with sufficient reserves to establish successfully under low-resource conditions (Kitajima 2002), to make a large seedling with a greater chance of escaping size-dependent mortality, and to recover from damage due to herbivory or falling debris (Harms and Dalling 1997). By contrast, small-seeded species produce a greater number of seeds per unit of reproductive effort (Moles et al. 2004) and are better colonizers of sites that are ephemeral in space and time (Dalling et al. 1998).

Specific leaf area is the light-capturing foliar area per unit of leaf biomass invested (see Plate 1). Species with high SLA tend to have high nutrient concentrations and mass-based photosynthesis and respiration rates (Reich et al. 1992, Wright et al. 2004, Poorter and Bongers 2006). Interspecific variation in seedling growth rate is largely driven by variation in SLA (Poorter and Van der Werf 1998, Wright and Westoby 1999). Low SLA leaves tend to be thick and dense, and thus physically robust and less attractive to herbivores than leaves with high SLA (Coley 1983, Wright and Westoby 2002). Consequently, low SLA leaves tend to be longer-lived, which by itself may lead to longer plant life spans (Sterck et al. 2006).

Wood density represents the biomass invested per unit wood volume. Low WD can contribute to higher stem growth rate because more volume is produced per unit biomass (King et al. 2005). Conversely, high-density wood tends to be constructed of small cells with thick walls and limited intercellular space (Castro-Díez et al. 1998). This makes stems more resistant to breakage (van Gelder et al. 2006) and to fungal and pathogen attack (Augsburger 1984), thus contributing to enhanced plant survival (Muller-Landau 2004). Finally, H_{\max} plays a fundamental role in access to light (Westoby 1998, Poorter et al. 2005). Light is a unidirectional resource and competition for light is highly asymmetric. Taller plant species intercept, on average, more light and thus potentially realize faster growth rates.

Although the functional value of these traits forms one of the central paradigms of comparative plant ecology (Westoby 1998, Reich et al. 2003), the relationships between these traits and vital rates such as growth

and mortality have rarely been evaluated under field conditions. This is especially the case for long-lived and slow-growing organisms such as trees for which the determination of vital rates requires monitoring large populations for long time periods.

Relationships among functional traits and vital rates may reflect direct effects, but it is more likely that both form part of a suite of coevolved traits (Reich et al. 2003). Life-history theory predicts that species specialized for ephemeral high-resource environments should have a strong ability to colonize and to preempt resources by having a copious production of small seeds, fast growth, small size at first reproduction, and rapid completion of their life cycle (Pianka 1970). In contrast, species specialized for stable low-resource environments should have large offspring, high survival, large size at reproduction, and long life span. Under low-resource conditions, selection favors allocation to storage and defense to maintain accumulated resources (Kitajima 1996). In tropical rain forests these two life-history extremes are represented by pioneer species that have high growth and mortality rates and regenerate in gaps and shade-tolerant species that have slow growth and low mortality rates that enable survival in the shaded understory (Condit et al. 1996, Wright et al. 2003). These life-history extremes also give rise to the growth/survival trade-off that is frequently observed among tropical tree species (Kitajima 1994, Wright et al. 2003).

This study is the first to quantify relationships between vital rates (growth and mortality) and key functional traits (seed volume, SLA, WD, and H_{\max}) across a large group of species in the post-regeneration stage and to assess whether similar trait–rate relationships exist in different plant communities. Data were collected for “large” trees (mostly between 10 and 50 cm diameter) of 240 species from five Neotropical forests. We pose two central questions. First, are functional traits known to be good predictors of demographic rates in the regeneration stage also good predictors of performance in the post-regeneration stage? Second, are there general trait–rate relationships across all five forests? Based on life-history theory and empirical studies (as cited here above) we predicted that (1) growth and mortality rates should decrease with an increase in seed size; (2) growth and mortality rates should increase with an increase in SLA; (3) growth and mortality rates should decrease with higher wood density; (4) growth rates should decrease with an increase in H_{\max} because species from disturbed microsites should be small and grow fast, and mortality rates should decrease with H_{\max} because species adapted to low-resource environments should be tall and long-lived; and (5) relationships between functional traits and demographic rates should be consistent across sites because these relationships express general convergent evolutionary patterns of adaptive value. All interspecific

TABLE 1. Environmental characteristics of the five rain forest sites.

Site	Forest type	Latitude	Longitude	MAT (°C)	Rainfall (mm/yr)	Length of dry period (mo)	PSP (ha)	Period (yr)
La Chonta, Bolivia ¹	MSE	15°45' S	62°60' W	24.8	1580	7	81 ha, >40 cm; 40.5 ha, >20 cm; 12 ha, >10 cm	2–4 (1)
BCI, Panama ²	MSE	9°10' N	79°85' W	26.2	2632	4	50 ha, >1 cm	5 (5)
Chajul, Mexico ³	ME	16°04' N	90°45' W	24.0	3000	4	14 ha, >10 cm	10 (1)
Fort Sherman, Panama ⁴	ME	9°17' N	79°58' W	26.2	3057	3	6 ha, >1 cm	3 (3)
Los Tuxtlas, Mexico ⁵	wet	18°35' N	93°06' W	24.6	4725	0	5 ha, >10 cm	8 (8)

Notes: Forest type (MSE, moist semi-evergreen; ME, moist evergreen), latitude, longitude, mean annual temperature (MAT), annual rainfall, length of dry period (number of months with <100 mm rain/mo), size of permanent sample plots (PSP) with the minimum diameter at breast height of trees included, and the monitoring period used to calculate demographic rates (measurement interval in parentheses) are given. The sites are ordered according to decreasing seasonality. Environmental data are (with some modifications) from Wright et al. (2007). Superscripts refer to the source for the site description. 1, Peña-Claros et al. (2008); 2, Leigh et al. (1982); 3, Ibarra-Manríquez and Martínez-Ramos (2002); 4, Condit et al. (2004); 5, Bongers et al. (1988).

relationships were examined using interspecific correlations and phylogenetically independent contrasts.

