GAP-DEPENDENT RECRUITMENT, REALIZED VITAL RATES, AND SIZE DISTRIBUTIONS OF TROPICAL TREES

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Abstract. In closed-canopy forests, plant morphology and physiology determine shade tolerance and potential growth and mortality rates; potential vital rates and ongoing gap dependence determine realized vital rates; and realized vital rates determine individual size distributions. This hypothesis was evaluated for the 73 most abundant canopy tree species from Barro Colorado Island, Panama. The percentage of recruits located in tree-fall gaps (P), sapling growth (G), and mortality (M) rates, and the coefficient of skewness of size distributions (g_1) were determined from censuses of all individuals >10 mm dbh in a 50-ha plot. Seven qualitative, bivariate predictions relating g_1, G, M, P, and wood density (W) were evaluated. Six of the seven predictions were substantiated in pairwise analyses. A path analysis integrated all seven predictions and explained 51% of the interspecific variation in g_1. Size distributions with many large individuals and a long tail of relatively rare, small individuals ($g_1 < 0$) characterized gap-dependent species with large fecundity, seed mortality, seedling mortality, G, M, and P. Size distributions with many small individuals and a long tail of relatively rare, large individuals ($g_1 > 0$) characterized shade-tolerant species with the opposite traits. The percentage of tropical tree species that require tree-fall gaps to regenerate has been estimated to range from <20% to >70% for old-growth forests. Our analyses suggest that there are not large numbers of functionally equivalent species at either extreme of the regeneration continuum. Rather, there are very few extremely shade-tolerant and extremely light-demanding species. Most species have intermediate light requirements and lifestyles.

Key words: Barro Colorado Island, Panama; functional groups; gap dependence; guilds; life history; ontogenetic shifts; Panama; shade tolerance; size distribution; tree-fall gap; tropical trees; wood density.

The tropics support 176 000 described and 40 000–100 000 undescribed species of flowering plants (Prance 1977, Prance et al. 2000, Govaerts 2001, Bramwell 2002). Life histories are unknown for the vast majority of these species. The problem is particularly acute in tropical forests where species density is greatest. Here, we return to an old hypothesis: Do size distributions correlate with life histories among tropical forest trees (Smith 1970)? If the answer is yes, then a single census could provide insight into the life histories of a community of tropical tree species. We evaluate this hypothesis for the large canopy trees of old-growth forest on Barro Colorado Island (BCI), Panama. We also evaluate attempts to categorize tropical trees by life history traits, possible shifts in life history traits during ontogeny, and a causal model that relates size distributions, habitat associations, morphology, and life history traits.

The degree to which regeneration depends on tree-fall gaps defines a fundamental axis of life history variation among tree species in closed-canopy forests

(Grubb 1977, Denslow 1987, Pacala et al. 1996). Gap-dependent or light-demanding species establish and thrive in tree-fall gaps where light levels are high and root competition is reduced, whereas shade-tolerant species establish widely and persist in the understory despite deep shade and often intense root competition. Contrasting physiology and morphology determine the potential growth and mortality rates of light-demanding and shade-tolerant species. Contrasting habitat associations and resource availability further modify potential vital rates during regeneration so that realized vital rates vary widely among species. Finally, realized growth and mortality rates determine tree size distributions (Harcombe 1987, Condit et al. 1998). This causal chain generates predictions that relate wood density, which we use as a proxy for physiological and morphological traits, gap dependence during early regeneration, realized sapling growth and mortality rates, and individual size distributions.

Most schemes developed to categorize tropical trees by life history traits have attempted to place species into functional groups defined by gap dependence during regeneration (Lieberman et al. 1985, Hubbell and Foster 1986, Swaine and Whitmore 1988, Van Clay 1991, Clark and Clark 1992, 1999, Condit et al. 1996*a*,

Gitay et al. 1999). Functional groups imply discontinuous or minimally multimodal trait distributions. We will examine life history trait distributions for discontinuities or multiple modes consistent with distinct functional groups.

Growth and mortality rates vary during ontogeny. Mortality rates generally decline with tree size or age, although mortality may pick up again for the very largest individuals (Harcombe 1987). Absolute stem diameter growth rates peak at intermediate sizes (Harcombe 1987), whereas relative stem diameter growth rates decline with size (H. C. Muller-Landau, *unpublished data*). An ontogenetic shift would occur if a species had a small vital rate relative to other species at one life history stage and a large vital rate relative to those same species at another life history stage (Clark and Clark 1992, 1999, Dalling et al. 2001). Ontogenetic shifts would complicate size distributions, with individuals accumulating in size classes characterized by slow growth or low mortality (Condit et al. 1998). We therefore search for evidence of ontogenetic shifts particularly among mortality rates, which we evaluate for three life history stages.

The coefficient of skewness (g_1) will be used to summarize the symmetry of tree size distributions (Bendel et al. 1989). It is positive for size distributions with abundant, small saplings and a long tail of rare, large adults, and is negative for distributions with a long tail of rare saplings and abundant adults. (For a definition of g_1, see *Methods: Size distributions*.) We will examine correlations between g_1 and fecundity, seed mortality, first-year seedling mortality, sapling growth (G), and sapling mortality (M).

We will then evaluate seven causal predictions that relate g_1, G, M, the percentage of sapling recruits located in tree-fall gaps (P), and wood density (W). We adopt a convention from path analysis in which a single-headed arrow points from the independent variable to the dependent variable. The seven qualitative predictions and their rationale follow.

$W \rightarrow G$. Dense wood requires more material to build. All else equal, this additional material requirement will slow growth in size. Therefore W and G are predicted to be negatively related (Favrichon 1994, Suzuki 1999; H. C. Muller-Landau, *unpublished data*).

$P \rightarrow G$. Light limits growth in closed-canopy forests. Light levels are greater in tree-fall gaps than in the shaded understory. Therefore, P and G are predicted to be positively related.

$W \rightarrow M$. Dense wood is less susceptible to pathogens and wood-boring insects (Bultman and Southwell 1976, Kitajima 1994). Therefore, W and M are predicted to be negatively related (H. C. Muller-Landau, *unpublished data*).

