

Functional traits and the growth–mortality trade-off in tropical trees

S. JOSEPH WRIGHT,^{1,16} KAORU KITAJIMA,^{1,2} NATHAN J. B. KRAFT,³ PETER B. REICH,⁴ IAN J. WRIGHT,⁵
DANIEL E. BUNKER,⁶ RICHARD CONDIT,¹ JAMES W. DALLING,^{1,7} STUART J. DAVIES,¹ SANDRA DÍAZ,⁸
BETTINA M. J. ENGELBRECHT,^{1,9} KYLE E. HARMS,^{1,10} STEPHEN P. HUBBELL,^{1,11} CHRISTIAN O. MARKS,¹²
MARIA C. RUIZ-JAEN,¹³ CRISTINA M. SALVADOR,¹⁴ AND AMY E. ZANNE¹⁵

¹Smithsonian Tropical Research Institute, Apartado 0843–03092, Balboa, Panama

²Department of Biology, University of Florida, Gainesville, Florida 32611 USA

³Department of Integrative Biology, University of California, Berkeley, California 94720 USA

⁴Department of Forest Resources, University of Minnesota, St. Paul, Minnesota 55108 USA

⁵Department of Biological Sciences, Macquarie University, Sydney, New South Wales 2109 Australia

⁶Department of Biological Sciences, New Jersey Institute of Technology, Newark, New Jersey 07102 USA

⁷Department of Plant Biology, University of Illinois, Champaign-Urbana, Illinois 61801 USA

⁸Instituto Multidisciplinario de Biología Vegetal, Consejo Nacional de Investigaciones Científicas y Técnicas and Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, Casilla de Correo 495, 5000 Córdoba, Argentina

⁹Department of Plant Ecology, University of Bayreuth, 95440 Bayreuth, Germany

¹⁰Department of Biological Sciences, Louisiana State University, Baton Rouge, Louisiana 70803 USA

¹¹Department of Ecology and Evolutionary Biology, University of California, Los Angeles, California 90095 USA

¹²Department of Ecology, Evolution and Behavior, University of Minnesota, St. Paul, Minnesota 55108 USA

¹³Department of Biology, McGill University, 1205 Dr. Penfield Avenue, Montreal, Quebec H3A 1B1 Canada

¹⁴Santa Fe Botanical Garden, P.O. Box 23343, Santa Fe, New Mexico 87502-3343 USA

¹⁵Department of Biology, One University Boulevard, University of Missouri, St. Louis, Missouri 63121 USA

Abstract. A trade-off between growth and mortality rates characterizes tree species in closed canopy forests. This trade-off is maintained by inherent differences among species and spatial variation in light availability caused by canopy-opening disturbances. We evaluated conditions under which the trade-off is expressed and relationships with four key functional traits for 103 tree species from Barro Colorado Island, Panama. The trade-off is strongest for saplings for growth rates of the fastest growing individuals and mortality rates of the slowest growing individuals ($r^2 = 0.69$), intermediate for saplings for average growth rates and overall mortality rates ($r^2 = 0.46$), and much weaker for large trees ($r^2 \leq 0.10$). This parallels likely levels of spatial variation in light availability, which is greatest for fast- vs. slow-growing saplings and least for large trees with foliage in the forest canopy. Inherent attributes of species contributing to the trade-off include abilities to disperse, acquire resources, grow rapidly, and tolerate shade and other stresses. There is growing interest in the possibility that functional traits might provide insight into such ecological differences and a growing consensus that seed mass (SM), leaf mass per area (LMA), wood density (WD), and maximum height (H_{\max}) are key traits among forest trees. Seed mass, LMA, WD, and H_{\max} are predicted to be small for light-demanding species with rapid growth and mortality and large for shade-tolerant species with slow growth and mortality. Six of these trait–demographic rate predictions were realized for saplings; however, with the exception of WD, the relationships were weak ($r^2 < 0.1$ for three and $r^2 < 0.2$ for five of the six remaining relationships). The four traits together explained 43–44% of interspecific variation in species positions on the growth–mortality trade-off; however, WD alone accounted for >80% of the explained variation and, after WD was included, LMA and H_{\max} made insignificant contributions. Virtually the full range of values of SM, LMA, and H_{\max} occurred at all positions on the growth–mortality trade-off. Although WD provides a promising start, a successful trait-based ecology of tropical forest trees will require consideration of additional traits.

Key words: Barro Colorado Island, Panama; growth rates; leaf mass per area; maximum height; maximum size; mortality rates; seed mass; seed size; wood density.

INTRODUCTION

A demographic trade-off between rates of growth vs. mortality is perhaps the best-established axis of life

history variation among tree species in closed-canopy forests (Grubb 1977, Hubbell and Foster 1992, Pacala et al. 1996, Wright et al. 2003, Kitajima and Poorter 2008). The trade-off is maintained by inherent differences among species in combination with spatial variation in light availability caused by treefalls and other canopy-opening disturbances. At one extreme, light-demanding species readily colonize forest gaps and grow quickly if

Manuscript received 19 December 2009; revised 29 March 2010; accepted 9 April 2010; final version received 12 May 2010.
Corresponding Editor: F. He.

¹⁶ E-mail: wrightj@si.edu

light levels remain high or die quickly if overtopped and shaded. At the other extreme, shade-tolerant species survive canopy-opening events as juveniles, have limited potential growth rates, and are overtopped by fast-growing, light-demanding species with limited impact on mortality risk. Thus, the trade-off concerns growth rates realized when resource availability is high (and other stresses are absent, henceforth “favorable conditions”) vs. mortality rates realized when resource availability is low (or other stresses are present, henceforth “unfavorable conditions”).

The inherent differences among species that contribute to this growth–mortality trade-off concern the abilities to disperse, to acquire resources and to grow rapidly, and to tolerate shade and other stresses. There is growing interest in the possibility that functional traits provide insight into these and other ecological differences among species, where functional traits refer to well-defined, measurable properties of organisms that strongly influence or are strongly coordinated with ecological performance (Lavorel and Garnier 2002, Reich et al. 2003, McGill et al. 2006, Westoby and Wright 2006). There is also a growing consensus that wood density (WD), seed mass (SM), leaf mass per area (LMA), and maximum adult height (H_{\max}) are key functional traits among forest trees providing insight into biogeochemical cycles (WD and LMA); life history variation (WD, SM, and LMA); and the ability to disperse to new sites (SM), acquire resources (LMA), grow quickly (WD and LMA), compete with neighbors (LMA, SM, and H_{\max}), and tolerate pests and other hazards (WD, SM, and LMA) (Hodgson et al. 1999, Weiher et al. 1999, Lavorel and Garnier 2002, Westoby et al. 2002, Cornelissen et al. 2003, Reich et al. 2003, Diaz et al. 2004, Westoby and Wright 2006, Wright et al. 2007, Chave et al. 2009).

The hundreds of sympatric tree species present in many tropical forests present an opportunity to evaluate hypothesized relationships between functional traits and life history variation as well as a challenge. The challenge concerns the initial documentation of life history variation. It is impractical to assess environmental conditions for enough individuals to evaluate a resource-dependent, growth–mortality trade-off for hundreds of species, particularly when most of those species are exceedingly rare. Instead, average growth rates and overall mortality rates are evaluated without reference to resource availability with the result that average growth–overall mortality relationships are often insignificant (Condit et al. 2006, Poorter et al. 2008). Here we evaluate the growth–mortality trade-off for growth rates of successively smaller subsets of the fastest growing individuals and mortality rates of successively smaller subsets of the individuals that grew most slowly in the previous census for six censuses of 368 122 trees on Barro Colorado Island (BCI), Panama. We predict that the growth–mortality trade-off will be stronger for these successively smaller subsets of individuals because

growth rates of the fastest growing individuals approximate potential growth rates under favorable conditions while mortality rates of the slowest growing individuals approximate the ability to survive unfavorable conditions.

After documenting each species position on the growth–mortality trade-off, we evaluated relationships with functional traits. Classical life history theory and common garden experiments from a wide range of vegetation types indicate that small SM, LMA, and WD characterize light-demanding or more generally high-resource-consuming species and that the opposite trait values characterize shade-tolerant or more generally stress-tolerant species (Grubb 1977, Kitajima 1994, Grime et al. 1997, Hodgson et al. 1999, Westoby et al. 2002, Cornelissen et al. 2003, Reich et al. 2003, Westoby and Wright 2006, Poorter et al. 2008, Chave et al. 2009, Muller-Landau 2010). Poorter et al. (2008) also hypothesized that growth and mortality rates should be inversely related to H_{\max} because species adapted to ephemeral forest gaps grow fast and should reproduce quickly at small adult sizes while species adapted to closed-canopy conditions grow slowly and should be tall and long-lived. Thus, we evaluated the predictions that growth rates, mortality rates, and position on the growth–mortality trade-off are inversely related to SM, LMA, WD, and H_{\max} .

Most tropical forest plant species are rare ecological ciphers, and the possibility that their life histories might be revealed by measurements of a few key functional traits has been greeted enthusiastically. Increasingly, studies of tropical trees evaluate relationships between mean growth rates and/or overall mortality rates and one or two functional traits, most frequently WD (reviewed in *Discussion*). Poorter et al. (2008) provide an exception in that they evaluated the same four functional traits considered here. In pairwise analyses, the individual traits consistently explained a small proportion of interspecific variation in mean growth and overall mortality rates of large trees from five Neotropical forests ($r^2 < 0.1$ for 60% and < 0.2 for 82.5% of comparisons). Collectively the four functional traits fared little better in multiple regression analyses explaining just 11% and 29% of interspecific variation in growth and mortality rates, respectively. Poorter et al. (2008) speculated that trait–performance relationships would be stronger for saplings than for the large trees that they considered. We evaluated the growth–mortality trade-off and relationships with functional traits for saplings as well as for large trees, for growth rates of successively smaller subsets of the most rapidly growing individuals to approximate potential growth rates under favorable conditions, and for mortality rates of successively smaller subsets of the most slowly growing individuals to approximate the potential to survive unfavorable conditions. Finally, we explored the range of trait combinations that characterize species at all points along the growth–mortality trade-off manifold.

METHODS

All free-standing woody plants with diameter at breast height (dbh) ≥ 1 cm were measured in a 50-ha plot on BCI in 1982, 1985, 1990, 1995, 2000, and 2005 (Hubbell and Foster 1992, Condit et al. 2006). Relative growth rates (RGR) equaled $\ln(\text{dbh}_f/\text{dbh}_i)/[(t_f - t_i)/365]$, where t is day of century and the subscripts f and i are final and initial values, respectively. Mortality rates (M) equaled $100 \times [1 - (N_f/N_i)]$ for N_i initial individuals and N_f survivors. Growth rates under favorable conditions equaled 95th percentile relative growth rates (RGR₉₅). Mortality rates under unfavorable conditions were calculated for the 25% of individuals of each species with the smallest RGR in the previous census interval (M_{25}). The first census interval lacked prior estimates of RGR so was not used to estimate mortality. We did not annualize mortality rates because subsequent census intervals were fixed at 5 yr. We also calculated mean RGR, RGR₉₀, overall mortality, and M_{50} . To limit sapling analyses to sterile individuals, we excluded individuals with dbh_i ≥ 5 cm and species with $H_{\max} < 5$ m. We also calculated mean RGR, RGR₉₀, RGR₉₅, overall mortality, M_{50} , and M_{25} for trees of the same large size ($10 \text{ cm} \leq \text{dbh}_i < 50 \text{ cm}$) evaluated by Poorter et al. (2008). We excluded palms because most palm species lack dbh growth, species with fewer than 100 observations to calculate M_{25} , RGR values for trees whose measurement height for dbh changed between censuses due to the growth of buttresses, and sapling RGR values involving the 1982 and 1985 censuses because dbh values < 5 cm were rounded down to the nearest 5 mm in these first two censuses.

