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TREE MORTALITY AND GROWTH IN 11 SYMPATRIC *MACARANGA* SPECIES IN BORNEO

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Abstract. Interspecific differences in tree performance due to variation in resource availability are expected to influence the structure and dynamics of tropical forest communities. Patterns of mortality and growth over 32 mo in 11 species of *Macaranga* were analyzed to investigate factors influencing tree spatial distributions and the dynamics of early successional communities. Tree performance was assessed in relation to variation in light levels, soil texture, and tree ontogeny. Rates of mortality and growth varied by over an order of magnitude among species. Species common in high-light microsites had higher mortality and growth rates. Higher low-light mortality for these species reflected lower shade tolerances, supporting the view that shade tolerance involves a trade-off between high-light growth and low-light mortality.

Logistic and multiple regressions were used to test for independent effects of tree size and microenvironment on performance in the 11 species. Mortality and growth were significantly related to tree size in nine and eight species, respectively. Higher mortality and lower growth rates for juvenile trees were common. Despite positive correlations between light availability and tree size, mortality rates increased in three species, and growth rates decreased in four species at larger tree sizes. This pattern was particularly strong in smaller statured shade-intolerant species and may reflect changes in biomass allocation following reproductive onset. Declines in growth at larger tree sizes for only some species resulted in changes in species' performance rankings through succession.

Low-light mortality rates were strongly correlated with species' distributions in the forest with respect to light levels, whereas biases in distributions with respect to soil texture were not supported by differential mortality. For all trees pooled and in several species, growth showed a threshold response to light levels, being light-limited in low light but not in high light. Across all light levels, soil texture significantly influenced growth in six species. Five species and all trees pooled had significantly lower growth on the more nutrient-poor and potentially drought-prone sandy soils. The dynamics of *Macaranga*-dominated early successional communities are strongly influenced by soil resource and light availability, coupled with species-specific ontogenetic trajectories of performance.

Key words: Borneo; gap dynamics, tree canopy; Lambir Hills National Park, Sarawak, Malaysia; life history; Macaranga; *pioneer trees; rain forest; resource availability; shade tolerance; succession; tropical tree demography.*

INTRODUCTION

Resource availability for tropical rain forest trees is heterogeneous over a wide range of spatial and temporal scales (Vitousek and Denslow 1986, Canham et al. 1994, Denslow et al. 1998), and species are differentially distributed according to this variation (Orians 1982, Swaine 1996, Clark et al. 1998, Sollins 1998). Differences in species' mortality and growth responses to variation in resources influence community structure and forest dynamics (Tilman 1988, Clark and Clark 1992), and may be important for the maintenance of tropical tree diversity (Denslow 1987). In this study, patterns of mortality and growth in relation to variation in resource availability were analyzed to investigate factors influencing the spatial distribution, and the community structure and dynamics of 11 sympatric species of early successional tropical trees of the genus *Macaranga* (Euphorbiaceae) in Borneo.

The performance of tropical rain forest tree species is influenced by a range of resources, including light, soil water, soil nutrients, as well as physical aspects of establishment microsites (Brokaw 1987, Núñez-Farfan and Dirzo 1988, Popma and Bongers 1988, Uhl et al. 1988, Denslow et al. 1990, Clark and Clark 1992, Condit et al. 1995, Becker et al. 1998). Mortality and growth of pioneer tree seedlings are considered to be particularly strongly influenced by light levels, as a suite of ecophysiological and allocational traits of these species are specialized for resource acquisition in high light (Bazzaz and Pickett 1980, Swaine and Whitmore 1988, Ackerly 1996). However, these traits may limit survival ability in low light, due to high respiration

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rates, and increased vulnerability to herbivores and physical damage (Kitajima 1994, Kobe et al. 1995, Walters and Reich 1996, Davies 1998). Soil nutrient availability may also affect tropical tree performance. In dipterocarp forests of southeast Asia, where the soils are of generally low fertility, the influence of soil properties on species' spatial patterning and performance has been much debated (Wong and Whitmore 1970, Austin et al. 1972, Baillie et al. 1987, Ashton and Hall 1992). Several greenhouse studies using forest soil suggest that nutrient availability may limit seedling growth of pioneer species more than later successional species (Turner 1991, Turner et al. 1993, Burslem et al. 1994, 1995), but it is unknown whether these results reflect performance differences in the forest. Nevertheless, the potential for significant effects of variation in resources other than light on tree mortality and growth exists, although few studies have considered the importance of variation in a range of resources on tropical tree performance (Clark and Clark 1992).

Performance also changes through ontogeny in many tropical tree species (Lieberman et al. 1985, Shukla and Ramakrishnan 1986, Swaine et al. 1987*b*, Korning and Balslev 1994, Milton et al. 1994). Resources such as light and humidity change along the vertical gradient from the forest floor to above the canopy (Yoda 1974, Chazdon and Fetcher 1984). Soil water and nutrient levels change during gap-phase cycles (Becker et al. 1988, Denslow et al. 1998). However, few studies have attempted to link these systematic fluctuations in resource availability to ontogenetic changes in tree performance (Clark and Clark 1992).