$P \rightarrow M$. Resource allocation to competing functions varies widely among tree species (Grubb 1977, Kitajima 1994). Shade-tolerant species tend to invest heavily in defenses against pests and in storage against resource fluctuations, which maximizes their survival everywhere but limits their potential growth rates when resources are plentiful. Light-demanding species tend to invest heavily in leaves, roots, and extension growth, which maximizes their potential growth rates when resources are ample, but limits their survival when resources are scarce. Light-demanding species are characterized by large P and large potential mortality rates. Light-demanding species also face an added mortality hazard when they are overtopped and shaded by another tree. Therefore P and M are predicted to be positively related.

$G \rightarrow M$. Species that risk high growth rates retain few resources to allocate to other functions that favor survival, and face a familiar trade-off leading to greater mortality. G and M are therefore predicted to be positively related (Hubbell and Foster 1992, Pacala et al. 1996).

$G \rightarrow g_1$. Rapid sapling growth moves individuals through the smaller size classes quickly, which reduces the number of small individuals and increases the number of large individuals. G and g_1 are therefore predicted to be negatively related (Condit et al. 1998).

$M \rightarrow g_1$. High sapling mortality reduces the number of trees in all larger size classes. M and g_1 are therefore predicted to be positively related.

Finally, path analysis will be used to evaluate a causal model that integrates these seven predictions (see *Methods: Analyses*).

METHODS

All trees >10 mm in dbh were identified and measured in 1982, 1985, 1990, 1995, and 2000 for a 50-ha plot located on Barro Colorado Island (BCI; 9°9′ N, 79°51′ W), Panama (for methods, see Condit 1998). The 2000 census data are not used here. The 50-ha plot includes 2 ha of young secondary forest (Hubbell and Foster 1986). The remainder is old growth disturbed minimally by humans for at least 1500 years (Piperno 1990). Detailed descriptions of BCI and the 50-ha plot can be found elsewhere (Croat 1978, Condit 1998, Leigh 1999). All analyses are restricted to the 73 tree species that reach into the forest canopy as adults (Condit et al. [1996b] identify canopy species) and that were represented by >25 individuals in the 1995 census. Wood density was available for 58 of these species (Muller-Landau, in review). Nomenclature follows Croat (1978), as updated by Condit et al. (1996b).

Size distributions (g_1)

Height is an appropriate measure of size for life history analyses of canopy trees because canopy trees become fully reproductive at threshold heights that place their upper foliage in full sun (Thomas 1996; S. J. Wright, *unpublished data*). Allometric relationships describe height–diameter relationships well for tropical trees (Brown et al. 1989). The relationship $H = b \times$ dbh^c, where H represents height and b and c are fitted

constants, explained 88% to 97% of the variation in height for each of 55 BCI tree species (O'Brien et al. 1995; S. T. O'Brien, *unpublished data*). For these reasons, we used the logarithm of dbh (measured in 1995) to quantify tree size.

The 10 mm dbh size threshold for inclusion in censuses of the 50-ha plot truncates tree size distributions. The coefficient of skewness (g_1) is the preferred statistic to summarize the evenness or symmetry of truncated lognormal distributions (Bendel et al. 1989). Henceforth, we will use g_1 to refer to the coefficient of skewness calculated for logarithms of dbh, where

$$g_1 = \frac{n \sum_i (x_i - \bar{x})^3}{(n - 1)(n - 2)s^3}$$

and n, x_i, $\bar{x}$, and s represent the number of individuals, the logarithm of dbh for individual i, the mean of the x_i, and the standard deviation of the x_i, respectively (Bendel et al. 1989). We calculated g_1 for the 73 canopy tree species represented by >25 individuals in 1995.

G, M, and P

Saplings were defined to have dbh of 10–39 mm at the beginning of a census interval. We estimated G for the 1990–1995 census interval because dbh was measured to the nearest millimeter for both censuses (previously dbh was measured to the nearest 5 mm). Sapling growth G equaled the mean annualized relative dbh increment (increase in dbh [in millimeters] per dbh [in millimeters] per year) and was estimated for the 71 species with three or more saplings surviving from 1990 to 1995. Sapling mortality M equaled annualized mortality (percentage dying per year) and was estimated for the 1990 to 1995 census interval for the 69 species represented by 15 or more saplings in 1990.

P equaled the percentage of sapling recruits located closest to a low-canopy site. Canopy height was measured at the intersections of a 5 × 5 m grid, which covered the 50-ha plot, every year from 1983 through 1995 with the exception of 1994 (for methods, see Welden et al. 1991). Low-canopy sites were grid intersections with maximum canopy height <10 m in at least one year between two consecutive censuses. P was estimated for the 60 species with 15 or more recruits summed over the 1982–1985, 1985–1990 and 1990–1995 census intervals.

Additional life history traits

Fecundity (number of seeds per square meter of basal area per year), seed establishment probability (number of seedlings per seed), and first-year seedling mortality (percentage per year) were estimated using 200 stations located in the 50-ha plot. Each station included one 0.5-m² seed trap and three 1-m² seedling plots. Stations were located at 13.5-m intervals along trails and randomly at 4–10 m from trails with a distance of 18.9 ± 3.6 m (mean ± 1 SD) between neighboring stations.

Seed traps were constructed of 1-mm mesh screen suspended on PVC frames. All seeds were identified and counted in weekly censuses conducted from 1 January 1987 through 31 December 1999 (Wright et al. 1999). Seedling plots were 2 m from each of three sides of each seed trap (the fourth side faced the nearby trail). All woody plants ≤50 cm tall were tagged and identified between January and March 1994. Survivors were remeasured and new recruits were tagged and identified between January and March each year from 1995 to 1999 (Harms et al. 2000).