METHODS

Research sites and species

Functional traits and demographic rates were compiled from permanent sample plots located in five Neotropical rainforests (Table 1). The forests span the latitudinal range of Neotropical rainforests, from 18° N (Los Tuxtlas, Mexico) to 15° S (La Chonta, Bolivia). Annual rainfall varies from 1580 to 4725 mm across sites, the length of the dry period (number of months with mean rainfall <100 mm) varies from 0 to 7 months, and the mean annual temperature varies from 24.8° to 26.2°C. At least one demographic rate and one functional trait were measured for 240 woody tree species, representing 146 genera, 46 families, and 21 orders. The delineation of genera followed Kew Botanic Gardens, and the delineation of higher taxonomic levels followed the Angiosperm Phylogeny Group (information available online).¹² Palms were excluded from the study because most have fixed trunk diameters and little secondary growth.

Functional traits

We evaluated four functional traits; seed volume (SV), specific leaf area (SLA), wood density (WD), and maximum adult height (H_{\max}). Site-specific data were obtained from the literature or collected in the field for each species. Measurement protocols occasionally varied among sites; hence, a concerted effort was made to standardize data to facilitate comparisons among sites. Here we describe methods of trait measurement only briefly; further details are reported by Wright et al. (2007).

Seed volume.—At most sites SV was calculated from seed lengths and widths, assuming an elliptical shape. For the Mexican sites, seeds including the seed coat were then dried and weighed. At Barro Colorado Island

(BCI) seed dry mass was taken from the literature (diaspore masses, Augspurger 1986; simple seed masses and diaspore masses, Kitajima 1992; diaspore masses without wings, Dalling et al. 1998) or obtained from seeds collected in the field (endosperm and embryo); then, seed mass was converted to volume using an allometric equation based on the Los Tuxtlas data ($\log_{10}[\text{mean seed volume}] = 0.043 - 1.027 \log_{10}[\text{mean seed mass}]$, $r^2 = 0.93$, $n = 272$) (Wright et al. 2007).

Specific leaf area.—Leaves were collected from 5–10 m tall trees at Los Tuxtlas (Bongers and Popma 1990), from 6–16 m tall trees at La Chonta (Rozendaal et al. 2006), and from canopy trees at Fort Sherman and BCI. Sun leaves were collected at all sites except BCI, where a mixture of sun and shade leaves was collected. Specific leaf area was calculated as the leaf blade area divided by the leaf dry mass, excluding the petiole. For compound-leaved species the rachis was included for La Chonta or only winged rachae were included for BCI and Fort Sherman. For some BCI species SLA was measured on leaf discs rather than whole leaves. Whole-leaf SLA was estimated for these species using the allometric equation for species with SLA for both discs and whole leaves ($\log_{10}[\text{whole-leaf SLA}] = 0.0129 - 0.972 \log_{10}[\text{leaf disc SLA}]$, $r^2 = 0.91$, $n = 101$) (Wright et al. 2007).

Wood density.—Wood density came from various published sources (Los Tuxtlas, Barajas-Morales 1985; BCI, Muller-Landau 2004, Chave et al. 2006). At La Chonta wood samples of tall species were collected from trees between 20 and 50 cm dbh (measured at 1.3 m above the ground surface); samples for shorter species were taken from plants close to the maximal dbh for each species. Fresh wood volume was determined with the water displacement method, after which samples were oven-dried at 70°C and weighed.

Maximum adult height.—At Los Tuxtlas, H_{\max} was visually estimated for the five largest trees or obtained from Ibarra-Manríquez and Sinaca (1995). At BCI and Chajul, H_{\max} was either measured directly, estimated from maximum dbh using a regression equation for all species pooled, or taken (for BCI only) from Croat (1978). At La Chonta, plant height was measured with a

¹² <http://www.mobot.org/MOBOT/research/APweb/>

clinometer for 25 mature trees per species and regressed against diameter using the asymptotic formula of Thomas (1996). H_{\max} was calculated for the tree with the largest diameter, using species-specific regression equations (Poorter et al. 2006).

Demographic rates

Demographic rates were determined for trees between 10 and 50 cm dbh for mapped plots at each site (Table 1). Plot size varied from 5 to 81 ha, measurement intervals from one to eight years, and the total evaluation period from two to 10 years. All plots supported mature forest without signs of recent human disturbance, excepting La Chonta, where low-impact logging of 1 tree/ha occurred in the 1970s. Annual mortality rates (MR) were calculated as $(\log[N_0] - \log[N_t])/\text{time}$ for species with 20 or more individuals, where N_0 and N_t are the numbers of individuals at the first and last measurement, respectively. Relative stem diameter growth rates (RGR, in millimeters per millimeter per year) were calculated as $(\log[\text{dbh}_t] - \log[\text{dbh}_0])/\text{time}$, where dbh_0 and dbh_t are the tree diameters at the first and last measurement, respectively. Mean RGR was calculated for all species that had 10 or more individuals. For Chajul and Los Tuxtlas, trees with resprouts were excluded.

Interspecific comparisons might potentially be hampered if growth is size dependent and if size distributions vary among species. We evaluated the potential magnitude of this problem for BCI by comparing absolute growth rates standardized to 25 cm dbh with the average RGR for the 10–50 cm dbh interval. We fit the logarithm of absolute growth rates to the logarithm of initial diameter for species with 20 or more individuals in the 10–50 cm dbh interval. We then used the log–log regression equations to estimate the absolute growth rate of 25 cm dbh trees. This estimated absolute growth rate and the average RGR observed for trees in the 10–50 cm DBH interval were strongly correlated (Pearson's $r = 0.95$, $P < 0.001$, $n = 73$), indicating that size-dependent growth does not bias the analysis.