We measured SM, WD, LMA, and H_{\max} following Cornelissen et al. (2003) with two exceptions. First, our SM refers to endosperm and embryo only while Cornelissen et al. (2003) recommend using diaspores. Our SM controls interspecific variation in allocation to endocarps and testa, which averaged $34\% \pm 21\%$ (mean ± 1 SD) of diaspore mass among BCI species. The second difference concerned LMA. We measured LMA for leaves taken from the tallest foliage of six of the smallest individuals of each species in the 50-ha plot. We did not use the sun-exposed leaves recommended by Cornelissen et al. (2003) because most BCI tree species reproduce in the understory and lack sun-exposed leaves (King et al. 2006b). We did, however, measure LMA for leaves from the tallest foliage of the six largest individuals of each species. The relationship between LMA for sun-exposed leaves and for the shaded understory leaves used here was strong ($r^2 = 0.57$, $P < 0.001$) for the 25 species with LMA determinations for five or more individuals in both light habitats. Maximum height, H_{\max} , equaled the mean height of the six largest (by dbh) individuals of each species in the 50-ha plot and a nearby (5 km) 38.4-ha plot (King et al. 2006b). To assess WD, we cored trees located within 15 km of BCI because increment borers are prohibited on BCI. We broke cores into pieces < 5 cm long, calculated

the specific gravity of each piece as oven-dried mass (100°C) divided by fresh volume (measured by water displacement), and estimated WD as an area-weighted average, where area refers to the annulus represented by each piece, assuming a circular trunk.

We performed correlation analyses to evaluate the growth–mortality trade-off and pairwise relationships between RGR₉₅, M_{25} , H_{\max} , LMA, WD, and SM for saplings using species values and phylogenetically independent contrasts (PICs) (Felsenstein 1985). We repeated the species-level correlation analyses for large trees to enable direct comparison with Poorter et al. (2008). We performed z tests to evaluate the hypothesis that correlation coefficients were equal.

We performed two principal components analyses. The first was for the RGR₉₅– M_{25} relationship. In subsequent analyses, species positions on the growth–mortality trade-off equaled their factor score on the first principal component of the RGR₉₅– M_{25} relationship. The second principal component analysis evaluated relationships among the four functional traits.

We performed three multiple regression analyses to evaluate relationships between traits (independent variables) and RGR₉₅, M_{25} , and position on the growth–mortality trade-off (three dependent variables) for saplings. The multiple regression analyses were repeated for species values and PICs. Multiple regression diagnostics were evaluated for collinearity, which occurs when condition indices (largest eigenvalue divided by each smaller eigenvalue) are > 30 or between 15 and 30 if variance proportions are large for two or more independent variables (Belsley et al. 1980). Collinearity was absent. The largest condition index of 17.0 occurred in a model that included all four traits with just one having a largish variance proportion. All condition indices were < 15 in models that excluded insignificant traits. The traits were effectively independent for the purposes of multiple regression analysis despite weak but significant correlations for two of the six trait pairs (see *Results: Functional traits*).

We performed a discriminant analysis to evaluate a standard practice in which tropical tree species are placed into light-demanding, shade-tolerant, and often one intermediate category. To approximate this practice, we divided ranked factor scores from the first principal component of the RGR₉₅– M_{25} relationship into thirds to represent light-demanding, intermediate, and shade-tolerant species (Fig. 1). The discriminant analysis then determined the proportion of species classified into these three categories correctly given species-specific values of SM, LMA, WD, and H_{\max} . The discriminant analysis is technically inappropriate because RGR₉₅– M_{25} factor scores are continuous rather than categorical. We included the discriminant analysis here because it is the most direct method to evaluate the standard practice of categorizing tropical trees by their supposed life histories.

We calculated PICs for a DNA barcode phylogeny based on three plastid markers (*rbcL*, *matK*, and *trnH-psbA*) for 281 species from the BCI 50-ha plot (Kress et al. 2009). The barcode phylogeny and the angiosperm phylogeny group current hypothesis resolved 97.5% vs. just 48.4% of nodes among these 281 species, respectively (Kress et al. 2009). We used the analysis of traits (AOT) module of the program Phylocom (Webb et al. 2008) to calculate contrasts. At polytomies, one trait was selected arbitrarily, its median value was used to divide the taxa involved in the polytomy into two groups, and the mean trait values for the two groups were used to calculate contrasts, as recommended by Pagel (1992).

All other analyses were performed with SYSTAT 11.0 (Richmond, California, USA) on untransformed values of H_{\max} , LMA, WD, and mortality rates and log-transformed values of SM and growth rates. We forced regressions of PIC data through the origin. This is necessary because the direction of subtraction is arbitrary when contrasts are calculated. A contrast with positive divergences in two traits would have negative divergences in both traits had the subtractions been performed the other way around. Due to this symmetry, regressions of contrast data have no intercept term; they are “forced” through the origin (Garland et al. 1992).

RESULTS

Growth–mortality trade-off in saplings

We calculated mean RGR, RGR_{90} , RGR_{95} , overall mortality, M_{50} , and M_{25} for saplings of 103 species with $H_{\max} > 5$ m (see Supplement). Interspecific standard deviations of growth and mortality rates and the strength of the growth–mortality trade-off increased consistently as RGR was calculated for ever-smaller subsets of the fastest growing individuals and as mortality rates were calculated for ever-smaller subsets of the slowest growing individuals. The trade-off between RGR_{95} and M_{25} ($r^2 = 0.691$, $P < 0.001$; Fig. 1) was significantly stronger ($z = 2.57$, $P < 0.01$) than the trade-off between mean RGR and overall mortality (not shown; $r^2 = 0.462$, $P < 0.001$). RGR_{95} and M_{25} varied nearly fivefold (0.073–0.34 $\text{cm}\cdot\text{cm}^{-1}\cdot\text{yr}^{-1}$) and 15-fold (5.5–87.5% per 5 yr) among species, respectively.

Growth–mortality trade-off in large trees

We calculated mean RGR, RGR_{90} , RGR_{95} , overall mortality, M_{50} , and M_{25} for large trees of 95 species (see Supplement). Interspecific standard deviations of growth and mortality rates increased consistently as RGR was calculated for ever-smaller subsets of the fastest growing individuals and as mortality rates were calculated for ever-smaller subsets of the slowest growing individuals. The strength of the growth–mortality trade-off was invariably modest. Coefficients of determination (r^2 values) varied from 0.01 for the relationship between mean RGR and overall mortality ($P = 0.21$) to a maximum of just 0.10 for the relationship between RGR_{90} and M_{25} ($P = 0.006$). This maximal

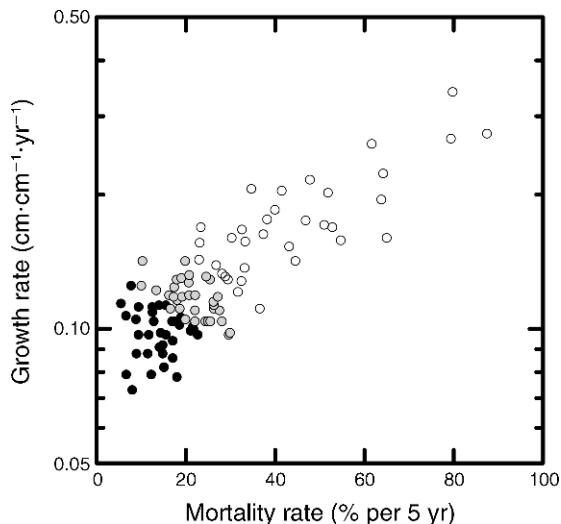


FIG. 1. The growth–mortality trade-off for saplings expressed as the 95th percentile relative growth rate (RGR_{95}) vs. the mortality rate of the slowest growing 25% of individuals (M_{25}) for 103 tree species with mean maximum height > 5 m on Barro Colorado Island, Panama. Open, shaded, and solid symbols represent species with factor scores in the top, middle, and bottom thirds, respectively, for the first principal component of the RGR_{95} – M_{25} trade-off. Minimum sample sizes are 100 trees/species for M_{25} and 333 trees/species for RGR_{95} .

difference in r^2 values was insignificant ($z = -1.24$, $P = 0.21$).

Functional traits

We determined H_{\max} , LMA, WD, and SM for 103, 103, 100, and 76 of the 103 sapling species, respectively (see Supplement). Maximum height varied sixfold (6.1–40.4 m), LMA fourfold (27–105 g/m^2), WD nearly threefold (0.31–0.84 g/cm^3), and SM by six orders of magnitude (0.00005–22 g). Small coefficients of determination characterized pairwise relationships among traits (Fig. 2); however, the LMA–WD (Fig. 2E) and LMA–SM (Fig. 2F) relationships were significant despite r^2 values of just 0.13 and 0.12 (Bonferroni-corrected P values = 0.001 and 0.014, respectively). Coefficients of determination were remarkably similar for PIC and species-level analyses of trait–trait relationships (not shown).

Two significant principal components explained 39.6% and 31.7% of variation among traits for the 75 sapling species with all four traits measured. The first component had large positive loadings for WD and LMA and the second had large positive loadings for H_{\max} and SM (Fig. 3).

Functional traits and demographic rates among saplings

In pairwise analyses, the direction of seven of the eight predictions (see *Introduction*) was confirmed although coefficients of determination were often small. Wood density was the strongest predictor of RGR_{95} and M_{25} ,