Fecundity was estimated as seed flux density (number of seeds per hectare per year) divided by 1995 basal area density (basal area [in square meters] per hectare) for the 53 species with seeds larger than the 1-mm trap mesh and 50 or more seeds captured in 13 years. Fecundity was standardized by basal area because reproductive biomass scales linearly with basal area (Niklas 1993). Establishment probability was estimated as recruit flux density (number of seedlings per square meter per year) divided by seed flux density (number of seeds per square meter per year) for the 41 species with seeds larger than the 1-mm mesh and 20 or more seeds captured in the appropriate years. None of these 41 species persists for more than one year in the soil seed bank (J. Dalling, *personal communication*). Seedling mortality was estimated as the percentage of recruits that survived their first year for the 32 species with >10 seedling recruits.

Analyses

Distributions of vital rates (G, M, fecundity, establishment probability, and seedling mortality) and their logarithms were evaluated for skewness and kurtosis and compared with normal distributions using one-sample Kolmogorov-Smirnov tests. The seven bivariate predictions (see *Introduction*) were evaluated using Pearson product-moment correlation coefficients. The Bonferroni correction was used to determine significance. Relationships between g_1 and fecundity, establishment probability, and seedling mortality were also evaluated using Pearson product-moment correlation coefficients. The relative variation in realized vital rates (G, M) explained by microhabitat association (P) and wood density (W) was evaluated using multiple regression. A principal components analysis was performed for mortality rates of saplings, seedlings, and seeds (i.e., seed establishment probability). Homoscedastic residuals were obtained for untransformed values of g_1, seedling mortality, and W, and for logarithms of the remaining variables. These analyses were performed with SYSTAT 10.0 (SPSS 2000).

A causal model, which integrated the seven bivariate predictions relating g_1, G, M, P, and W, was evaluated using path analysis. The five variables generate 10 bivariate relationships, leaving three possible paths unaccounted for. We anticipate no direct causal relation between W and g_1, nor between P and g_1. Path analysis
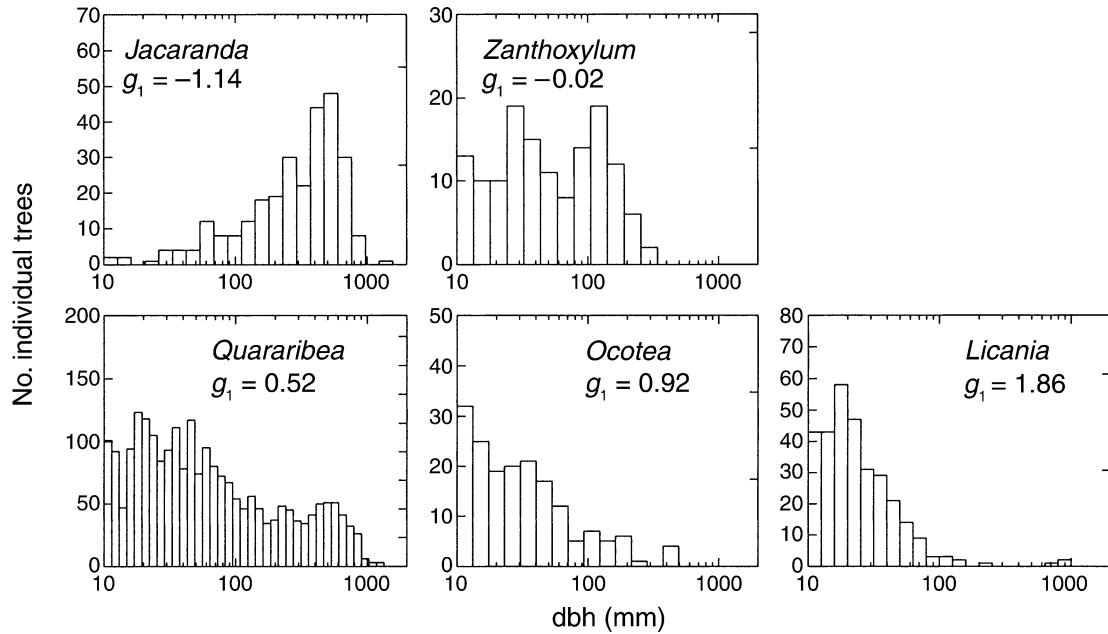
FIG. 1.   Distributions of the logarithm of diameter at breast height for selected tree species from Barro Colorado Island, Panama. *Jacaranda copaia* had the most negative skewness (coefficient g_1), with large numbers of adults and a long tail of rare juveniles. *Licania platypus* had the most positive skewness, with large numbers of juveniles and a long tail of rare adults. *Zanthoxylum procerum*, *Quararibea asterolepis*, and *Ocotea puberula* represent the 25th, 50th, and 75th percentiles of the distribution of g_1 for the 73 canopy tree species represented by >25 individuals.

requires an unanalyzed covariance path between the exogenous variables W and P (Li 1975). This covariance could arise if, for example, species with low-density wood produced greater numbers of seeds and hence reached a greater percentage of tree-fall gaps. We will not consider possible causes of a relationship between W and P here and instead treat the relationship between W and P as an unanalyzed covariance. The path analysis was repeated using pairwise and listwise correlation coefficients, following the recommendation of Mitchell (2001). Collinearity among the predictor variables was evaluated using variance inflation factors, collinearity condition indices, and proportions of variance explained for each predictor variable by the remaining predictor variables (Petraitis et al. 1996). The path analysis was performed with SAS PROC CALIS (SPSS 2000).

Results

Size distributions

Fig. 1 presents size distributions for five representative canopy tree species. Visual inspection suggested that distributions of logarithms of dbh were generally unimodal for each tree species (e.g., Fig. 1). Fig. 2A presents the distribution of g_1 for the 73 species represented by >25 individuals.

A prolonged dry period in central Panama offered an opportunity to evaluate the stability of size distributions in the face of environmental variation. BCI experienced unusually dry conditions for 30 years be-

ginning in the 1960s and an unprecedented 6-month drought during the 1982–1983 El Niño event (Windsor 1990). This caused declines of up to 5% per year in the population sizes of moisture-sensitive tree species between 1982 and 1990 (Condit et al. 1996b). The species with the greatest population decline and the most extreme change in g_1 was *Poulsenia armata*. With each successive census, g_1 declined from 0.135 in 1982 to −0.192 in 2000. This 18-year decline represents just 11% of the interspecific variation in g_1 observed among tree species (Figs. 1 and 2A). Size distributions were relatively stable despite dramatic changes in the population sizes of moisture-sensitive species.