Analyses

We used three types of analyses (correlation, ANCOVA, and multiple regression) to provide different insights. First, Pearson correlations were used to evaluate interspecific relationships between demographic rates and functional traits at each site (a so-called “cross-species analysis”). This analysis identifies statistically significant demographic-trait relationships and permits a first comparison of the direction and strength (r^2) of these relationships within and across sites. These within-site correlations are also free of any between-site biases that might be introduced by the small differences in census intervals used to estimate vital rates and the differences in protocols used to measure traits. Logarithmic transformations of RGR and SV and an angular transformation of MR satisfied the normality assumption.

Twenty species had zero mortality; for these species the population sizes were apparently too small (median $n = 26$) to get a reliable estimate of mortality rate, and they were therefore excluded from MR analyses. Studentized residuals were >3 in three instances, and these cases were excluded.

Second, we used ANCOVA models to test the null hypothesis that all sites showed similar trait–rate relationships. In these models, RGR or MR were dependent variables, functional traits were covariates, and site was a grouping factor with five levels. A significant site \times covariate interaction would indicate that the slope of the trait–rate relationship differs among sites. When the interaction was insignificant the homogeneity of slopes assumption of ANCOVA was met and the analysis was repeated without the insignificant interaction term to determine whether the intercept of the trait–rate relationship differed among sites. Generalized linear interactive modeling (GLIM) enabled a binomial error and logit link function for analyses involving MR and a normal error and an identity link function for analyses involving RGR. We weighted species by the number of individuals used to determine RGR or MR for the ANCOVA analyses because the precision of vital rate estimates increases with the sample size.

Third, forward multiple regressions were performed to evaluate relationships between demographic rates and combinations of functional traits. The multiple regression analyses were performed for all five sites combined (with site as a dummy variable) and for BCI and La Chonta only (because too few species had all four functional traits measured at the three remaining sites).

Trait–rate correlations were also assessed using phylogenetically independent contrasts (PIC). In cross-species analyses, each species contributes a single data point. In PIC analyses, each independent contrast (evolutionary divergence) contributes a data point, allowing one to ask (1) whether evolutionary shifts in one trait have tended to be associated throughout history with evolutionary shifts in another trait and (2) whether results from cross-species analyses largely reflect trait differences among clades (Westoby 1999). A phylogenetic tree describing the hypothesized evolutionary relationships among species was constructed using Phylomatic (Webb and Donoghue 2005; based on the conservative angiosperm phylogeny, C20040402). Where relationships among genera within a given family were not fully resolved they were treated as polytomies. Relationships among species within genera were also treated as polytomies. Analyses were conducted with the “Analysis of Traits” (version 3.0) module in Phylocom version 3.22 (Webb et al. 2006). Phylogenetic branch lengths were set to 1 and polytomies were resolved to provide one contrast, following Pagel (1992). 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

TABLE 2. Pearson correlation coefficients between functional traits and relative diameter growth rate (RGR) and mortality rate (MR) for five rain forest sites, for all sites combined (All), for all sites combined but taking average values for species that occur at several sites (Species means), and for phylogenetically independent contrasts (Ind. contrasts).

Rain forest site	SV-RGR		SV-MR		SLA-RGR		SLA-MR		WD-RGR		WD-MR		H_{\max} -RGR		H_{\max} -MR	
	<i>r</i>	<i>N</i>	<i>r</i>	<i>N</i>	<i>r</i>	<i>N</i>	<i>r</i>	<i>N</i>	<i>r</i>	<i>N</i>	<i>r</i>	<i>N</i>	<i>r</i>	<i>N</i>	<i>r</i>	<i>N</i>
La Chonta	-0.43	45	-0.46	36	0.16	34	0.40	28	-0.45	46	-0.30	36	0.30	46	-0.26	36
BCI	-0.02	125	-0.36	92	0.24	44	-0.14	34	-0.35	81	-0.15	63	0.34	133	-0.16	95
Chajul	-0.33	40	-0.70	23	-0.07	14	-0.03	8	-0.19	21	-0.40	12	0.28	41	-0.14	26
Fort Sherman	0.10	38	-0.10	23	-0.03	25	0.27	17	-0.58	27	0.25	14	0.55	30	-0.23	19
Los Tuxtlas	-0.28	12	-0.74	15	0.36	11	0.27	14	-0.10	11	-0.58	14	-0.62	12	0.12	15
All	-0.15	260	-0.43	189	-0.20	128	0.03	101	-0.37	186	-0.22	139	0.38	262	-0.08	191
Species means	-0.15	219	-0.42	164	-0.17	107	0.05	87	-0.38	149	-0.19	115	0.38	220	-0.11	166
Ind. contrasts	-0.18	93	-0.25	72	-0.33	55	-0.13	48	-0.15	70	-0.27	58	0.34	97	0.01	72

Notes: *N* indicates the number of species. Functional traits included are seed volume (SV), specific leaf area (SLA), wood density (WD), and maximum adult height (H_{\max}). Logarithms of RGR and seed volume and the angular transformation of MR achieved normality. Significant correlations are in boldface type ($P < 0.05$) or in boldface italic type ($P < 0.01$).

number of internal nodes (i.e., PICs) providing contrasts.

RESULTS

Relative growth rate and MR were measured for 278 (236 different species) and 198 (173 species) species-site combinations, respectively. Maximum height, SV, WD, and SLA were measured for 268, 266, 191, and 132 of these species-site combinations, respectively. There was considerable variation in sample size for the four functional traits and the two demographic rates both within and among sites (Table 2).