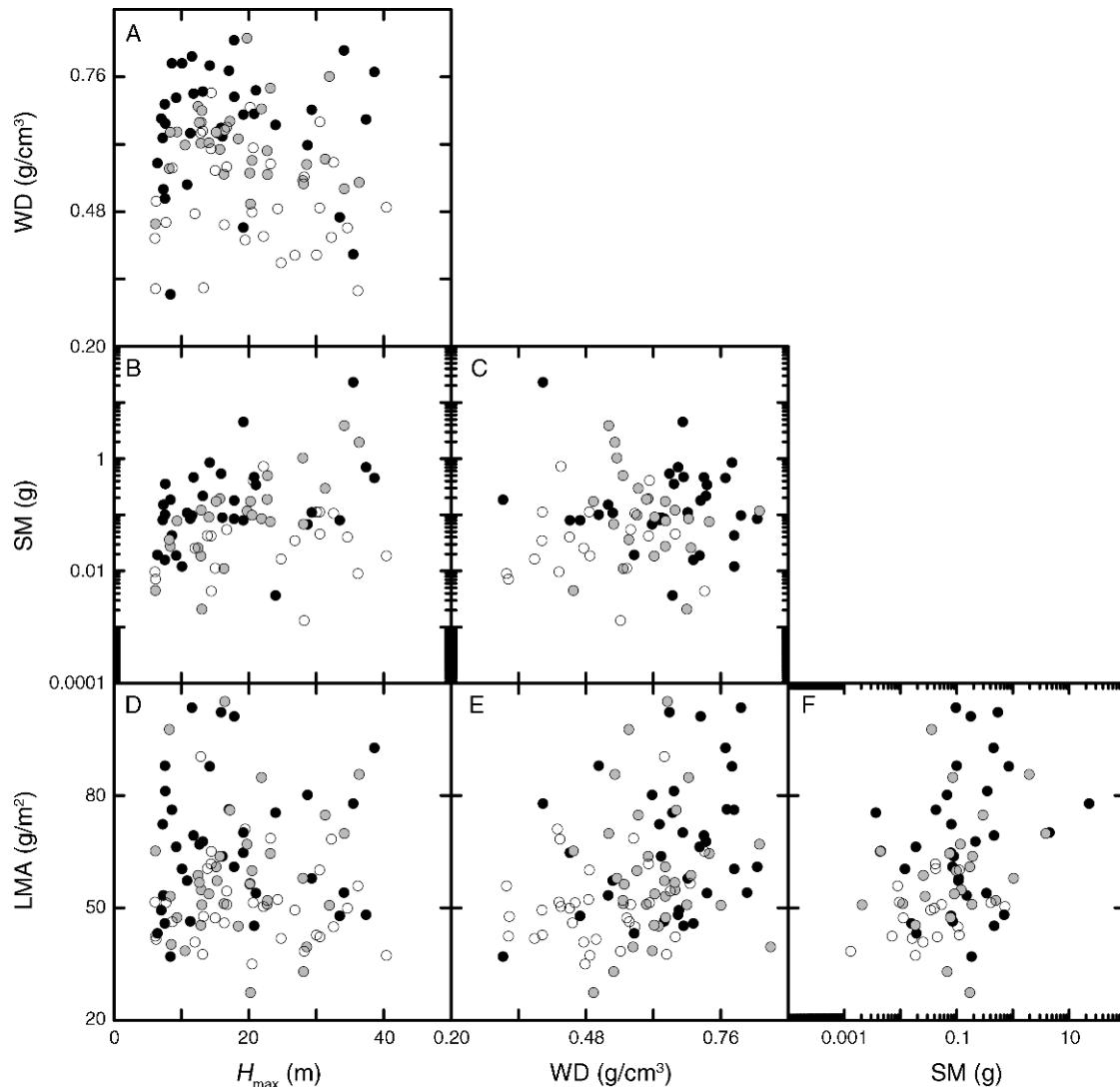


FIG. 2. Pairwise relationships among maximum height (H_{\max}), wood density (WD), seed mass (SM), and leaf mass per area (LMA) for trees on Barro Colorado Island, Panama. Open, shaded, and solid symbols are as in Fig. 1 and illustrate the wide range of trait values found at all positions on the growth–mortality trade-off. Coefficients of determination (r^2) are (A) 0.017, (B) 0.052, (C) 0.0056, (D) 0.00068, (E) 0.13, and (F) 0.12.

explaining 29–41% of interspecific variation in species-level and PIC analyses (Table 1). Leaf mass per area was the next strongest single predictor, explaining 18–24% of interspecific variation in species-level analyses and 9–13% in PIC analyses. Seed mass and H_{\max} were considerably weaker predictors of both RGR_{95} and M_{25} . The RGR_{95} – H_{\max} relationship was positive, not negative as predicted, but with a coefficient of determination of just 0.076 (Table 1A). Seed mass explained 15% of interspecific variation in M_{25} in the species-level analysis (Table 1A); however, this fell to 4.1% in the PIC analysis (Table 1B). In contrast, coefficients of determination were similar for PIC and species-level analyses for the seven remaining pairwise relationships between traits and demographic rates (Table 1).

In multiple regression analyses, the four traits collectively explained 39–43% of interspecific variation in RGR_{95} , M_{25} , and position on the growth–mortality trade-off in species-level analyses and 34–50% in PIC analyses (Table 1). Wood density accounted for 66–89% of the total variation explained by significant traits across the six multiple regression analyses. Leaf mass per area explained significant additional variation after WD in just two of the six multiple regressions despite being a consistently strong predictor of demographic rates in pairwise analyses. In contrast, SM explained significant additional variation after WD in four of the six multiple regressions despite weak relationships with vital rates in three of the four pairwise analyses. Once again, H_{\max} contributed little.

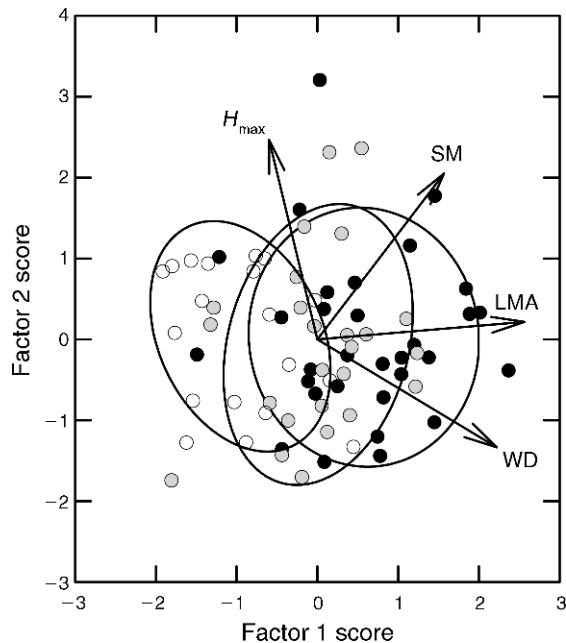


FIG. 3. Principal components analysis for maximum height (H_{max}), seed mass (SM), leaf mass per area (LMA), and wood density (WD) for tropical trees on Barro Colorado Island, Panama. Arrows represent principal components loadings. Open, shaded, and solid symbols are as in Fig. 1 and illustrate the wide range of trait values found at all positions on the growth-mortality trade-off. The broadly overlapping ellipses represent one sample standard deviation for species in the three inferred life history categories: light-demanding (open symbols), intermediate (gray symbols), and shade-tolerant (black symbols) species.

The discriminant analysis classified 58%, 32%, and 68% of shade-tolerant, intermediate, and light-demanding species correctly where these species had small, intermediate, and large factor scores on the first principal component of the $RGR_{95}-M_{25}$ relationship, respectively (Fig. 3). This compares with 33% correct classification expected by chance given three categories. The classification of BCI trees species into light-demanding, intermediate, and shade-tolerant categories is fraught with error even when informed by extensive trait data.

Functional traits and demographic rates among large trees

Table 2 contrasts three estimates of the strength of relationships between functional traits and demographic rates for large BCI trees ($10\text{ cm} \leq \text{dbh}_i < 50\text{ cm}$). Coefficients of determination for mean RGR and overall mortality are rather similar in Poorter et al. (2008) and in this study, with the notable exception of the SM-mortality relationship (see *Discussion: Seed mass*). Coefficients of determination for M_{25} and RGR_{95} tend to be larger than those obtained using mean RGR and overall mortality; however, the differences are not significant.

Relationships between functional traits and M_{25} and RGR_{95} are evaluated for saplings in the second and third columns of Table 1A and for large trees in the final two columns of Table 2. The correlation coefficients are marginally significantly larger for saplings for the WD- M_{25} , LMA- M_{25} , and LMA- RGR_{95} relationships and for large trees for the H_{max} - RGR_{95} relationship ($\text{abs}|z| > 1.7, P < 0.10$).

TABLE 1. Coefficients of determination (r^2) for pairwise correlation and multiple regression analyses of relationships between key functional traits, growth rates, mortality rates, and position on the growth-mortality trade-off for tree saplings from Barro Colorado Island, Panama: (A) species values and (B) phylogenetically independent contrasts.

Independent variable	Correlation analyses		Multiple regression analyses		
	M_{25}	RGR_{95}	M_{25}	RGR_{95}	$RGR_{95}-M_{25}$ factor score
A) Species values					
WD	-0.31***	-0.33***	-0.31***	-0.33***	-0.36***
SM	-0.15**	-0.066*	-0.12***	...	-0.087**
LMA	-0.17***	-0.24***	...	-0.076**	...
H_{max}	0.0004	+0.076*
Adjusted multiple R^2	0.41	0.39	0.43
B) Phylogenetically independent contrasts					
WD	-0.29***	-0.41***	-0.29***	-0.40***	-0.40***
SM	0.041	-0.067*	...	-0.055**	-0.050*
LMA	-0.090**	-0.13***	-0.060*
H_{max}	0.004	+0.056*	...	+0.062**	...
Adjusted multiple R^2	0.34	0.50	0.44

Notes: Significant entries are preceded by the sign of the relationship. For multiple regressions, only significant terms in models with all four independent variables are presented. The independent variables are wood density (WD), seed dry mass (SM), maximum height (H_{max}), and leaf mass per area (LMA). The dependent variables are mortality rates of the slowest-growing 25% of saplings (M_{25}), 95th percentile sapling growth rates (RGR_{95}), and factor scores on the first principal component for the $RGR_{95}-M_{25}$ relationship. Multiple regression analyses included all independent variables; entries are provided for significant independent variables only. The final row provides the adjusted multiple R^2 for the multiple regression models.

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

TABLE 2. Relationships between functional traits and growth and mortality rates for large trees (10 cm \leq dbh < 50 cm) from Barro Colorado Island, Panama.

Demographic variable	Poorter et al. (2008)		This study ($N = 67$ species)			
	Overall mortality	Mean RGR	Overall mortality	Mean RGR	M_{25}	RGR ₉₅
WD	0.023	-0.12*	-0.061*	-0.19***	-0.081*	-0.26***
SM	-0.13**	0.0004	0.0036	-0.072*	0.014	-0.094*
LMA	0.020	0.056	0.020	0.0079	0.017	-0.067*
H_{\max}	0.026	+0.12**	0.019	+0.17***	0.0029	+0.28***

Notes: Entries are coefficients of determination (r^2) preceded by the sign of significant relationships. The independent variables are wood density (WD), seed dry mass (SM), leaf mass per area (LMA), and maximum height (H_{\max}). The dependent variables are overall mortality rates, average relative growth rates (RGR), the mortality rate of the slowest growing 25% of individuals (M_{25}) and 95th percentile RGR (RGR₉₅).

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

DISCUSSION

A trade-off between growth rates and mortality rates is perhaps the best established axis of life history variation among forest tree species (Grubb 1977, Hubbell and Foster 1992, Pacala et al. 1996, Wright et al. 2003, Kitajima and Poorter 2008). We have shown that the strength of this trade-off depends strongly on the plants evaluated. The trade-off is strongest for saplings when growth rates of the fastest growing individuals and mortality rates of the slowest growing individuals are evaluated ($r^2 = 0.69$; Fig. 1), intermediate for saplings when average growth rates and overall mortality rates are evaluated ($r^2 = 0.46$), and much weaker for large trees ($r^2 \leq 0.10$). The environmental conditions responsible for the growth–mortality trade-off in closed-canopy forests are well aligned with the observed differences in the strength of the trade-off.

Light availability is a key environmental variable in closed-canopy forests because light limits photosynthetic carbon gain, which in turn influences growth and mortality. Light availability varies spatially with treefalls and other canopy-opening disturbances. The degree of spatial variation in light availability declines predictably with height above the forest floor as background light levels increase (Yoda 1974). The foliage of saplings is in the understory where light availability is most variable. The foliage of large trees is in the subcanopy and canopy where spatial variation in light availability is greatly reduced. Thus, interspecific variation in light availability is potentially greater for saplings than for large trees. In addition, mean growth and overall mortality rates integrate performance over the entire range of light levels encountered by each species. In contrast, the fastest and slowest growing individuals tend to be associated with high and low light levels, respectively, thereby capturing spatial variation in light availability. Thus, the growth–mortality trade-off is expressed more strongly among saplings than among large trees and when growth rates of the fastest growing individuals are contrasted with mortality rates of the slowest growing individuals.

Relationships between functional traits and demographic rates

Relationships between functional traits and demographic rates were generally in the direction predicted (see *Introduction* for predictions), tended to be stronger for saplings than for large trees, but tended to have modest r^2 values even for saplings (Tables 1 and 2). We used unprecedented sample sizes to quantify demographic rates (e.g., ≥ 400 and 333 trials for sapling mortality and RGR, respectively), measured H_{\max} directly rather than using qualitative values as is often done, and measured traits for each species on BCI (or within 15 km for WD) rather than using values from remote sites, thereby avoiding geographic variation (Patiño et al. 2009). For these reasons, the modest r^2 values that characterized trait–demography relationships are likely to be real.