Vital rates

Skewness, kurtosis, and one-sample Kolmogorov-Smirnov tests were not significantly different from normality for g_1, seedling mortality, and wood density, or for logarithms of *G, M, P,* fecundity, and establishment probability ($P > 0.15$). Visual inspection further suggested that all vital rates as well as g_1, *P,* and wood density were continuously distributed with strong central tendencies (Fig. 2). There is no evidence for the discontinuous or multimodal distributions that might suggest distinct functional groups.

Bivariate analyses

Six of the seven bivariate predictions (see *Introduction*) were substantiated for both listwise and pairwise correlation analyses (Table 1, Figs. 3, 4, and 5). The
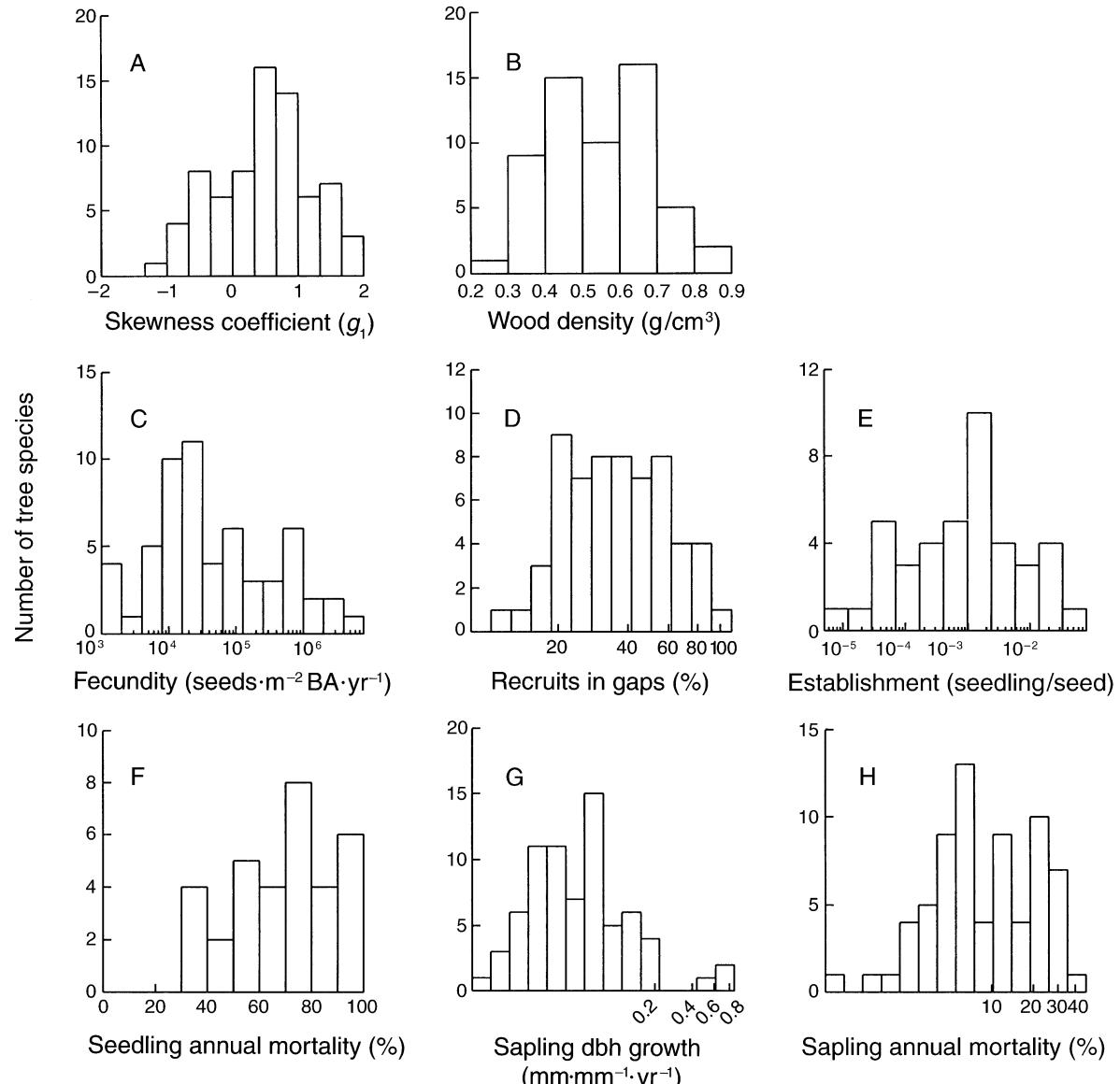
FIG. 2. Frequency histograms for (A) the coefficient of skewness of the logarithm of diameter at breast height (g_1); (B) wood density; (C) fecundity quantified as the number of seeds produced per square meter of basal area per year; (D) the percentage of sapling recruits located in tree-fall gaps; (E) seed establishment probability; (F) first-year seedling mortality; (G) relative sapling dbh growth; and (H) sapling mortality for large canopy tree species from Barro Colorado Island, Panama. The distributions are approximately normal or lognormal. Note the x-axis log scales in panels C–E, G, and H.

exception was the relationship between M and g_1, which was predicted to be positive but was, in fact, negative (Fig. 5A). We will return to this relationship later (see *Results: Path analysis*). The seven bivariate relationships explained a minimum of 24% and a maximum of 62% of variation in the dependent variable (Table 1, Figs. 3, 4, and 5).

There were also significant relationships between g_1 and life history traits involving non-sapling life stages: g_1 was negatively related to fecundity (Fig. 6A; $r = -0.32$, $P < 0.05$) and to seedling mortality (Fig. 6C; $r = 0.66$, $P < 0.002$), and was positively related to

establishment probability (Fig. 6B; $r = 0.46$, $P < 0.005$). *Alseis blackiana* was an outlier (absolute value of studentized residual > 2.5) from the relationships with fecundity and establishment probability (Fig. 6A,B). We will return to *A. blackiana* (see *Discussion: Ontogenetic consistency*).