MR vs. RGR

Mortality rate and RGR were significantly positively correlated for all sites combined (Fig. 1) and for La Chonta alone ($r = 0.44$, $P = 0.008$, $n = 36$). For the other sites the relationship was positive but not significant (Fort Sherman, $r = 0.29$, $P = 0.17$, $n = 24$; BCI, $r = 0.12$, $P = 0.24$, $n = 94$; Chajul, $r = 0.33$, $P = 0.086$, $n = 28$; Los Tuxtlas, $r = 0.07$, $P = 0.83$, $n = 12$). To check whether all sites show a similar relationship between MR and RGR, we did an ANCOVA analysis with site as factor and RGR as covariate and weighted for the number of individuals per species. Mortality rate did not vary with site ($F_{4,184} = 2.06$, $P = 0.088$) and RGR ($F_{1,184} = 2.77$, $P = 0.098$), but there was a significant site \times RGR interaction ($F_{4,184} = 12.5$, $P = 0.044$).

Relationships between functional traits and RGR

Relative growth rate was significantly negatively correlated with SV when all sites were combined and also for La Chonta and Chajul alone (Table 2, Fig. 2, Appendix A). In the ANCOVAs, the interactions between site and the covariates or functional traits were always insignificant, the homogeneity of slopes assumption of ANCOVA was always satisfied, and the analyses were performed again without the insignificant site-covariate interactions. This final step of the ANCOVA indicated that intercepts differed significantly among sites for the RGR-SV relationship (Table 3). Chajul and La Chonta had significantly lower intercepts and lower

RGR than the other three forests (post hoc test, $P < 0.05$). Relative growth rate was also significantly lower at Chajul and La Chonta than at the other sites when the other functional traits were used as covariates (Table 3).

Relative growth rate was significantly negatively correlated with SLA when all sites were combined (Table 2). This significant relationship was caused by the combination of relatively high SLA and low RGR for species from La Chonta. The ANCOVA takes such site differences into account. In the ANCOVA, site had a highly significant effect on RGR, SLA was also significant, and the slope of the RGR-SLA relationship was reversed and became positive (Table 3). Deciduous species had a slightly higher SLA ($12.6 \text{ mm}^2/\text{mg}$) than evergreen species ($11.5 \text{ mm}^2/\text{mg}$; ANOVA, $F_{1,101} = 4.11$,

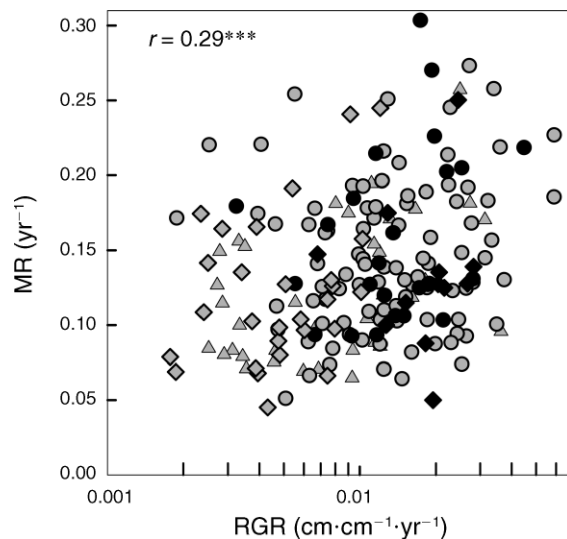


FIG. 1. Relationship between mortality rate (MR) and relative diameter growth rate (RGR) of tree species at five Neotropical forest sites (gray triangles, La Chonta; gray circles, Barro Colorado Island; black circles, Fort Sherman; gray diamonds, Chajul; black diamonds, Los Tuxtlas). Note the logarithmic scale for RGR. Pearson correlation coefficient and significance level are shown.