These trait–demography relationships might be inherently weak for at least three reasons. First, each functional trait might influence demographic rates at a different life stage; we might be evaluating an important trait but at the wrong life stage (Grime et al. 1997, Poorter 2007). Second, functional traits might be involved in multiple trade-offs with contradictory effects on demographic rates (Marks and Lechowicz 2006). Third, SM, LMA, WD, and H_{\max} are “soft” in contrast to “hard” traits. “Hard” or fundamental traits are mechanistically linked to performance but are often difficult to measure and are replaced by easier-to-measure “soft” traits that experience suggests serve as adequate proxies (Hodgson et al. 1999, Weiher et al. 1999, Lavorel and Garnier 2002, Cornelissen et al. 2003, Reich et al. 2003). Here we evaluate these three possible explanations of weak trait–demography relationships for each trait.

Wood density

The strongest trait–demography relationships were consistently for WD. Growth rates and WD are negatively related at all stages of development after germination (Kitajima 1994, Muller-Landau 2004,

Poorter et al. 2008, Alvarez-Clare and Kitajima 2009, Chave et al. 2009). Possible mechanisms include greater construction costs as well as lower xylem conductance and hence lower photosynthetic potentials with greater WD (reviewed by Chave et al. 2009).

The relationship between WD and mortality was substantially stronger for saplings ($r^2 = 0.31$) than for large trees ($r^2 = 0.081$) in this study. We hypothesize that this reflects coordination between WD and shade tolerance (reviewed by Chave et al. 2009) combined with relief from light limitation and associated mortality among large trees whose foliage reaches into the canopy or subcanopy. Possible mechanisms relating WD and mortality include greater structural strength as well as greater pest resistance with greater WD (reviewed by Chave et al. 2009). In sum, WD contributed directly to the growth–mortality trade-off observed among saplings through relatively strong negative correlations with both growth and mortality rates.

Leaf mass per area

Leaf mass per area was the second best predictor of growth and mortality rates of saplings (Table 1). Leaf mass per area was also negatively correlated with both growth and mortality rates and might be expected to contribute directly to the growth–mortality trade-off; however, this was not the case in multiple regression analyses (Table 1). There was a weak positive relationship between LMA and WD ($r^2 = 0.13$; Fig. 2E). Much of the variation in demographic rates explained by LMA in pairwise analyses was apparently explained by WD in multiple regression analyses.

Leaf mass per area illustrates two of the reasons that trait–demography relationships might be inherently weak at the sapling stage. The first is ontogenetic. There is a strong negative relationship between LMA and early seedling growth rates; however, direct limitation of growth rates by large LMA decreases in importance as trees mature and leaf number increases (Lambers and Poorter 1992, Reich et al. 1992, Poorter et al. 2009). In this study, the LMA–RGR₉₅ relationship was substantially stronger for saplings ($r^2 = 0.24$) than for large trees ($r^2 = 0.067$). The LMA– M_{25} relationship was also substantially stronger for saplings ($r^2 = 0.18$) than for large trees ($r^2 = 0.017$). This is consistent with ongoing declines in the importance of LMA for demographic rates as trees mature.

The second reason LMA–demography relationships might be inherently weak is because LMA is a “soft” trait. Other leaf traits are sometimes better correlated with growth and mortality rates, particularly in closed-canopy forests (Reich et al. 1992, 2003, Poorter and Bongers 2006). Leaf life span, leaf tissue density, leaf nitrogen concentration, photosynthetic capacity, and dark respiration rates all contribute to shade tolerance (Grime 1965, Reich et al. 1995, 2003, Lusk and Reich 2000, Poorter and Bongers 2006, Kitajima and Poorter 2010). High CO₂ exchange rates are associated with the

fast-growth, high-mortality end of the growth–mortality trade-off while low respiratory carbon losses and long leaf lifetimes are associated with the slow-growth, low-mortality end of the trade-off. These “hard” leaf traits are mechanistically linked to carbon economy and might be better predictors of demographic rates than is LMA.

Seed mass

Relationships between SM and demographic rates were weak or inconsistent. Seed mass–growth relationships were significant but with coefficients of determination of just 6–9% (Tables 1 and 2). The SM–mortality relationships were highly variable. The SM–mortality relationship for large BCI trees was relatively strong in Poorter et al. (2008) and insignificant in this study (Table 2). Visual inspection of Fig. 2 in Poorter et al. (2008) suggests their BCI seed size–mortality relationship depends on three outliers with minute seeds and high mortality. The sapling SM– M_{25} relationship was relatively strong for species-level values but insignificant for phylogenetically independent contrasts (Tables 1 and 2). There is no evidence for coordinated evolutionary changes in SM and sapling mortality.

Weak and inconsistent relationships between SM and demographic rates are perhaps not surprising given the limited role of seeds at sapling and later life stages. There is a strong positive relationship between SM and the survival of seeds and first-year seedlings on BCI (King et al. 2006b); however, as seedlings mature and seed reserves are depleted, the seed no longer has any direct impact on performance. Subsequent effects of SM on performance must be indirect rather than causal and might be mediated by multi-trait trade-offs that involve SM (Shipley and Peters 1990, Westoby et al. 2002, Wright et al. 2004, Poorter et al. 2006).

Seed mass also illustrates interactions among trade-offs that affect performance. Consider the well-established seed number–seed mass trade-off in which many small seeds enable colonization ability while fewer larger seeds enable survival under a variety of hazards (Westoby et al. 2002, Muller-Landau 2010). This trade-off rests on the irrefutable but incomplete logic that seed number per gram of seed produced cannot be increased without a decrease in individual seed mass. This logic is incomplete because allocation to reproduction is not limited to seeds. In addition to seeds, reproduction involves pedicels to enhance flower and fruit displays; flowers, nectar, and pollen to enhance outcrossing; and exocarps, mesocarps, and endocarps to protect seeds and enhance dispersal. The seed number–seed mass trade-off is embedded in a large number of potential trade-offs that could compromise subsequent seed mass–performance relationships. As just one example, increased allocation to flowers might entail reduced allocation to seeds and smaller seed size but enhance outcrossing so that lifelong performance was actually greater for smaller but outcrossed seeds. Relationships

between SM and performance are contingent on both ontogenetic stage and values of other traits.

Maximum plant size

The weakest trait–demographic rate relationships were for H_{\max} . All mortality rates were independent of H_{\max} ($r^2 \leq 0.026$; Tables 1 and 2). Maximum height was also the weakest predictor of growth rates of saplings (Table 1); however, H_{\max} was the strongest predictor of growth rates of large trees (Table 2). Poorter et al. (2008) speculated that the H_{\max} –RGR relationship among large trees might depend on the inclusion of small species whose maximum sizes are not much larger than the lower 10-cm dbh threshold used to define large trees. There are many small tree species on BCI (King et al. 2006b). To explore their contribution to the H_{\max} –RGR relationship, we first included all 67 species with H_{\max} and RGR for large trees ($r^2 = 0.28$, $P < 0.001$; Table 2) then 60 of those species with $H_{\max} > 15$ m ($r^2 = 0.090$, $P = 0.021$), and finally 49 species with $H_{\max} > 20$ m ($r^2 = 0.014$, $P = 0.40$). The H_{\max} –RGR relationship for large trees became insignificant as a few small tree species were excluded. We conclude that growth and mortality rates are generally independent of H_{\max} on BCI. Bohlman and O'Brien (2006) reached the same conclusion in an earlier study of BCI saplings.

Other studies find stronger H_{\max} –RGR relationships. This includes significant H_{\max} –RGR relationships for large trees from three Neotropical forests, which might have been an artifact of the inclusion of small species as discussed in the previous paragraph (Poorter et al. 2008). At the Pasoh Forest Reserve, Malaysia, H_{\max} and RGR are positively correlated within five speciose genera (Thomas 1996), and a dbh-based index of maximum size is positively correlated with sapling RGR in a community-wide analysis but with an r^2 value of just 0.18 (King et al. 2006a). In sum, the evidence for correlations between H_{\max} and growth rates is mixed. This does not mean that H_{\max} is unimportant. Rather, several other traits tend to covary with H_{\max} and the strongest correlations between H_{\max} and growth rates are contingent on values of other traits (Thomas 1996, Poorter et al. 2006).

Conclusions

We have established that on BCI (1) there is a strong trade-off between rapid growth under favorable conditions and low mortality under unfavorable conditions for saplings (Fig. 1) but not large trees; (2) wood density explains a significant and substantial proportion of interspecific variation in position along the sapling growth–mortality trade-off (Table 1); and (3) after wood density is incorporated, three other supposedly key functional traits (seed mass, leaf mass per area, and maximum height) add little to the explained variation (Table 1). A wide range of seed masses, maximum heights, and leaf mass per area characterizes species at

all positions along the growth–mortality trade-off (Figs. 2 and 3).

This does not mean that seed mass, leaf mass per area, and maximum height are unimportant. The saplings evaluated here have already passed through several life history stages including seed arrival, germination, establishment, and growth and survival as seedlings. An obvious next step will be to evaluate trait–demography relationships at these early life stages (Kitajima 1994, Reich et al. 2003, King et al. 2006b, Muller-Landau et al. 2008).

Another important step will incorporate microhabitat-dependent performance. Ecological filters at the germination, establishment, and seedling stages restrict saplings to species-specific subsets of the available microhabitats. As an example, low light levels exclude most species from some proportion of potential regeneration sites with the proportion increasing from shade-tolerant to light-demanding species (Rüger et al. 2009). We only observed saplings of light-demanding species in relatively bright microhabitats. An analysis that controlled variation in light availability might yet detect stronger trait–performance relationships than observed here.

The search for traits that provide additional predictive ability at each life stage should also be expanded. Traits that are well correlated with performance in common garden experiments on young plants might not be correlated with performance at later life stages in real forests. We might need to return to the chemical, physiological, and allometric traits that are mechanistically linked to performance. We might also need to consider the possibility that relationship between any one trait and performance is contingent on values of other possibly unidentified traits (Marks and Lechowicz 2006).

We end with a philosophical question. How much variation do simple traits need to explain to serve as a useful foundation for building conceptual and quantitative models of ecological strategies? If traits explain 20%, 30%, or 50% of all variation in important species-level performance metrics, is the glass partially full or partially empty? Perhaps the answer is both. A simple trait-based approach can provide a meaningful first step toward a more predictive and quantitative science that can be further advanced by consideration of other more complex traits as well as ecological factors outside the plant trait envelope.

ACKNOWLEDGMENTS

Rolando Perez, Salomon Aguilar, and Javier Ballesteros determined wood densities. The F. H. Levinson Fund supported plant trait measurements. The National Science and MacArthur Foundations supported 50-ha plot censuses.