Multivariate analyses

Multiple regression analyses evaluated contributions of P and W to variation in G and M. P and W were not significantly related ($r = -0.217$, $P = 0.15$, $N = 46$ species). Together P and W explained 54.5% of the
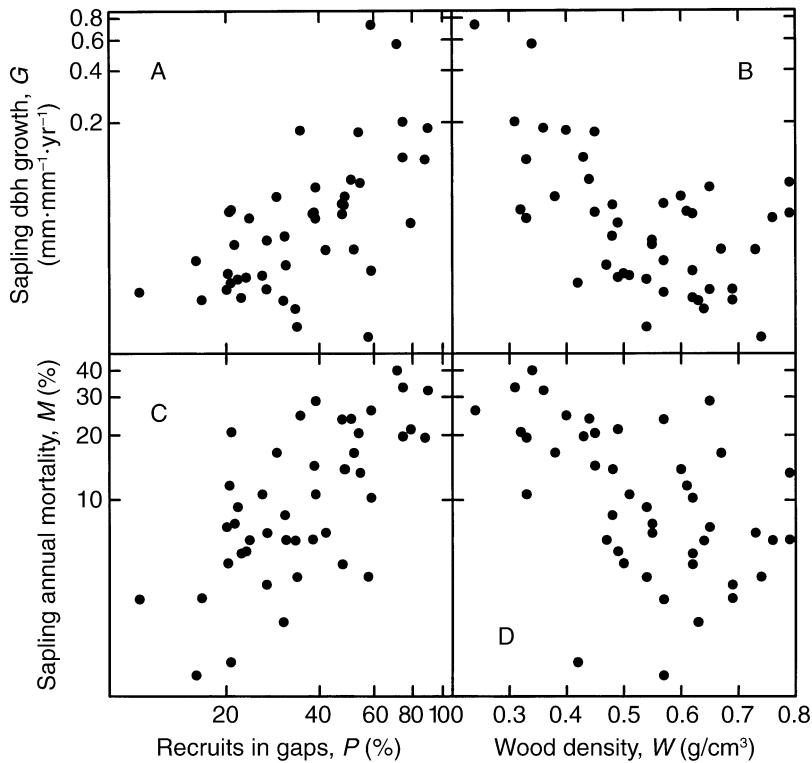
Fig. 3. Relationships between sapling performance (log scale), the percentage of sapling recruits located in gaps (log scale), and wood density for canopy tree species from Barro Colorado Island, Panama. Sapling dbh growth rates were positively related to the percentage of recruits located in gaps (A) and negatively related to wood density (B). Sapling mortality rates were also positively related to the percentage of recruits located in gaps (C) and negatively related to wood density (D). Panel labels cross reference the predictions in Table 1, where correlation coefficients and significance levels are given.

variation in G and 55.4% of the variation in M; P entered both multiple regressions first, and W explained a significant portion of the remaining variation for both G ($F_{1,43} = 16.6$, $P < 0.001$) and M ($F_{1,42} = 9.7$, $P < 0.01$). Both resource availability associated with microhabitat (P) and morphological differences among species (W) contribute to realized growth (G) and mortality (M) rates of saplings.

The first principal component explained 55.4% of the variability in seed establishment probability, first-

year seedling mortality, and sapling mortality (Fig. 7). Relative mortality rates were consistent across these three ontogenetic stages. The largest residual was once again for *A. blackiana*, which had unexpectedly low establishment probability (Fig. 7).

Path analysis

Appendix A presents the listwise and pairwise correlation coefficients and sample sizes required to perform the path analyses. Appendix B presents the spe-

TABLE 1. The seven qualitative, bivariate predictions summarized. The Bonferroni procedure was used to determine significance.

Variables		Predicted relationship	Listwise r†	Pairwise		
Independent	Dependent			r	N‡	Fig.
P	G	positive	0.59***	0.59***	60	3A
W	G	negative	−0.58***	−0.56***	56	3B
P	M	positive	0.67***	0.62***	58	3C
W	M	negative	−0.49**	−0.53***	55	3D
G	M	positive	0.79***	0.68***	67	4
M	g_1	positive	−0.58***	−0.57***	69	5A
G	g_1	negative	−0.71***	−0.57***	71	5B

** $P < 0.01$; *** $P < 0.001$.
† Sample size includes 45 species that fulfilled all criteria in *Methods*: G, M, and P.
‡ Samples size includes species that fulfilled pairwise criteria in *Methods*: G, M, and P.
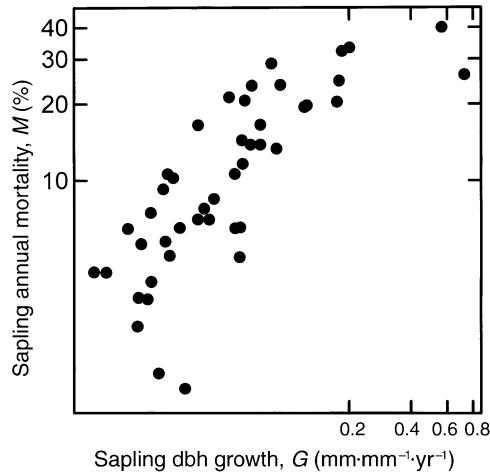
FIG. 4. Sapling mortality rates (log scale) were positively related to sapling dbh growth rates (log scale) for canopy tree species from Barro Colorado Island, Panama. The correlation coefficient and significance level are given in Table 1.

cies-level data used to calculate these correlation matrices.

The correlation matrices satisfied the requirements of path analysis (Petraitis et al. 1996). The largest variance inflation factor (3.2) was well below the critical value of 10, the proportion of variation explained was less for the predictor variables than for the complete model, and the largest condition index (19.2) was well below the critical value (30) recommended by both SAS and SYSTAT (SPSS 2000). The causal model described the correlation structure among g_1, G, M, P, and W reasonably well ($\chi_2^2 = 0.87$ and $\chi_2^2 = 0.62$ for the listwise and pairwise analyses, respectively; $P \geq 0.65$). However, the significance of two path coeffi-

cients and the covariance path between W and P differed between the listwise and pairwise analyses. We followed the recommendation of Mitchell (2001) and report the results of the listwise analysis when the results of listwise and pairwise analyses differ.