*** $P < 0.001$.

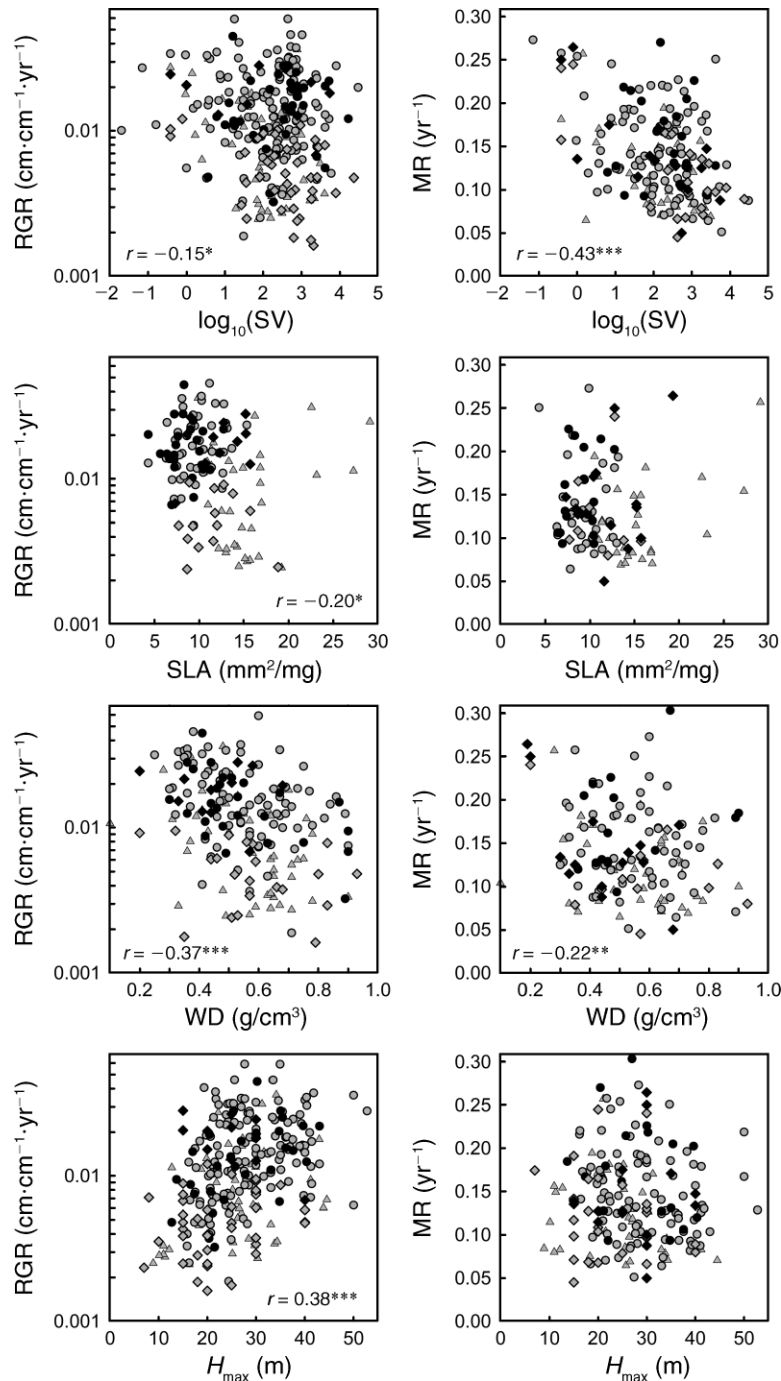


FIG. 2. Trait correlations between relative diameter growth rate (RGR), angular-transformed mortality rate (MR), and functional traits of tree species at five Neotropical forest sites (gray triangles, La Chonta; gray circles, Barro Colorado Island; black circles, Fort Sherman; gray diamonds, Chajul; black diamonds, Los Tuxtlas). Functional traits included are seed volume (SV; measured in mm^3 prior to log-transformation), specific leaf area (SLA), wood density (WD), and maximum adult height (H_{max}). Note the logarithmic scale for RGR. The Pearson correlation coefficient is shown if significant.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

$P = 0.045$). To evaluate the possibility that the RGR–SLA relationship differed between evergreen and deciduous species, we redid the ANCOVA with site and deciduousness as factors, SLA as a covariate, and the

interaction between deciduousness and SLA. All main factors were significant, but the interaction effect was insignificant ($F_{1,101} = 0.04$, $P = 0.84$), indicating that evergreen and deciduous species have similar relation-

TABLE 3. Relationships between relative stem diameter growth rate (RGR), mortality rate (MR), and four functional traits for tree species from five rain forest sites.

Dependent variable and covariate	Site main effect			Covariate			Slope	r^2	Site				
	F	df	χ^2	F	df	χ^2			LC	BCI	CH	FS	LT
RGR													
SV	25.0***	4, 261		6.4*	1, 261		−0.047	0.32	a	b	a	b	b
SLA	30.0***	4, 134		9.5**	1, 134		0.014	0.49	a	b	a	b	b
WD	21.8***	4, 182		18.1***	1, 182		−0.53	0.37	a	b	a	b	b
H_{\max}	26.5***	4, 258		18.4***	1, 258		0.008	0.33	a	b	a	b	b
MR													
SV		4, 187	27.2***		1, 187	36.4***	−0.309	0.22	a	b	ab	ab	ab
SLA		4, 96	19.6***		1, 96	1.2NS	0.03	0.14	a	b	ab	ab	ab
WD		4, 135	22.6***		1, 135	21.8***	−1.91	0.24	a	b	ab	ab	ab
H_{\max}		4, 189	23.2***		1, 189	14.2***	−0.026	0.16	a	b	ab	b	ab

Notes: Functional traits included are seed volume (SV), specific leaf area (SLA), wood density (WD), and maximum adult height (H_{\max}). Dependent variables are RGR and MR, site is a grouping factor, and the functional traits are covariates in ANCOVA models implemented with generalized linear interactive modeling (GLIM). All interactions between site and functional traits were insignificant, the homogeneity of slopes assumption of ANCOVA was satisfied, and the analyses were redone without the interaction term. The F values (for RGR), χ^2 (for MR), P values, degrees of freedom, the slope of the covariate, and coefficients of determination of the full model (r^2) are shown. Sites (LC, La Chonta; BCI, Barro Colorado Island; CH, Chajul; FS, Fort Sherman; LT, Los Tuxtlas) followed by a different letter are significantly different (Bonferroni, $P < 0.05$). Relative growth rate and SV were log-transformed, and MR was angular transformed prior to analyses.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS, $P > 0.05$.

ships between SLA and RGR. The interaction between deciduousness and SLA was also insignificant when MR was the dependent variable ($F_{1,76} = 1.97$, $P = 0.16$).

Relative growth rate was significantly negatively correlated with WD when all sites were combined and also for three of the five sites alone (Table 2). Relative growth rate was significantly positively correlated with H_{\max} when all sites were combined and also for three of the five sites alone (Table 2). These results for WD and H_{\max} were confirmed by the ANCOVAs in which both site and the covariate effects were highly significant (Table 3).

To determine which trait was the best predictor of interspecific variation in RGR, we used stepwise multiple regression analyses, which included site as a

dummy variable (Table 4). The first variable included was site, which explained 48% of the variation in RGR. The second variable entered was WD, which had a negative effect on RGR and explained an additional 11% of the variation. Seed volume, SLA, and H_{\max} did not contribute significantly to the model. The overall model predicted RGR reasonably well, explaining 59% of the variation. The model was confined to 110 species because SLA was available for relatively few species. We therefore repeated the multiple regression analysis without SLA, thus expanding the sample size to include 178 species. Wood density was again an important factor, but this time H_{\max} and SV were also significant. Maximum height had a positive effect and SV a negative effect on RGR (Table 4). The multiple regression

TABLE 4. Stepwise multiple regression relating relative diameter growth rate (RGR) and mortality rate (MR) to site and functional traits.