LITERATURE CITED

- Alvarez-Clare, S., and K. Kitajima. 2009. Susceptibility of tree seedlings to biotic and abiotic hazards in the understory of a moist tropical forest in Panama. *Biotropica* 41:47–56.
- Belsley, D. A., E. Kuh, and R. E. Welsch. 1980. Regression diagnostics: identifying influential data and sources of

- collinearity. John Wiley and Sons, New York, New York, USA.
- Bohman, S., and S. O'Brien. 2006. Allometry, adult stature and regeneration requirement of 65 tree species on Barro Colorado Island, Panama. *Journal of Tropical Ecology* 22: 123–136.
- Chave, J., D. Coomes, S. Jansen, S. L. Lewis, N. G. Swenson, and A. E. Zanne. 2009. Towards a worldwide wood economics spectrum. *Ecology Letters* 12:351–366.
- Condit, R., et al. 2006. The importance of demographic niches to tree diversity. *Science* 313:98–101.
- Cornelissen, J. H. C., et al. 2003. Handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* 51:335–380.
- Díaz, S., et al. 2004. The plant traits that drive ecosystems: evidence from three continents. *Journal of Vegetation Science* 15:295–304.
- Felsenstein, J. 1985. Phylogenies and the comparative method. *American Naturalist* 125:1–15.
- Garland, T., P. H. Harvey, and A. R. Ives. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Systematic Biology* 41:18–32.
- Grime, J. P. 1965. Shade tolerance in flowering plants. *Nature* 208:161–163.
- Grime, J. P., et al. 1997. Integrated screening validates primary axes of specialisation in plants. *Oikos* 79:259–281.
- Grubb, P. J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Reviews* 52:107–145.
- Hodgson, J. G., P. J. Wilson, R. Hunt, J. P. Grime, and K. Thompson. 1999. Allocating C-S-R plant functional types: a soft approach to a hard problem. *Oikos* 85:282–294.
- Hubbell, S. P., and R. B. Foster. 1992. Short-term dynamics of a neotropical forest: why ecological research matters to tropical conservation and management. *Oikos* 63:48–61.
- King, D. A., S. J. Davies, and M. N. Nur Sapardi. 2006a. Growth and mortality are related to adult tree size in a Malaysian mixed dipterocarp forest. *Forest Ecology and Management* 223:152–158.
- King, D. A., S. J. Wright, and J. H. Connell. 2006b. The distribution of maximum tree heights in tropical vs. temperate forests: Cause or consequence of tropical diversity? *Journal of Tropical Ecology* 22:11–24.
- Kitajima, K. 1994. Relative importance of photosynthetic and allocation traits as correlates of seedling shade tolerance of 15 tropical tree species. *Oecologia* 98:419–428.
- Kitajima, K., and L. Poorter. 2008. Functional basis for resource niche partitioning by tropical trees. Pages 172–188 in W. P. Carson and S. A. Schnitzer, editors. *Tropical forest community ecology*. Blackwell, Oxford, UK.
- Kitajima, K., and L. Poorter. 2010. Tissue-level leaf toughness, but not lamina thickness, predicts sapling leaf lifespan and shade tolerance of tropical tree species. *New Phytologist*, in press. [doi: 10.1111/j.1469-8137.2010.03212.x]
- Kress, W. J., et al. 2009. Plant DNA barcodes and a community phylogeny of a tropical forest dynamics plot in Panama. *Proceedings of the National Academy of Sciences USA* 106: 18627–18632.
- Lambers, H., and H. Poorter. 1992. Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. *Advances in Ecological Research* 23:187–261.
- Lavorel, S., and E. Garnier. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology* 16: 545–556.
- Lusk, C. H., and P. B. Reich. 2000. Relationships of leaf dark respiration with light environment and tissue nitrogen content in juveniles of 11 cold-temperate tree species. *Oecologia* 123:318–329.
- Marks, C. O., and M. J. Lechowicz. 2006. Alternative designs and the evolution of functional diversity. *American Naturalist* 167:55–66.
- McGill, B. J., B. J. Enquist, E. Weiher, and M. Westoby. 2006. Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution* 21:178–185.
- Muller-Landau, H. C. 2004. Interspecific and inter-site variation in wood specific gravity of tropical trees. *Biotropica* 36: 20–32.
- Muller-Landau, H. C. 2010. The tolerance–fecundity tradeoff and the maintenance of diversity in seed size. *Proceedings of the National Academy of Sciences USA*, in press.
- Muller-Landau, H. C., S. J. Wright, O. Calderon, R. Condit, and S. P. Hubbell. 2008. Interspecific variation in primary seed dispersal in a tropical forest. *Journal of Ecology* 96:653–667.
- Pacala, S. W., C. D. Canham, J. Saponara, J. A. Silander, R. K. Kobe, and E. Ribbens. 1996. Forest models defined by field measurements: estimation, error analysis and dynamics. *Ecological Monographs* 66:1–43.
- Pagel, M. D. 1992. A method for the analysis of comparative data. *Journal of Theoretical Biology* 156:431–442.
- Patiño, S., et al. 2009. Branch xylem density variations across the Amazon Basin. *Biogeosciences* 6:545–568.
- Poorter, H., Ü. Niinemets, L. Poorter, I. J. Wright, and R. Villar. 2009. Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. *New Phytologist* 182: 565–588.
- Poorter, L. 2007. Are species adapted to their regeneration niche, adult niche or both? *American Naturalist* 169:433–442.
- Poorter, L., and F. Bongers. 2006. Leaf traits are good predictors of plant performance across 53 rain forest species. *Ecology* 87:1733–1743.
- Poorter, L., L. Bongers, and F. Bongers. 2006. Architecture of 54 moist forest tree species: traits, trade-offs, and functional groups. *Ecology* 87:1289–1301.
- Poorter, L., et al. 2008. Are functional traits good predictors of demographic rates? Evidence from five Neotropical forests. *Ecology* 89:1908–1920.
- Reich, P. B., D. S. Ellsworth, and C. Uhl. 1995. Leaf carbon and nutrient assimilation and conservation in species of differing successional status in an oligotrophic Amazonian forest. *Functional Ecology* 9:65–76.
- Reich, P. B., M. B. Walters, and D. S. Ellsworth. 1992. Leaf lifespan in relation to leaf, plant and stand characteristics among diverse ecosystems. *Ecological Monographs* 62:365–392.
- Reich, P. B., I. Wright, J. Cavender-Bares, J. Craine, J. Oleksyn, M. Westoby, and M. B. Walters. 2003. The evolution of plant functional variation: traits, spectra, and strategies. *International Journal of Plant Sciences* 164:S143–S164.
- Rüger, N., A. Huth, S. P. Hubbell, and R. Condit. 2009. Response of recruitment to light availability across a tropical lowland rain forest community. *Journal of Ecology* 97:1360–1368.
- Shipley, B., and R. H. Peters. 1990. The allometry of seed weight and seedling relative growth rate. *Functional Ecology* 4:523–539.
- Thomas, S. C. 1996. Asymptotic height as a predictor of growth and allometric characteristics in Malaysian rain forest trees. *American Journal of Botany* 83:556–566.
- Webb, C. O., D. D. Ackerly, and S. W. Kembel. 2008. Phylocom: software for the analysis of phylogenetic community structure and trait evolution. *Bioinformatics* 24:2098–2100.
- Weiher, E., A. van der Werf, K. Thompson, M. Roderick, E. Garnier, and O. Eriksson. 1999. Challenging Theophrastus: a common core list of plant traits for functional ecology. *Journal of Vegetation Science* 10:609–620.

- Westoby, M., D. S. Falster, A. T. Moles, P. A. Vesk, and I. J. Wright. 2002. Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology and Systematics* 33:125–159.
- Westoby, M., and I. J. Wright. 2006. Land-plant ecology on the basis of functional traits. *Trends in Ecology and Evolution* 21:261–268.
- Wright, I. J., et al. 2004. The worldwide leaf economics spectrum. *Nature* 428:821–827.
- Wright, I. J., et al. 2007. Relationships among key dimensions of plant trait variation in seven Neotropical forests. *Annals of Botany* 99:1003–1015.
- Wright, S. J., H. C. Muller-Landau, R. Condit, and S. P. Hubbell. 2003. Gap-dependent recruitment, realized vital rates, and size distributions of tropical trees. *Ecology* 84: 3174–3185.
- Yoda, K. 1974. Three-dimensional distribution of light intensity in a tropical rain forest of West Malaysia. *Japanese Journal of Ecology* 24:247–254.

SUPPLEMENT

All data used in analyses of relationships among functional traits and demographic rates for trees and saplings from Barro Colorado Island, Panama (*Ecological Archives* E091-257-S1).

S. Joseph Wright, Kaoru Kitajima, Nathan J. B. Kraft, Peter B. Reich, Ian J. Wright, Daniel E. Bunker, Richard Condit, James W. Dalling, Stuart J. Davies, Sandra Díaz, Bettina M. J. Engelbrecht, Kyle E. Harms, Stephen P. Hubbell, Christian O. Marks, Maria C. Ruiz-Jaen, Cristina M. Salvador, and Amy E. Zanne. 2010. Functional traits and the growth–mortality trade-off in tropical trees. *Ecology* 91:3664–3674.

Supplement

All data used in analyses of relationships among functional traits and demographic rates for trees and saplings from Barro Colorado Island, Panama.
***Ecological Archives* E091-257-S1.**

[Copyright](#)

[Authors](#)

[File list \(downloads\)](#)

[Description](#)

Author(s)

S. Joseph Wright
Smithsonian Tropical Research Inst.
Apartado 0843–03092
Balboa
Republic of Panama
Tel: +507-212-8132
Fax: +507-212-8148
Email: wrightj@si.edu

Kaoru Kitajima
Dept of Biology
Univ. of Florida
Gainesville, FL 32611
USA

Nathan J. B. Kraft
Dept of Integrative Biology
Univ. of California, Berkeley, 94720
USA

Peter B. Reich
Dept of Forest Resources
Univ. of Minnesota
St Paul, MN 55108
USA

Ian J. Wright

Dept of Biological Sciences
Macquarie Univ.
Sydney, NSW 2109
Australia

Dan E. Bunker
Dept. Biological Sciences
New Jersey Inst. of Technology
Newark, NJ 07102
USA

Richard Condit
Smithsonian Tropical Research Inst.
Apartado 0843-03092
Balboa
Republic of Panama

James W. Dalling
Dept of Plant Biology
Univ. of Illinois
Champaign-Urbana, IL 61801
USA

Stuart J. Davies
Smithsonian Tropical Research Inst.
Apartado 0843-03092
Balboa
Republic of Panama

Sandra Diaz
Instituto Multidisciplinario de Biología Vegetal (CONICET-UNC) and FCEFyN
Universidad Nacional de Córdoba
Casilla de Correo 495, 5000 Córdoba
Argentina

Bettina M. J. Engelbrecht
Dept Plant Ecology
Univ Bayreuth
95440 Bayreuth
Germany

Kyle E. Harms
Dept of Biological Sciences
Louisiana State Univ.
Baton Rouge, LA 70803
USA

Stephen P. Hubbell
Dept of Ecology and Evolutionary Biology
UCLA
Los Angeles, CA 90095
USA

Christian O. Marks
Dept of Ecology, Evolution and Behavior

Univ. of Minnesota
St Paul, MN 55108
USA

Maria C. Ruiz-Jaen
Dept of Biology
McGill Univ
1205 Dr Penfield Ave
Montreal, Quebec H3A 1B1
Canada

Christina M. Salvador
Santa Fe Botanical Garden
PO Box 23343
Santa Fe NM 87502-3343
USA

Amy E. Zanne
Dept of Biology
One University Blvd.
Univ. of Missouri - St. Louis
St. Louis, MO 63121
USA

File list

[Supplement_20100505.txt](#)

Description

The `Supplement_20100505.txt` file is a tab-delimited ASCII file. The file contains nomenclature, wood specific gravity, seed mass, maximum height and leaf mass per area for each species. The file also contains average, 90th percentile and 95th percentile diameter growth rates and sample sizes for saplings and large trees of each species. The file also contains overall mortality rates and mortality rates of the slowest growing 50% and 25% of individuals in the previous census interval and sample sizes for saplings and large trees of each species.

Missing values for functional traits and values that would be based on inadequate sample sizes for demographic variables are represented as "-99".