The causal model explained 51% of the interspecific variation in g_1 in the listwise path analysis (Fig. 8, Table 2). G alone explained 46% of the variation in g_1 or nearly 92% of the explained variation in g_1. P and W each explained a substantial proportion of variation in G. The path coefficient between M and g_1 approached zero, which suggests that the significant negative, bivariate correlation between M and g_1 was driven by other correlations. This final suggestion is suspect, however, because the path coefficient between M and g_1 was negative and significant in the pairwise analysis. We will return to the M–g_1 relation in the *Discussion*.

DISCUSSION

The relationship among gap-dependent regeneration, realized vital rates, and tree size distributions can be summarized as follows. Light-demanding species are relatively rare as seedlings and saplings because seedlings and saplings are ephemeral, either dying quickly if shaded, or growing rapidly into larger size classes if light levels remain high. In contrast, shade-tolerant species are relatively abundant as seedlings and saplings because seedlings and saplings are persistent, with most surviving and growing slowly in deep shade.

We evaluated seven bivariate predictions distilled from this hypothesis for canopy trees from Barro Colorado Island, Panama. Six of the seven predictions were substantiated, with $0.24 \leq r^2 \leq 0.62$ (Table 1). By comparison, the mean percentage of variation explained in the ecological and evolutionary literature is
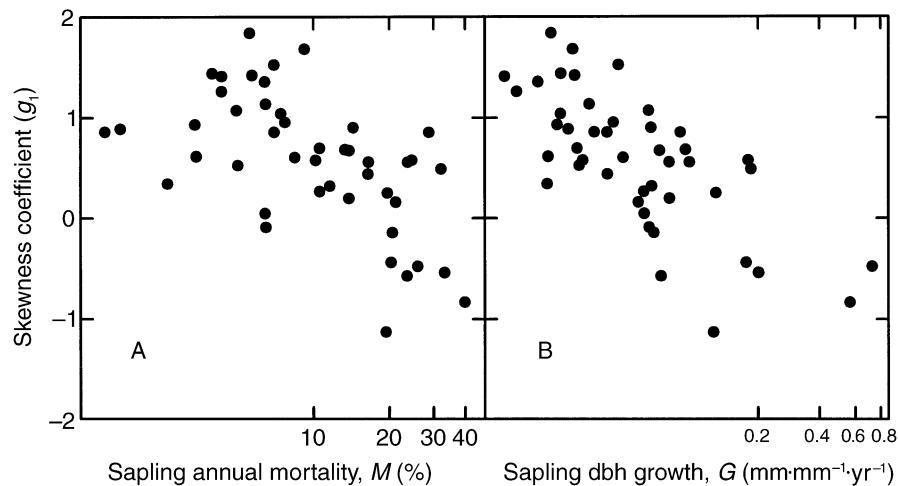
FIG. 5. Relationships between size distributions and realized sapling vital rates (log scale) for canopy tree species from Barro Colorado Island, Panama. The coefficient of skewness of the logarithm of diameter at breast height (g_1) summarizes tree size distributions. Relationships between g_1 and sapling mortality rates (A) and sapling dbh growth rates (B) were both negative. Panel labels cross reference the predictions in Table 1, where correlation coefficients and significance levels are given.
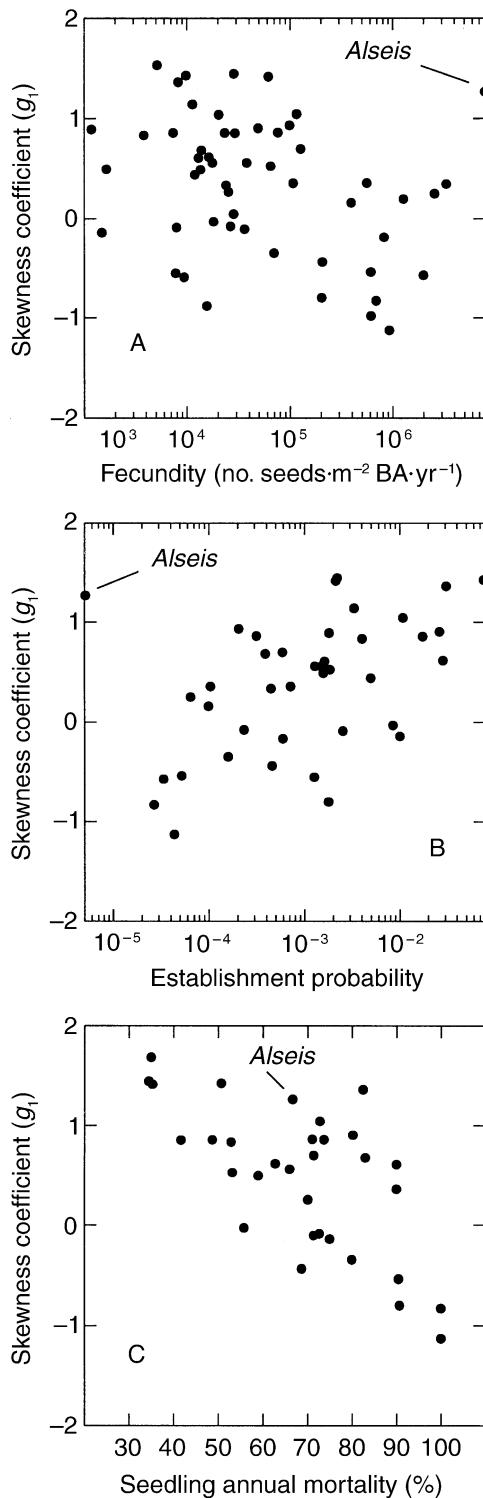
FIG. 6. Relationships between size distributions and fecundity (log scale), seed establishment probability (log scale), and first-year seedling mortality for canopy tree species from Barro Colorado Island, Panama. The coefficient of skewness of the logarithm of diameter at breast height (g_1) summarizes tree size distributions; it was negatively related to fecundity (A), positively related to seed establishment probability (B), and negatively related to first-year seedling mortality (C).

an order of magnitude lower, ranging from 2.5% to 5.4% depending on discipline (Møller and Jennions 2002). Cohen (1988) further suggested that large effects are characterized by r^2 values of 0.25, near the lower end of our observed r^2 values. Figs. 3–6 present strong ecological relationships.