Variable	Including SLA						Excluding SLA					
	RGR			MR			RGR			MR		
	b	r^2	P	b	r^2	P	b	r^2	P	b	r^2	P
Site	—	0.476	***	—	—	—	—	0.302	***	—	0.118	***
SV	—	—	—	-0.019	0.067	***	-0.032	0.021	*	-0.018	0.146	***
SLA	—	—	—	-0.007	0.144	***	—	—	—	—	—	—
WD	-0.724	0.109	***	-0.166	0.276	***	-0.501	0.055	***	-0.106	0.088	***
H_{\max}	—	—	—	-0.002	0.056	**	0.006	0.031	**	-0.002	0.059	***
Model		0.585	***		0.543	***		0.409	***		0.411	***
df model		5			4			7			7	
df error		104			82			170			128	

Notes: Functional traits included were seed volume (SV), specific leaf area (SLA), wood density (WD), and maximum adult height (H_{\max}). Dependent variables were weighted by sample size. The analysis was repeated twice, with SLA and without SLA. Regression slopes (b), partial r^2 , and significance levels (P) are shown. The number of species for RGR and MR are 110 and 87 for the analysis with SLA, and 178 and 136 for the analysis without SLA. Relative growth rate and SV were log-transformed, and MR was angular-transformed prior to analyses. When the site main effect was significant, the corresponding r^2 is shown. A dash indicates that independent variables were not significant and were excluded from the final model.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.



PLATE 1. *Pourouma cecropiifolia* leaf capturing sunlight in the La Chonta forest, Bolivia. A high specific leaf area is important to enhance the leaf display per unit of leaf biomass invested. Photo credit: M. Peña-Claros.

analysis was also carried out for the two sites (La Chonta and BCI) that had complete data for a sufficient number of species. Relative growth rate was negatively related to WD for La Chonta ($r^2 = 0.29$) and negatively related to WD, SLA, and SV for BCI ($r^2 = 0.42$; Appendix C).

Relationships between functional traits and MR

Mortality rate was significantly negatively related to SV when all sites were combined and for four of the five sites alone (Fig. 2, Table 2, Appendix B). Seed volume also had a highly significant negative effect on MR in the ANCOVA (Table 3). La Chonta had a significantly lower intercept and therefore lower MR than BCI (post hoc tests, $P < 0.05$), and the same results were obtained when other functional traits were used as covariates. Mortality rate was unrelated to SLA for the combined sites and positively related to SLA for La Chonta alone (Tables 2 and 3). Mortality rate was significantly negatively related to wood density when all sites were combined and for Los Tuxtlas alone (Tables 2 and 3). Finally, MR was significantly negatively related to H_{\max} for all sites combined, but only when intersite differences in MR were incorporated in the ANCOVA model

(Table 3). There were no significant interactions between site and any of the covariates or functional traits in the four ANCOVA analyses.

Wood density entered the stepwise multiple regression model first and explained 28% of the variation in MR (Table 4). Specific leaf area, SV, and H_{\max} explained an additional 14%, 7%, and 6% of the variation in MR, respectively. Only site did not contribute significantly to the multiple regression model. The relationships between MR and the four functional traits were all negative. Overall, the model explained 54% of the variation in MR. The multiple regression analysis was repeated without SLA, thus including a larger number (178) of species. Again the three remaining functional traits had significant negative effects on MR. Multiple regression analysis at individual sites showed that MR was negatively related to WD and H_{\max} ($r^2 = 0.50$) for La Chonta and that MR was negatively related to SV and SLA ($r^2 = 0.24$) for BCI (Appendix C).

Independent contrasts

Correlations based on independent contrasts were generally similar to the cross-species correlations presented in Table 2. Two significant cross-species correla-

tions (RGR vs. SV and RGR vs. WD) were no longer significant when phylogeny was taken into account; however, for the RGR–SV relationship the magnitude of the phylogenetic correlation was larger than for the cross-species correlation, suggesting that the change in significance was due to lower power. Correlation coefficients for RGR vs. SLA and MR vs. WD also increased in magnitude with independent contrasts.

DISCUSSION

The four morphological traits were each significantly correlated with relative growth rates and/or mortality rates, suggesting either direct functional effects or indirect correlations mediated by species life histories. Analyses based on independent contrasts did not lead to consistent reductions in the magnitude of the correlations, indicating that the relationships arose through repeated evolutionary divergences and functional convergences.

Comparison among sites: similar trade-offs, different vital rates

The relationships between demographic rates and functional traits were statistically similar across a wide range of Neotropical forests (Table 3). This result strongly suggests that species from different sites face similar trade-offs and converge on similar sets of solutions (cf. ter Steege and Hammond 2001, Reich et al. 2003, Wright et al. 2004). La Chonta and Chajul had slower growth rates than the other sites (Table 3). La Chonta is more seasonal than the other sites (Table 1), and growth might slow during the seven dry months, leading to lower annual growth rates. Slow growth at La Chonta might also be attributed to the relatively poor soils in the Amazon compared to Central America (Powers 2005). Slow growth rates at Chajul might also be explained by soils. Most Chajul trees grew on low hills with sandy, acidic, phosphorous-poor soil or on karst with shallow soils and poor water-holding capacity.