Column definitions follow:

- 1 = GENUS\$ - genus (truncated at 12 letters)
- 2 = SPECIES\$ - species (truncated at 12 letters)
- 3 = FAMILY\$ - family (truncated at 12 letters)
- 4 = WSG - Mean wood specific gravity (g cm⁻³)
- 5 = SEEDMASS - Mean seed dry mass (g)
- 6 = HEIGHT - Mean height of six largest individuals (m)
- 7 = LMA - Mean leaf mass per area determined from leaf discs for the six smallest individuals of each species (g m⁻²)

- 8 = RGR95SAP - 95th percentile relative growth rate for saplings (cm cm-1 yr-1)
- 9 = RGR90SAP - 90th percentile relative growth rate for saplings (cm cm-1 yr-1)
- 10 = RGRAVGSAP - Mean relative growth rate for saplings (cm cm-1 yr-1)
- 11 = N_RGRSAP - sample size to determine relative growth rates for saplings
- 12 = MRT25SAP - Mortality rate for the 25% of saplings with the slowest growth rates in the previous census (% 5 yr-1)
- 13 = MRT50SAP - Mortality rate for the 50% of saplings with the slowest growth rates in the previous census (% 5 yr-1)
- 14 = MRTALLSAP - Mortality rate for all saplings (% 5 yr-1)
- 15 = N_MRTSAP - sample size to determine mortality rates for saplings
- 16 = RGR95TRE - 95th percentile relative growth rate for large trees (cm cm-1 yr-1)
- 17 = RGR90TRE - 90th percentile relative growth rate for large trees (cm cm-1 yr-1)
- 18 = RGRAVGTRE - Mean relative growth rate for large trees (cm cm-1 yr-1)
- 19 = N_RGRTRE - sample size to determine relative growth rates for large trees
- 20 = MRT25TRE - Mortality rate for the 25% of large trees with the slowest growth rates in the previous census (% 5 yr-1)
- 21 = MRT50TRE - Mortality rate for the 50% of large trees with the slowest growth rates in the previous census (% 5 yr-1)
- 22 = MRTALLTRE - Mortality rate for all large trees (% 5 yr-1)
- 23 = N_MRTTRE - sample size to determine mortality rates for large trees

Check sum values are:

For the first row, there are 9 missing values and Checksum = 4459.035

For the final row, there are zero missing values and Checksum = 1501.341

For the fourth column, there are 5 missing values and Checksum = 74.980

For the seventh column, there is one missing value and Checksum = 7425.420

GENUS\$ - genus (truncated at 12 letters)

SPECIES\$ - species (truncated at 12 letters)

FAMILY\$ - family (truncated at 12 letters)

WSG - Mean wood specific gravity (g cm^{-3})

SEEDMASS - Mean seed dry mass (g)

HEIGHT - Mean height of six largest individuals (m)

LMA - Mean leaf mass per area determined from leaf discs for the six smallest individuals of each species (g m^{-2})

RGR95SAP - 95th percentile relative growth rate for saplings ($\text{cm cm}^{-1} \text{yr}^{-1}$)

RGR90SAP - 90th percentile relative growth rate for saplings ($\text{cm cm}^{-1} \text{yr}^{-1}$)

RGRAVGSAP - Mean relative growth rate for saplings ($\text{cm cm}^{-1} \text{yr}^{-1}$)

N_RGRSAP - sample size to determine relative growth rates for saplings

MRT25SAP - Mortality rate for the 25% of saplings with the slowest growth rates in the previous census ($\% 5 \text{yr}^{-1}$)

MRT50SAP - Mortality rate for the 50% of saplings with the slowest growth rates in the previous census ($\% 5 \text{yr}^{-1}$)

MRTALLSAP - Mortality rate for all saplings ($\% 5 \text{yr}^{-1}$)

N_MRTSAP - sample size to determine mortality rates for saplings

RGR95TRE - 95th percentile relative growth rate for large trees ($\text{cm cm}^{-1} \text{yr}^{-1}$)

Aspidosperma	spruceanum	Apocynaceae	0.770	0.453950	38.6	92.7					
	0.088	0.065	0.025	1634	11.4	10.5	9.4	1313	0.057	0.045	0.0202
	239	12.8	9.6	4.8	189						
Astronium	graveolens	Anacardiaceae	0.808	0.017660	34.8	35.1	-99				
	-99	-99.000	-99	-99.0	-99.0	-99.0	-99.0	0.037	0.028	0.0101	
	169	9.1	6.0	2.9	136						
Beilschmiedi	pendula	Lauraceae	0.528	3.876056	34.2	69.8					
	0.115	0.089	0.032	7878	26.2	24.1	18.0	6533	0.044	0.032	0.0113
	1282	17.6	11.5	7.3	1048						
Brosimum	alicastrum	Moraceae	0.672	0.701005	37.4	48.1	0.114				
	0.092	0.036	2173	5.5	4.9	4.4	1761	0.038	0.026	0.0069	786
	13.8	11.0	6.8	621							
Calophyllum	longifolium	Clusiaceae	0.541	1.950110	36.4	85.6	0.131	0.1			
	0.040	3052	24.6	20.1	14.9	2233	0.049	0.041	0.0155	221	47.8
	37.0	22.2	185								
Capparis	frondosa	Capparaceae	0.633	0.080482	7.2	72.3	0.082				
	0.062	0.018	13974	15.1	13.1	10.9	11576	-99.0	-99.0	-99.0000	-
	99.0	-99.0	-99.0	-99.0	-99.0						
Casearia	aculeata	Flacourtiace	0.690	0.002075	13.1	50.8					
	0.113	0.086	0.029	1402	26.3	22.8	18.6	1135	-99.0	-99.0	-99.0000
	-99.0	-99.0	-99.0	-99.0	-99.0						
Casearia	arborea	Flacourtiace	0.562	0.001150	22.5	27.5	-99				
	-99	-99.000	-99	-99.0	-99.0	-99.0	-99.0	0.056	0.038	0.0156	
	461	38.1	29.2	18.4	392						
Casearia	sylvestris	Flacourtiace	0.662	-99.000000	16.4	70.4	-99				
	-99	-99.000	-99	-99.0	-99.0	-99.0	-99.0	0.03	0.023	0.0099	
	258	35.2	23.9	16.4	220						
Cassipourea	elliptica	Rhizophorace	0.660	0.003657	24.0	75.4					
	0.112	0.086	0.032	3399	9.4	8.5	5.8	2674	0.043	0.036	0.0169
	356	17.6	14.6	9.1	275						
Cecropia	insignis	Cecropiaceae	0.551	-99.000000	30.6	-99.0	-99				
	-99	-99.000	-99	-99.0	-99.0	-99.0	-99.0	0.086	0.062	0.0250	
	831	34.5	25.7	17.2	688						
Celtis	schippii	Ulmaceae	0.579	-99.000000	20.7	51.5	-99	-99			
	-99.000	-99	-99.0	-99.0	-99.0	-99.0	-99.0	0.045	0.035	0.0140	160
	32.3	23.8	14.8	128							
Cestrum	megalophyllu	Solanaceae	0.424	0.009621	6.1	51.5	0.16				
	0.12	0.042	430	65.0	64.2	53.5	404	-99.0	-99.0	-99.0000	-
	99.0	-99.0	-99.0	-99.0	-99.0						
Chamguava	schippii	Myrtaceae	-99.000	-99.000000	12.7	66.9					
	0.113	0.09	0.035	1158	15.5	11.0	8.1	854	-99.0	-99.0	-99.0000
	-99.0	-99.0	-99.0	-99.0	-99.0						
Chrysochlamy	eclipes	Clusiaceae	0.507	0.100268	7.6	87.9					
	0.091	0.065	0.022	1511	14.0	12.9	9.1	1239	-99.0	-99.0	-99.0000
	-99.0	-99.0	-99.0	-99.0	-99.0						
Chrysophyllu	argenteum	Sapotaceae	0.736	0.075110	23.2	64.5	0.13				
	0.091	0.030	1932	19.0	16.2	12.5	1493	0.038	0.032	0.0100	367
	20.3	14.9	8.4	298							
Coccoloba	manzinellens	Polygonaceae	0.716	0.018820	9.2	66.3					
	0.104	0.078	0.025	1498	17.0	15.8	13.1	1241	-99.0	-99.0	-99.0000
	-99.0	-99.0	-99.0	-99.0	-99.0						
Cordia	alliodora	Boraginaceae	0.455	0.005611	31.6	30.5	-99				
	-99	-99.000	-99	-99.0	-99.0	-99.0	-99.0	0.069	0.059	0.0236	
	260	28.8	21.0	11.4	211						

Cordia	bicolor	Boraginaceae	0.373	0.016216	24.8	41.8	0.26			
	0.181	0.066	1338	61.6	55.7	39.3	1172	0.068	0.05	0.0196
	18.4	13.9	9.6	1026						1323
Cordia	lasiocalyx	Boraginaceae	-99.000	0.042325	13.9	60.5				
	0.167	0.127	0.049	2880	32.6	29.3	20.3	2400	0.026	0.019
	1620	32.4	30.0	20.8	1394					0.0061
Coussarea	curvigemma	Rubiaceae	0.622	0.018453	12.9	45.3	0.119			
	0.091	0.035	6664	16.2	13.5	9.6	5233	0.027	0.024	0.0083
	15.9	15.9	13.5	178						233
Croton	billbergianu	Euphorbiaceae	0.478	-99.000000	20.5	35.0				
	0.34	0.269	0.117	810	79.8	74.2	60.1	716	0.08	0.068
	203	78.6	72.9	59.1	171					0.0325
Cupania	seemannii	Sapindaceae	0.665	0.120431	13.0	54.8	0.118			
	0.093	0.033	3798	17.2	15.2	11.0	3021	0.038	0.032	0.0061
	3.4	3.4	2.5	119						161
Dendropanax	arboreus	Araliaceae	0.411	0.006140	24.5	65.5	-99	-99		
	-99.000	-99	-99.0	-99.0	-99.0	-99.0	-99.0	0.034	0.028	0.0099
	24.4	19.1	12.7	347						411
Desmopsis	panamensis	Annonaceae	0.536	0.108017	10.9	57.2	0.102			
	0.079	0.029	46091	18.6	16.8	13.2	36989	-99.0	-99.0	-99.0000
	99.0	-99.0	-99.0	-99.0	-99.0					-
Drypetes	standleyi	Euphorbiaceae	0.618	0.067596	28.7	80.1				
	0.098	0.076	0.027	7060	14.3	12.6	9.5	5773	0.041	0.034
	1211	10.3	6.3	4.2	930					0.0146
Erythrina	costaricensi	Fabaceae:Pap	0.500	-99.000000	9.4	19.4				
	-99	-99	-99.000	-99	-99.0	-99.0	-99.0	-99.0	0.021	0.016
	0.0009		142	16.1	19.4	20.0	125			
Erythroxyllum	macrophyllum	Erythroxyllac	0.643	-99.000000	12.9					
	90.4	0.111	0.083	0.028	938	36.6	34.1	27.0	788	-99.0
	99.0000	-99.0	-99.0	-99.0	-99.0	-99.0				-
Erythroxyllum	panamense	Erythroxyllac	0.703	0.015756	7.6	45.8				
	0.094	0.074	0.025	441	17.1	17.1	13.4	352	-99.0	-99.0
	-99.0	-99.0	-99.0	-99.0	-99.0					-99.0000
Eugenia	coloradoensi	Myrtaceae	0.693	0.085297	21.9	84.8				
	0.111	0.088	0.028	2451	26.2	24.2	17.5	2063	0.051	0.042
	348	26.5	17.5	16.0	275					0.0186
Eugenia	galalonensis	Myrtaceae	0.636	0.088920	16.1	63.8				
	0.104	0.078	0.027	5533	12.8	11.5	9.6	4181	-99.0	-99.0
	-99.0	-99.0	-99.0	-99.0	-99.0					-99.0000
Eugenia	nesiotica	Myrtaceae	0.732	0.340890	21.1	53.9	0.097			
	0.068	0.020	1880	15.5	15.1	12.7	1526	0.043	0.032	0.0105
	12.8	9.5	5.8	191						238
Eugenia	oerstediana	Myrtaceae	0.656	-99.000000	16.7	54.4	0.129			
	0.096	0.033	6830	29.4	27.6	19.4	5719	0.063	0.05	0.0211
	43.4	31.8	19.5	518						670
Faramea	occidentalis	Rubiaceae	0.609	0.193216	15.7	63.7				
	0.122	0.098	0.040	82728	13.3	10.4	7.2	66503	0.027	0.022
	6896	27.4	21.3	14.2	5337					0.0081
Ficus	tonduzii	Moraceae	0.357	-99.000000	11.2	76.3	-99	-99		
	99.000	-99	-99.0	-99.0	-99.0	-99.0	0.03	0.022	0.0029	
	28.6	24.0	100							113
										25.0
Garcinia	intermedia	Clusiaceae	0.654	0.541000	15.9	102.2	0.097			
	0.074	0.029	17020	9.4	8.6	7.0	13486	0.031	0.026	0.0103
	17.8	15.1	10.2	294						392