Several sources of unexplained variation remain nonetheless. First, vital rates were estimated from small sample sizes for many species (Appendix B). Second, vital rates and size distributions vary temporally with pathogen outbreaks, drought, and other sources of environmental variation (Gilbert et al. 1994, Condit et al. 1996b). Small sample size and temporal variation will introduce variation into each relationship examined here. The third source of unexplained variation affects relationships involving the percentage of recruits in gaps (P). Low canopy ($<$10 m tall) at the nearest point on a 5 × 5 m grid is a crude index of microhabitat and resource availability (Welden et al. 1991). Light availability is now being evaluated using canopy photographs to estimate light dependence during seedling recruitment. A fourth source of unexplained variation concerns the number of traits involved in ecological trade-offs. Trade-offs involving multiple traits will introduce variation into trade-offs among subsets of those traits. Temperate trees display a five-way trade-off among dispersal, sapling survival in shade, shade cast by adults, height growth in full sun, and height growth in deep shade (Pacala et al. 1996). Similar multiway trade-offs are likely to contribute to unexplained variation in the two-trait relationships involving wood density (W), sapling growth (G), and sapling mortality (M) considered here. Multiway trade-offs remain to be examined for tropical trees.

A final source of unexplained variation concerns relationships among sapling growth (G), sapling mortality (M), and the coefficient of skewness of size distributions (g_1). Growth and mortality of all size classes influence size distributions. Our analyses ignored growth and mortality of plants $>$39 mm in dbh. We speculate that species-specific changes in mortality rates among larger size classes may explain the negative relation observed between M and g_1 (Fig. 5A). Recall that this relation was predicted to be positive because greater M reduces the number of individuals in all larger size classes, which increases g_1. Mortality rates decline with tree size (Harcombe 1987). This decline is greatest for light-demanding species (S. J. Wright, *unpublished analysis*). We speculate that this is true because saplings of light-demanding species die quickly when overtopped and shaded, whereas conspecific adults escape this mortality hazard as they reach the canopy. Shade-tolerant species suffer less

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Alseis blackiana was an outlier (studentized residual > 2.5) from the relationships in panels A and B.
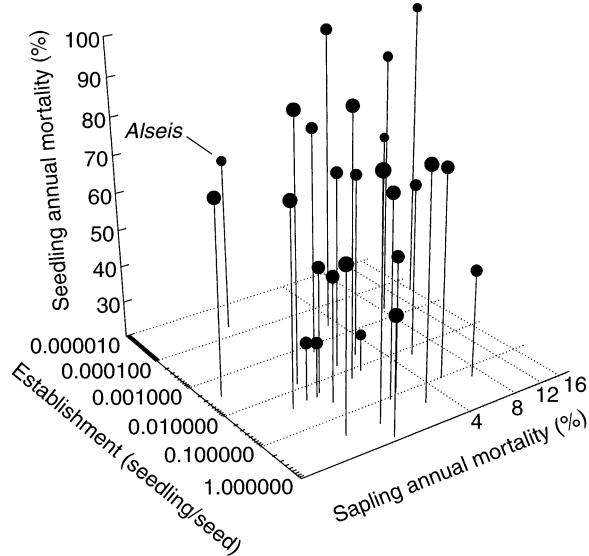
FIG. 7. The relationships among seed establishment probability (log scale), seedling mortality, and sapling mortality (log scale) for canopy tree species from Barro Colorado Island, Panama. The axes are arranged so that species with the greatest mortality at all three stages fall in the upper right rear and species with the greatest survival at all three stages fall in the lower left front. The first principal component explained 55.4% of the overall variation. *Alseis blackiana* had extremely low establishment probability.

from being overtopped and therefore gain less as they reach the canopy. The relation between size distributions and growth and mortality rates of all size classes is now being explored (H. C. Muller-Landau, *unpublished data*).

Ontogenetic shifts in life history traits

An ontogenetic shift would occur if a species were shade tolerant with low growth and mortality rates at

one juvenile stage, and light-demanding with high growth and mortality rates at a second juvenile stage. Ontogenetic shifts undoubtedly occur (Clark and Clark 1992, 1999). *Alseis blackiana* provides an example from BCI (Dalling et al. 2001). This species produces copious numbers of minute seeds (240 seeds·m^{-2}·yr^{-1}), which require high light levels to establish. Established seedlings and saplings are then shade tolerant (Dalling et al. 2001; see *Results: Multivariate analyses* and Fig. 6). Shade-tolerant tropical trees with minute seeds occur elsewhere (Metcalfe and Grubb 1994) and may provide additional examples of ontogenetic shifts, with high light levels required for initial establishment and with seedlings becoming shade tolerant sometime thereafter.

We found little evidence for ontogenetic shifts after saplings reach 10 mm in dbh, but rather evidence consistent with ontogenetic constancy. Ontogenetic shifts would cause multimodal size distributions, with few individuals in size classes with rapid growth and high mortality, and many individuals in size classes with slow growth and low mortality (Condit et al. 1998). There was no evidence for multimodal size distributions among the large canopy trees of old-growth forest on BCI (Fig. 1). With the exception of *A. blackiana*, mortality rates tended to be consistent across all juvenile stages, as demonstrated by the strong relationship among seed establishment probability, first-year seedling mortality, and sapling mortality (Fig. 7). If life history traits prove to be consistent through ontogeny for most species, then a reasonably small number of axes of variation may describe tree life histories (Pacala et al. 1996).

Can life histories be inferred from tree size distributions?