Seed volume

Growth and mortality rates decreased with larger SV both within and across forest sites, in agreement with our first prediction (see *Introduction*). Seed size is an important component of plant regeneration strategies. Seed size directly affects seedling survival and indirectly affects seedling growth, as small-seeded species have limited seed reserves and must deploy roots and leaves rapidly to become autotrophic. Many small-seeded species have photosynthetic cotyledons (Ibarra-Manríquez et al. 2001) and high SLA and leaf area ratio (LAR), which all fuel growth. Correlations between RGR and seed size are therefore especially high just after germination (Paz et al. 2005), but disappear over time as the initial SLA and LAR differences vanish (Baraloto et al. 2005, Poorter and Rose 2005). Seed size is also correlated with the growth and mortality rates of large trees because seed size is closely linked with a suite

of traits that enhance shade tolerance (Troup 1921, Hammond and Brown 1995, Osunkoya 1996). Shade-tolerant species have large seeds to regenerate successfully in the shade and inherently slower growth and mortality rates compared to light-demanding species. Not all species fit this paradigm. Shade-tolerant species can have minute seeds, and pioneer species can have large seeds (Metcalf and Grubb 1995). The consistent negative relationships observed between large tree mortality and seed volumes suggest, however, that such outliers are rare (Table 2).

Specific leaf area

The relationship between SLA and the growth and mortality of large trees was ambiguous. Relative growth rate was negatively related to SLA when sites were pooled because La Chonta tended to have the highest SLA and lowest RGR values. The ANCOVA incorporates such site differences, and RGR–SLA was reversed and was positive in the ANCOVA, which is consistent with our second hypothesis. However, in the multiple regression analysis for the combined sites, SLA had no effect on RGR and a negative effect on MR, which is inconsistent with our second hypothesis. The ambiguous and modest effect of SLA on demographic rates is surprising because SLA is considered to be a key trait influencing plant performance (e.g., Lambers and Poorter 1992, Grime et al. 1997, Wright et al. 2004) and is routinely included in screening studies of plant traits (e.g., Weiher et al. 1999). Growth was expected to scale positively with SLA, because SLA indicates the efficiency of biomass investment for light interception. Mortality rate was expected to scale positively with SLA, because high SLA leaves are less tough and suffer from higher herbivory rates (Coley 1983). Studies with seedlings under controlled conditions invariably show that SLA is a good predictor of interspecific variation in growth and survival (e.g., Kitajima 1994). Poorter and Bongers (2006) evaluated the performance of saplings of 53 rain forest species in the field and found that SLA was a reasonable predictor of interspecific variation in height growth ($r^2 = 0.18$) and mortality ($r^2 = 0.26$). Specific leaf area may be important for the performance of small plants, as leaf removal has a large impact on their survival (e.g., Pearson et al. 2003), but less important for the performance of large trees that have substantial reserves to recuperate from photosynthetic biomass loss (Würth et al. 2005). Similarly, SLA may be more important for light interception of saplings for which it determines to a large extent the total leaf area and leaf area ratio, but less so for large trees, for which leaf area and light interception are largely determined by branching patterns, the number of meristems, and tree architecture (Sterck and Bongers 2001).

Wood density

Both growth and mortality rates declined with higher WD, in line with the third prediction. The negative

relationship between RGR and WD was significant for three of our five sites ($0.12 \leq r^2 \leq 0.34$), and the two sites for which this relationship was insignificant had the smallest sample sizes. In the all-species regression and in the ANCOVA, WD was negatively correlated with both RGR and MR. Similar negative relationships between absolute growth rates of trees and WD have been reported from tropical rain forests from Guyana ($r^2 = 0.25$), Surinam ($r^2 = 0.37$) and Borneo ($r^2 = 0.19$, summarized in ter Steege 2003), Amazonia ($r^2 = 0.13$, Nascimiento et al. 2004), and Malaysia ($r^2 = 0.51$, King et al. 2006). Wood density was the best predictor of RGR (Table 4, Appendix A), presumably because it is directly related to the construction costs of the wood. All else being equal, species with dense wood grow more slowly than do species with soft wood, and wood density therefore sets an upper limit to potential diameter growth. Interspecific variation in wood density is mainly caused by spaces within and between cells. Soft-wooded species also grow more rapidly because their large vessel diameters enhance hydraulic conductance and water transport capacity and, hence, photosynthetic rates (Santiago et al. 2004).

Mortality rate has been found to be negatively related to WD for seedlings growing under controlled conditions ($r^2 = 0.50$, Kitajima 1994), for saplings growing in the field ($r^2 = 0.19$, Muller-Landau 2004), and in this study for larger-sized trees ($r^2 = 0.05$, all sites combined, Table 2). High-density wood is less vulnerable to stem breakage caused by falling debris or strong winds (Putz et al. 1983) and less vulnerable to stem rot and pathogens (Augsburger 1984). Small seedlings and saplings are more vulnerable to damage from falling debris and pathogens than are large trees, which might explain why WD is a better predictor for MR in the juvenile phase. Finally, WD is closely related to shade tolerance (van Gelder et al. 2006). Shade-tolerant species may combine well-defended, long-lived tissues with a long life span and low inherent mortality rates (Loehle 2000). Osunkoya (1996) found wood density to be the best predictor of light requirements for regeneration among 89 Australian rain forest tree species. Foresters have long been aware of this association and use wood density to classify species into different shade tolerance groups.

Maximum height

Growth increased with an increase in H_{\max} both within and among forests, which contradicts the prediction made on the basis of life-history theory. Growth consistently increased with H_{\max} at three sites and decreased at one site (Los Tuxtlas). Maximum height was available for just 12 Los Tuxtlas species, and one (*Nectandra ambigens*) was an outlier; when this outlier was removed the H_{\max} –RGR relationship was insignificant for Los Tuxtlas. Life-history theory predicts that organisms with larger H_{\max} should have slower growth rates. This relationship is apparent when

small, annual herbaceous plants are compared with large, long-lived trees, but is not found when only trees are compared. Studies from Malaysian rain forest also indicate that the growth rate of trees increases with H_{\max} (Thomas 1996, King et al. 2006). Light increases exponentially with height in forest canopies, and taller species may, on average, intercept a disproportionate amount of light compared to smaller species (Poorter et al. 2005). This, in combination with their larger crown area (Poorter et al. 2006), may allow taller species to realize faster growth rates than shorter species, when compared at similar diameters. Tall species may also have higher inherent growth rates because they are more demanding of light (Poorter et al. 2005, Sheil et al. 2006).