Garcinia	madruno	Clusiaceae	0.649	-99.000000	16.4	105.1	0.11			
	0.089	0.035	1804	22.0	17.2	22.0	1490	-99.0	-99.0	-99.0000
	99.0	-99.0	-99.0	-99.0	-99.0					-
Guapira	standleyana	Nyctaginaceae	0.511	0.061173	32.2	38.0	-99			
	-99	-99.000	-99	-99.0	-99.0	-99.0	-99.0	0.057	0.042	0.0144
	406	3.7	4.3	3.0	328					
Guarea	bullata	Meliaceae	0.668	-99.000000	17.2	76.1	0.097			
	0.072	0.024	4288	29.6	27.6	22.1	3720	0.023	0.017	0.0060
	37.1	30.8	19.8	288						335
Guarea	guidonia	Meliaceae	0.560	-99.000000	20.2	56.2	0.119			
	0.091	0.033	5222	22.1	20.5	15.1	4274	0.035	0.025	0.0077
	15.5	10.8	6.4	1371						1705
Guatteria	dumetorum	Annonaceae	0.446	0.040030	34.6	49.9	0.157			
	0.116	0.042	2978	33.3	30.3	21.9	2599	0.054	0.042	0.0151
	35.3	24.7	16.5	861						1027
Guazuma	ulmifolia	Sterculiaceae	0.495	0.001297	23.1	37.8	-99			
	-99	-99.000	-99	-99.0	-99.0	-99.0	-99.0	0.101	0.077	0.0270
	130	8.3	6.1	4.0	100					
Guettarda	foliacea	Rubiaceae	0.618	-99.000000	10.6	38.5	0.119			
	0.092	0.034	863	20.7	19.1	12.9	744	0.033	0.022	0.0046
	8.3	12.3	10.5	294						353
Gustavia	superba	Lecythidaceae	0.612	5.661719	20.6	44.7	-99			
	-99	-99.000	-99	-99.0	-99.0	-99.0	-99.0	0.021	0.016	0.0059
	3089	6.4	4.7	3.0	2494					
Hasseltia	floribunda	Flacourtiaceae	0.565	0.011230	15.0	47.3				
	0.128	0.099	0.038	1454	32.4	31.1	25.2	1328	0.042	0.031
	1008	32.1	23.6	15.8	840					0.0117
Heisteria	concinna	Olacaceae	0.719	0.179125	17.9	101.1	0.125			
	0.104	0.047	2356	7.7	5.9	4.7	1921	0.031	0.025	0.0101
	12.2	8.7	5.8	1018						1284
Herrania	purpurea	Sterculiaceae	0.308	0.184663	8.4	37.0				
	0.112	0.082	0.029	2073	12.5	11.0	11.1	1673	-99.0	-99.0
	-99.0	-99.0	-99.0	-99.0	-99.0					-99.0000
Hieronyma	alchorneoides	Euphorbiaceae	0.585	0.000960	34.3	35.2				
	-99	-99	-99.000	-99	-99.0	-99.0	-99.0	-99.0	0.064	0.039
	0.0178		165	12.1	6.0	3.0	135			
Hirtella	triandra	Chrysobalana	0.606	0.188107	22.7	50.9				
	0.124	0.097	0.036	15074	17.4	14.2	10.0	12256	0.037	0.03
	2879	13.2	9.2	5.7	2212					0.0120
Hura	crepitans	Euphorbiaceae	-99.000	-99.000000	35.0	27.6	-99			
	-99	-99.000	-99	-99.0	-99.0	-99.0	-99.0	0.047	0.033	0.0123
	432	5.8	4.1	2.9	345					
Hybanthus	prunifolius	Violaceae	0.580	0.019299	6.5	43.2	0.1			
	0.075	0.024	152207	21.7	21.0	17.2	126446			-99.0
	99.0000	-99.0	-99.0	-99.0	-99.0	-99.0				-99.0
Inga	acuminata	Fabaceae:Mim	0.321	-99.000000	13.3	47.7	0.169	0.14		
	0.062	1016	23.4	15.2	9.6	790	-99.0	-99.0	-99.0000	-99.0
	99.0	-99.0	-99.0	-99.0						-
Inga	goldmanii	Fabaceae:Mim	0.557	0.499075	22.8	51.9	0.118			
	0.094	0.036	1192	27.1	25.0	17.7	1009	0.066	0.051	0.0184
	48.7	46.2	31.6	158						180
Inga	marginata	Fabaceae:Mim	0.486	-99.000000	24.3	52.2	0.223			
	0.163	0.063	1405	64.2	60.0	45.1	1285	0.132	0.105	0.0524
	60.7	47.2	29.6	247						321

Inga	nobilis	Fabaceae:Mim	0.645	0.172580	15.2	60.9	0.132						
			0.101	0.038	2202	20.7	17.5	12.0	1879	0.041	0.03	0.0113	232
			31.0	22.6	15.3	170							
Inga	sapindoides	Fabaceae:Mim	0.612	0.406354	20.7	51.3	0.163	0.12					
			0.044	645	37.3	31.6	22.7	572	0.058	0.049	0.0173	296	40.7
			29.4	17.6	239								
Inga	umbellifera	Fabaceae:Mim	0.665	-99.000000	12.7	56.7	0.118	0.09					
			0.033	3193	19.1	18.0	13.3	2685	-99.0	-99.0	-99.0000	-99.0	-
			99.0	-99.0	-99.0	-99.0							
Jacaranda	copaia	Bignoniaceae	0.374	0.002070	31.8	48.1	-99						
			-99	-99.000	-99	-99.0	-99.0	-99.0	-99.0	0.088	0.069	0.0288	
			1066	18.2	10.7	6.9	860						
Lacistema	aggregatum	Flacourtiace	0.558	0.011052	16.3	51.1	0.11						
			0.081	0.028	5851	27.5	25.1	19.9	4848	0.027	0.023	0.0080	150
			37.1	32.3	19.2	125							
Lacmellea	panamensis	Apocynaceae	0.502	0.227051	21.8	52.6	-99	-99					
			-99.000	-99	-99.0	-99.0	-99.0	-99.0	0.055	0.047	0.0190	207	
			7.7	5.1	3.2	158							
Laetia	thamnia	Flacourtiace	0.727	0.004359	14.5	65.0							
			0.133	0.106	0.040	1566	28.1	24.1	18.9	1312	-99.0	-99.0	-99.0000
			-99.0	-99.0	-99.0	-99.0	-99.0						
Licania	hypoleuca	Chrysobalana	0.836	0.084700	17.8	60.9							
			0.109	0.072	0.024	415	12.5	10.9	8.1	332	-99.0	-99.0	-99.0000
			-99.0	-99.0	-99.0	-99.0	-99.0						
Licania	platypus	Chrysobalana	0.682	4.502960	19.2	70.1							
			0.101	0.076	0.027	1103	21.5	20.0	15.1	900	-99.0	-99.0	-99.0000
			-99.0	-99.0	-99.0	-99.0	-99.0						
Lindackeria	laurina	Flacourtiace	0.693	0.037742	17.3	66.8	-99						
			-99	-99.000	-99	-99.0	-99.0	-99.0	-99.0	0.031	0.02	0.0031	
			293	20.0	14.9	10.7	244						
Lonchocarpus	heptaphyllus	Fabaceae:Pap	0.666	0.045275	30.6								
			42.2	0.131	0.096	0.035	2235	28.8	26.2	19.5	1857	0.041	0.03
			0.0108	553	26.1	21.2	14.9	463					
Luehea	seemannii	Tiliaceae	0.572	0.001115	32.4	58.5	-99	-99					
			-99.000	-99	-99.0	-99.0	-99.0	-99.0	0.058	0.044	0.0142	343	
			15.9	10.1	6.1	277							
Maquira	guianensis	Moraceae	0.643	-99.000000	15.3	57.2	0.125						
			0.099	0.039	4320	10.0	8.6	6.4	3486	0.023	0.016	0.0036	770
			26.1	23.3	17.9	637							
Miconia	affinis	Melastomatac	0.570	-99.000000	8.7	46.2							
			0.204	0.163	0.064	1195	41.5	36.7	27.3	987	-99.0	-99.0	-99.0000
			-99.0	-99.0	-99.0	-99.0	-99.0						
Miconia	argentea	Melastomatac	0.697	-99.000000	20.2	56.5							
			0.267	0.228	0.096	1314	79.4	71.6	55.8	1165	0.067	0.059	0.0266
			223	50.0	40.5	30.6	170						
Mosannonna	garwoodii	Annonaceae	0.730	0.216420	13.2	67.7	0.107						
			0.083	0.033	1294	6.6	6.1	4.8	979	-99.0	-99.0	-99.0000	-
			99.0	-99.0	-99.0	-99.0	-99.0						
Mouriri	myrtilloides	Melastomatac	0.788	0.042875	8.6	76.2							
			0.097	0.073	0.024	29556	22.6	20.9	17.8	24178	-99.0	-99.0	-99.0000
			-99.0	-99.0	-99.0	-99.0	-99.0						
Nectandra	cissiflora	Lauraceae	0.421	-99.000000	19.5	71.1	0.176						
			0.151	0.059	743	38.2	36.3	28.2	663	-99.0	-99.0	-99.0000	-
			99.0	-99.0	-99.0	-99.0	-99.0						