Size distributions with many large individuals and a long tail of relatively rare, small individuals ($g_1 < 0$)
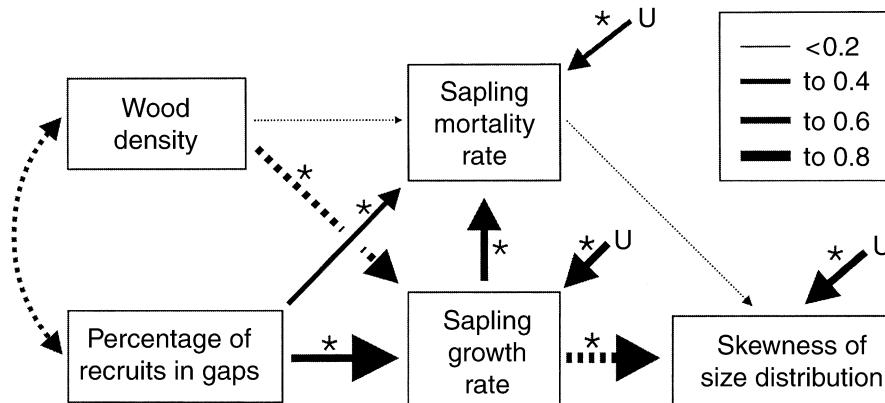
FIG. 8. Path diagram incorporating seven a priori predictions relating the percentage of recruits located in tree-fall gaps, wood density, sapling growth and mortality rates, and tree size distributions for canopy tree species from Barro Colorado Island, Panama. Solid lines represent positive effects, and dashed lines represent negative effects. The width of each line is proportional to the strength of the relationship. Asterisks mark paths that differ significantly from zero ($P < 0.05$). Table 2 presents the values of the path coefficients. An unanalyzed covariance path connects wood density and the percentage of recruits located in gaps. The U's represent residual variation.

TABLE 2. Direct (D), indirect (I), and total (T) effects from the listwise path analysis; the direct effects represent path coefficients.

Variable	Sapling growth (G)			Sapling mortality (M)			Skewness coefficient (g_1)		
	D	I	T	D	I	T	D	I	T
W	−0.45		−0.45	−0.09	−0.24	−0.33		0.32	0.32
P	0.47		0.47	0.33	0.25	0.58		−0.34	−0.34
G				0.54		0.54	−0.68	−0.02	−0.70
M							−0.04		−0.04

Note: R^2 values are 0.54 for sapling growth, 0.69 for sapling mortality, and 0.51 for the skewness coefficient.

characterized light-demanding species with high fecundity, rapid sapling growth, and high mortality of seeds, seedlings, and saplings (Figs. 5 and 6). Size distributions with many small individuals and a long tail of relatively rare, large individuals ($g_1 > 0$) characterized shade-tolerant species with lower fecundity, slower sapling growth, and lower mortality of seeds, seedlings, and saplings. Life history traits and size distributions are correlated for canopy trees on BCI.

Size distributions of BCI trees also appear to be fairly robust during population fluctuations. Many moisture-sensitive species declined substantially over an 18-year period that overlapped a 30-year dry spell and included an unprecedented 6-month drought (Condit et al. 1996*b*). Their size distributions were relatively stable despite these declines (see *Results: Size distributions*). Foresters and ecologists have, in the past, used tree size distributions to predict future population change (reviewed by Condit et al. 1998). Populations dominated by small (vs. large) individuals were predicted to grow (vs. crash) in the future. Condit et al. (1998) demonstrated that changes in population size observed over a 13-year interval were independent of initial size distributions for BCI trees. The observed size distributions of *Licania platypus* and *Jacaranda copaia* do not anticipate future population explosions and crashes, respectively (Fig. 1). Rather, these extreme size distributions appear to be stable characteristics of species that differ dramatically in shade tolerance.

Implications

The current paradigm posits a dominant axis of life history variation among tree species in closed-canopy forests with light-demanding pioneers and shade-tolerant climax species at the two end points (reviewed by Denslow 1987). Our analyses are consistent with this paradigm. Uncertainty concerns the distribution of species between the end points. Hartshorn (1980) believed that 71% of the canopy tree species at the La Selva Biological Station required high light levels to regenerate. In contrast, Hubbell and associates have previously argued that >80% of BCI tree species regenerated from the deeply shaded understory and were functionally equivalent (Hubbell and Foster 1986, Welden et al. 1991, Condit et al. 1996*b*). Our analyses suggest a third possibility. There are not large numbers of species at either extreme of the pioneer–climax continuum. Rather, there are very few extreme species. Most BCI tree species have intermediate light requirements and life styles (Fig. 2).

Three methodological problems have limited the attempts to evaluate consequences of life history variation and gap dynamics for the coexistence of tropical trees. First, continuous environmental variation in space has been described by two or three arbitrary habitat categories, (gap, gap edge, non-gap; Lieberman et al. 1989, Young and Hubbell 1991). Second, continuous environmental variation in time has been reduced to a single event: Did a gap form? And, third, continuous life history variation among species has been described by two or three arbitrary categories (pioneer, intermediate, and climax species). This caricature of environmental variation and tree responses has failed to explain tropical tree diversity (Brown and Jennings 1998, Hubbell et al. 1999). Yet, tree diversity has been shown to increase after disturbance in several tropical forests (Vandermeer et al. 2000, Molino and Sabatier 2001). We believe that it is now time to set aside the caricature of environmental variation and tree responses that led Brown and Jennings (1998) and Hubbell et al. (1999) to conclude that gap dynamics do not influence tree diversity. Future attempts to evaluate the relationship between gap dynamics and tree diversity must quantify continuous variation in tree responses to continuous variation in microenvironments in space and time. Static size distributions may aid this effort by providing insight into the relative positions of species along a continuum of species-specific responses to environmental variation.

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APPENDIX A

Correlation matrices required for the path analysis are available in ESA's Electronic Data Archive: *Ecological Archives* E084-085-A1.

APPENDIX B

Raw data used for the path analysis and for Figs. 3, 4, and 5 are available in ESA's Electronic Data Archive: *Ecological Archives* E084-085-A2.