Mortality rate decreased with an increase in H_{\max} for all sites combined in the ANCOVA and multiple regression analysis (Tables 3 and 4), which is consistent with life-history theory (tall, long-lived species should have low inherent mortality rates). Similar results have been observed for an Ecuadorian rain forest (Korning and Balslev 1994). There are two other possible explanations for the negative H_{\max} –MR relationship. First, small species might have higher mortality rates because they are close to their maximal size for the diameter range considered (10–50 cm) and many individuals might be senescent (cf. King et al. 2006). Environmental conditions might also contribute to the higher mortality rates observed among smaller species if small plants have less access to resources and hence higher mortality. As a consequence, smaller species have faster population turnover, with higher recruitment and mortality rates (Kohyama et al. 2003).

Growth vs. mortality and the relative importance of functional traits

There were fewer significant correlations between functional traits and MR (six of 20 comparisons) than between functional traits and RGR (nine of 20), and the explained variation was also much lower ($r^2 = 0.14$ – 0.24 for MR compared to $r^2 = 0.32$ – 0.49 for RGR; Table 3). The relationships with MR are probably weaker because of the difficulties to get an accurate estimate of MR. Mortality is a highly stochastic, slow process, and therefore either a large sample size or a long evaluation period is needed to get accurate mortality estimates.

Given this limitation, it is surprising how well four functional traits predicted mortality rates when all sites were combined (overall $r^2 = 0.54$). Wood density was the best predictor of MR, followed by SLA, SV, and H_{\max} . All functional traits had negative effects on MR, which is consistent with our predictions for all traits except SLA. When the multiple regression analysis was carried out for individual sites, only WD and H_{\max} were significant for La Chonta and only SLA and SV were significant for BCI. Discrepancies among these three regression analyses are probably due to the smaller number of species that could be included for La Chonta

and BCI (ca. 30 species per site had complete trait data). Smaller sample sizes reduce statistical power and increase the possibility that unusual species might have influenced the results.

The trade-off between growth and survival might contribute to the coexistence of forest trees (Kitajima and Poorter 2008), although this trade-off may be stronger for small seedlings and saplings (Kitajima 1994, Wright et al. 2003, Poorter and Bongers 2006) than for large trees (Fig. 1). Wood density was also the best predictor of RGR (Table 4) and was the only functional trait considered that directly contributed to the growth/survival trade-off for large trees, as it affected survival positively and growth negatively (Nascimento et al. 2005). In contrast, leaf traits are also important determinants of the growth/survival trade-off in the seedling stage (Kitajima 1994, Poorter 1999, Sterck et al. 2006). Wood density may fulfill such a central role, because it is closely related to shade tolerance and to a range of plant functions, including defense, stability, water relations, carbon gain, and growth (Santiago et al. 2004).

Small seedlings vs. large trees

Results from the literature suggest that trait–rate relationships are much stronger for small plants than for large trees (as found in this study). One reason is that interspecific variation in demographic rates is much larger for small plants than for large trees, which makes it statistically easier to detect trait–rate relationships. A second reason is that tree size tends to swamp more subtle trait differences. As mentioned above, SLA may be the strongest determinant of total leaf area, light interception, and growth in the seedling stage, but crown size and branching pattern may be the strongest determinant in the adult stage. A third reason that trait–rate relationships might be stronger for seedlings than for adults concerns the contrasting light environments in which seedlings of different species regenerate in the field (Wright et al. 2003); for example, seedlings of pioneers have high population-level mortality rates because all individuals that establish in the shaded understory die and high population-level diameter growth rates because those individuals that survive do so in gaps, where they can realize high growth rates. In contrast, adult trees tend to experience more similar irradiance levels and hence, more similar growth and mortality rates because they are all in the (sub)canopy.

Data from this study come from five well-studied tropical forest sites. In putting together the data matrix, the number of species with complete data decreased dramatically with the number of variables included. We know surprisingly little about functional traits and demographic rates of large suites of tree species. Comparative, standardized research on large sets of species is therefore needed to advance our understanding of the salient features that drive species coexistence, community composition, and dynamics.

ACKNOWLEDGMENTS

We thank all the people who one way or another have contributed data to this study and who have made the tremendous effort to maintain the long-term demographic plots at the different forest sites. We also thank Robin Chazdon and Kaoru Kitajima for helpful comments on the manuscript. This paper is the result of the NCEAS working group “Life-history variation and community structure in Neotropical rainforest communities: ecological and phylogenetic influences.” NCEAS is supported by NSF grant DEB-94-21535, UCSB, and the State of California. L. Poorter was supported by Veni grant 863.02.007 from NWO and a fellowship from the Wageningen Graduate School Production Ecology and Resource Conservation. Data from Chajul and Los Tuxtlas were obtained from PAPIIT-DGAP-UNAM and MacArthur Foundation grants to M. Martínez-Ramos and with the technical support of J. Rodríguez-Velazquez.

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APPENDIX A

Figures showing trait correlations between relative diameter growth rate and functional traits of tree species at five Neotropical forest sites (*Ecological Archives* E089-111-A1).

APPENDIX B

Figures showing trait correlations between mortality rate and functional traits of tree species at five Neotropical forest sites (*Ecological Archives* E089-111-A2).

APPENDIX C

Multiple regression relating relative diameter growth rate and mortality rate to functional traits for La Chonta and Barro Colorado Island (*Ecological Archives* E089-111-A3).