Ocotea	cernua	Lauraceae	0.610	0.041760	14.4	61.7	0.142				
	0.105	0.040	802	44.5	42.1	33.9	696	-99.0	-99.0	-99.0000	-
99.0	-99.0	-99.0	-99.0	-99.0							
Ocotea	puberula	Lauraceae	0.389	0.034480	26.8	49.4	0.175				
	0.145	0.054	504	46.8	48.9	39.0	459	-99.0	-99.0	-99.0000	-
99.0	-99.0	-99.0	-99.0	-99.0							
Ocotea	whitei	Lauraceae	0.426	-99.000000	32.3	68.3	0.169				
	0.127	0.055	1431	52.8	46.4	34.5	1342	0.082	0.063	0.0247	659
	20.2	15.5	10.6	518							
Ouratea	lucens	Ochnaceae	0.802	0.097000	11.6	103.5	0.078	0.06			
	0.018	5182	18.0	13.6	11.3	4165	-99.0	-99.0	-99.0000	-99.0	-
99.0	-99.0	-99.0	-99.0								
Palicourea	guianensis	Rubiaceae	0.320	0.007087	6.2	42.4	0.274				
	0.236	0.114	1344	87.5	88.0	83.6	1150	-99.0	-99.0	-99.0000	-
99.0	-99.0	-99.0	-99.0	-99.0							
Pentagonia	macrophylla	Rubiaceae	0.454	0.004479	6.1	65.2	0.098				
	0.065	0.019	1593	29.9	26.7	22.1	1371	-99.0	-99.0	-99.0000	-
99.0	-99.0	-99.0	-99.0	-99.0							
Perebea	xanthochyma	Moraceae	0.623	0.091272	14.1	53.7	0.129				
	0.099	0.037	846	17.9	15.0	10.5	695	-99.0	-99.0	-99.0000	-
99.0	-99.0	-99.0	-99.0	-99.0							
Picramnia	latifolia	Simaroubacea	0.699	0.025705	12.5	58.7					
	0.104	0.08	0.026	3884	25.5	23.3	17.9	3200	0.038	0.03	0.0104
	174	31.4	28.2	16.8	143						
Platymiscium	pinnatum	Fabaceae:Pap	0.761	0.145200	29.7	33.4					
	-99	-99	-99.000	-99	-99.0	-99.0	-99.0	-99.0	0.035	0.025	
	0.0077		249	20.4	15.2	10.9	211				
Platypodium	elegans	Fabaceae:Pap	0.703	0.334896	35.1	36.1	-99				
	-99	-99.000	-99	-99.0	-99.0	-99.0	-99.0	0.045	0.035	0.0087	
	174	19.4	15.7	14.1	142						
Poulsenia	armata	Moraceae	0.315	0.008913	36.2	55.8	0.185				
	0.143	0.061	2422	39.9	30.5	23.1	2247	0.047	0.036	0.0118	3033
	40.1	32.3	22.3	2536							
Pouteria	reticulata	Sapotaceae	0.761	-99.000000	32.0	50.7	0.104				
	0.079	0.025	5126	28.1	26.4	21.3	4365	0.063	0.052	0.0231	793
	12.9	8.7	5.1	622							
Pouteria	stipitata	Sapotaceae	-99.000	0.777521	22.4	58.6	-99				
	-99	-99.000	-99	-99.0	-99.0	-99.0	-99.0	0.041	0.027	0.0111	
	143	7.1	5.3	4.3	115						
Prioria	copaifera	Fabaceae:Cae	0.391	22.869184	35.5	77.8					
	0.105	0.079	0.028	3837	8.8	8.0	5.6	3167	0.054	0.042	0.0180
	1554	9.6	5.8	3.1	1216						
Protium	costaricense	Burseraceae	0.452	-99.000000	16.4	45.9					
	0.156	0.112	0.041	2276	23.1	21.4	16.1	1902	0.042	0.031	0.0106
	441	23.0	27.4	18.2	352						
Protium	panamense	Burseraceae	0.447	0.079495	19.2	64.7	0.113				
	0.086	0.030	11126	13.9	12.2	10.6	8972	0.034	0.026	0.0071	197
	32.5	27.2	21.5	163							
Protium	tenuifolium	Burseraceae	0.586	0.098637	20.5	59.9	0.127				
	0.099	0.037	9236	20.6	17.5	12.9	7506	0.043	0.034	0.0126	1604
	13.7	10.6	8.2	1263							
Pterocarpus	rohrrii	Fabaceae:Pap	0.496	0.172620	20.3	27.3					
	0.129	0.094	0.032	5403	25.4	23.9	19.0	4450	0.034	0.022	0.0044
	338	35.2	32.2	23.2	293						

Quararibea	asterolepis	Bombacaceae	0.468	0.079973	33.5	47.8	0.104				
	0.081	0.031	5282	17.7	14.7	10.8	4323	0.053	0.04	0.0126	2714
	15.4	10.1	6.9	2186							
Quassia	amara	Simaroubacea	0.527	0.150680	7.3	53.3	0.097				
	0.067	0.024	377	11.7	10.3	7.6	314	-99.0	-99.0	-99.0000	-
99.0	-99.0	-99.0	-99.0	-99.0							
Randia	armata	Rubiaceae	0.643	0.085212	11.3	46.4	0.106				
	0.081	0.030	2696	18.9	17.1	12.2	2243	0.026	0.02	0.0069	1088
	16.2	13.1	9.6	871							
Rinorea	sylvatica	Violaceae	0.673	-99.000000	7.0	49.3	0.086				
	0.064	0.020	10587	17.0	16.0	12.9	8650	-99.0	-99.0	-99.0000	-
99.0	-99.0	-99.0	-99.0	-99.0							
Simarouba	amara	Simaroubacea	0.390	0.111140	30.1	42.7	0.216				
	0.164	0.065	2679	47.8	41.6	32.0	2169	0.078	0.063	0.0293	1089
	30.9	26.4	20.0	881							
Siparuna	pauciflora	Monimiaceae	0.458	-99.000000	7.7	51.4	0.153				
	0.111	0.042	747	43.1	38.5	29.8	578	-99.0	-99.0	-99.0000	-
99.0	-99.0	-99.0	-99.0	-99.0							
Sloanea	terniflora	Elaeocarpace	0.815	-99.000000	34.1	54.1					
	0.079	0.055	0.017	1767	12.2	10.1	9.2	1471	0.034	0.021	0.0074
	342	14.1	11.3	7.4	285						
Sorocea	affinis	Moraceae	0.646	0.077688	9.4	47.4	0.111				
	0.084	0.031	11108	16.5	15.0	12.0	9288	0.016	0.013	-0.0002	122
	34.6	32.2	25.9	108							
Spondias	radlkoferi	Anacardiaceae	0.363	0.016950	30.8	48.4	-99				
	-99	-99.000	-99	-99.0	-99.0	-99.0	-99.0	0.058	0.045	0.0186	
	280	10.9	8.2	5.9	221						
Stylogyne	turbacensis	Myrsinaceae	0.569	0.035900	8.2	97.6	0.104				
	0.076	0.024	2661	24.9	23.5	20.3	2153	-99.0	-99.0	-99.0000	-
99.0	-99.0	-99.0	-99.0	-99.0							
Swartzia	simplex_var.	Fabaceae:Pap	0.773	-99.000000	17.1	76.3					
	0.088	0.065	0.023	9540	8.9	7.3	6.0	7518	0.027	0.019	0.0068
	998	7.2	6.5	3.8	796						
Swartzia	simplex_var.	Fabaceae:Pap	0.784	0.849488	14.2	87.8					
	0.079	0.058	0.020	10532	6.6	6.0	4.8	8434	0.022	0.016	0.0044
	568	7.1	4.5	3.4	445						
Symphonia	globulifera	Clusiaceae	0.545	1.028950	28.0	57.9	0.116				
	0.099	0.043	498	18.0	20.4	16.4	403	-99.0	-99.0	-99.0000	-
99.0	-99.0	-99.0	-99.0	-99.0							
Tabebuia	guayacan	Bignoniaceae	0.790	-99.000000	36.8	22.9	-99				
	-99	-99.000	-99	-99.0	-99.0	-99.0	-99.0	0.047	0.03	0.0123	
	139	0.0	3.7	2.8	109						
Tabebuia	rosea	Bignoniaceae	0.489	0.018505	40.4	37.3	0.137				
	0.102	0.037	656	33.1	29.0	20.8	553	0.042	0.027	0.0092	295
	23.8	16.1	10.9	238							
Tabernaemont	arborea	Apocynaceae	0.538	0.068031	28.1	32.9					
	0.142	0.104	0.037	4060	19.8	17.0	11.8	3212	0.073	0.058	0.0232
	1288	11.7	10.1	7.0	996						
Tachigali	versicolor	Fabaceae:Cae	0.582	0.105295	32.6	44.9					
	0.121	0.097	0.035	10339	31.7	30.6	22.9	8756	0.087	0.068	0.0316
	346	34.3	24.4	15.1	271						
Talisia	nervosa	Sapindaceae	0.663	0.353484	7.6	81.2	0.073				
	0.055	0.018	3392	8.0	7.2	6.3	2762	-99.0	-99.0	-99.0000	-
99.0	-99.0	-99.0	-99.0	-99.0							

Talisia	princeps	Sapindaceae	0.725	0.463500	11.8	69.3	0.088			
	0.064	0.021	2451	14.8	13.9	14.0	1982	-99.0	-99.0	-99.0000
	99.0	-99.0	-99.0	-99.0						
Terminalia	oblonga	Combretaceae		0.634	-99.000000	35.4	29.5	-99		
	-99	-99.000	-99	-99.0	-99.0	-99.0	-99.0	0.059	0.041	0.0177
	153	6.5	7.9	5.5	127					
Tetragastris	panamensis	Burseraceae	0.589	0.294750	31.3	74.8				
	0.111	0.086	0.030	13928	18.6	16.6	12.4	11034	0.043	0.034
	1616	9.6	7.5	5.2	1259					
Trattinnicki	aspera	Burseraceae	0.439	0.006370	29.0	54.6	-99			
	-99	-99.000	-99	-99.0	-99.0	-99.0	-99.0	0.076	0.049	0.0236
	189	34.2	27.6	17.5	154					
Trichilia	pallida	Meliaceae	0.573	0.054078	16.7	50.9	0.139			
	0.103	0.040	1591	26.8	22.2	15.1	1336	0.042	0.035	0.0126
	18.6	11.4	8.2	281						358
Trichilia	tuberculata	Meliaceae	0.692	0.109507	29.3	57.8	0.099			
	0.075	0.027	39824	21.0	18.8	14.7	32273	0.037	0.029	0.0113
	25.8	18.6	12.4	6425						7745
Triplaris	cumingiana	Polygonaceae		0.529	-99.000000	28.1	40.8	-99		
	-99	-99.000	-99	-99.0	-99.0	-99.0	-99.0	0.048	0.033	0.0116
	598	11.1	8.9	5.5	472					
Trophis	caucana	Moraceae	0.475	0.025370	12.0	40.8	0.158			
	0.118	0.049	520	54.7	43.2	32.2	488	0.033	0.03	0.0079
	31.6	21.4	19.3	114						144
Trophis	racemosa	Moraceae	0.631	-99.000000	18.4	45.1	0.105			
	0.076	0.024	959	19.7	18.5	14.7	789	0.028	0.019	0.0048
	36.4	32.8	23.5	136						156
Turpinia	occidentalis	Staphyleaceae		0.407	0.004135	22.6	38.4			
	-99	-99	-99.000	-99	-99.0	-99.0	-99.0	-99.0	0.079	0.061
	0.0213		221	44.4	30.8	22.3	184			
Unonopsis	pittieri	Annonaceae	0.428	0.724820	22.2	50.3	0.16			
	0.121	0.047	1728	30.3	25.0	19.3	1484	0.046	0.035	0.0141
	19.4	15.1	9.3	557						709
Virola	sebifera	Myristicaceae	0.487	0.111661	30.5	60.1				
	0.143	0.106	0.041	4593	22.9	18.9	13.9	4024	0.048	0.036
	2684	24.2	17.0	11.2	2181					0.0138
Virola	surinamensis	Myristicaceae		0.407	1.580256	37.3	49.5			
	-99	-99	-99.000	-99	-99.0	-99.0	-99.0	-99.0	0.065	0.049
	0.0192		619	20.9	13.5	8.8	520			
Xylopia	macrantha	Annonaceae	0.840	0.116775	19.8	67.0	0.142			
	0.116	0.053	3241	10.2	8.0	5.8	2502	0.037	0.031	0.0130
	6.7	5.7	4.0	424						574
Xylosma	oligandra	Flacourtiaceae		-99.000	-99.000000	8.5	40.2			
	0.104	0.082	0.029	425	24.4	20.6	18.4	380	-99.0	-99.0
	-99.0	-99.0	-99.0	-99.0	-99.0					-99.0000
Zanthoxylum	acuminatum	Rutaceae	0.579	-99.000000	23.2	68.6	0.206			
	0.167	0.063	393	34.7	31.0	22.9	350	0.068	0.052	0.0218
	69.2	53.8	32.1	106						131
Zanthoxylum	ekmanii	Rutaceae	0.435	-99.000000	31.1	52.3	-99	-99		
	-99.000	-99	-99.0	-99.0	-99.0	-99.0	-99.0	0.131	0.11	0.0464
	37.5	23.9	16.9	419						529
Zanthoxylum	panamense	Rutaceae	0.552	0.001300	28.2	38.4	0.202			
	0.132	0.049	354	51.9	53.0	35.3	329	0.072	0.062	0.0261
	39.7	28.2	18.6	236						288