The spatial distributions of the 11 *Macaranga* species considered in this study were strongly correlated with fine-scale variation in resource availability (Davies et al. 1998). Species differed in distributions along a continuum with respect to light availability, by whether they were more common on sandy or clay soils, and in maximum tree size that reflected differences in light availability through ontogeny. In the present study, I analyze mortality and growth rates over a 32-mo period for the same 11 species to address the following questions: (1) Are tree mortality and growth influenced by microenvironmental variation? (2) Is performance among microenvironments linked to the biases in species' spatial distributions? (3) Are there among-species trade-offs between performance in different resource microenvironments? And, (4) are there differences in mortality and growth through ontogeny with respect to microenvironmental variation? The consequences of species' differences in resource-dependent performance through ontogeny are then considered for the dynamics of *Macaranga*-dominated early successional communities.

METHODS

Study site, species, microenvironment, and plant attributes

This study was conducted in Lambir Hills National Park (Lambir), Sarawak, Malaysia (4°20′ N, 113°50′ E). Lambir is dominated by an exceptionally diverse, lowland, mixed dipterocarp forest (Lee et al. 1999). The climate is aseasonal, with mean rainfall >100 mm for all months, and high even temperatures.

The eleven species of *Macaranga* (Euphorbiaceae) selected for this study were locally abundant pioneer trees of large or small forest gaps (see further description in Davies et al. 1998). Trees were monitored over ~ 32 mo, from November 1991 to August 1994, in a series of permanent plots in Lambir: a 52-hectare plot and seven smaller plots. Methods of establishment and monitoring of these plots are described in Manokaran et al. (1990) and Davies et al. (1998), respectively.

Mortality and growth rates of individual trees through ontogeny and across a range of microenvironmental variation are described. Light levels of individual trees were assessed by assigning a crown illumination (CI) index on a scale of 5 (high light) to 1 (low light) to each tree following Clark and Clark (1992). Hemispherical photographs ($n = 101$) were taken across a wide range of canopy openness levels to calibrate the CI index. All five CI levels differed significantly in average percent canopy openness ($P = 0.001$; Davies et al. 1998), and CI was strongly positively correlated with canopy openness ($r_s = 0.82$). While this method provided a rapid and repeatable technique to estimate light availability for trees of all sizes, light in tropical rain forests varies along a continuum, and attempts to categorize it result in reduced precision of light availability measurement. Soil textural variation in the 52-ha plot was assessed by assigning 1300 soil samples (one per 20×20 m quadrat) to one of four soil texture classes from 1 (high clay content) to 4 (high sand content) based on a field evaluation of apparent sand content, slipperiness, and stickiness (Kimmins 1987). Analysis of sand, silt, and clay fractions for 145 representative soil samples using a LaMotte soil texture unit (LaMotte, Chesterton, Maryland) found significant differences in soil texture among the soil classes (percent sand/clay contents: class 1: 39/36; class 2: 45/19; class 3: 51/27; class 4: 64/13; see Davies et al. 1998 for further details). Soil texture varied across the 52-ha plot but did not show much variation within most quadrats (S. J. Davies, *personal observation*), so each tree in the plot was assigned the texture class of its quadrat. The microenvironment of subsamples of trees of each species were assessed, and consequently not all trees were included in all analyses presented.

Data analysis

Mortality.—Annual mortality rates were calculated as $m = 1 - (N_t/N_o)^{1/t}$, where N_o and N_t were numbers of trees alive at the start and end of the survey period, respectively (Sheil et al. 1995). The exact time interval, t in years, varied for each tree due to the time periods over which both plot establishment and remeasurement occurred. Population levels of mortality were therefore estimated with $t =$ the median time interval for each species (Condit et al. 1995). Confidence intervals of mortality rates were estimated using F ratios from the binomial distribution (Alder 1995), and rates were compared using chi-square tests. *Macaranga havilandii* is clonal so mortality refers to stem death, and not to genet death.

Logistic regression was used to model the probability of tree mortality (P_m) in relation to species, tree size, and microenvironment. The binary variable (dead/alive) was modeled against species ($n = 11$, unordered), initial tree size (diameter at breat height [dbh], continuous), crown light levels (CI index, $n = 5$, ordered), and soil texture ($n = 4$, ordered) using the logistic model $P_m = 1/(1 + e^{-z})$ where $z = a + bx_1 + cx_2 + \ldots + dx_n$, and $x_1, x_2 \ldots x_n$ are explanatory variables. Explanatory variables were included by stepwise addition to each model, and log-likelihood ratio chi-square tests were used to assess the significance of their contributions to the model (Trexler and Travis 1993, Legendre and Legendre 1998). Tree diameter (dbh) was $\log_e$-transformed prior to analysis. Preliminary analyses that also included untransformed dbh resulted in significantly improved fit for the model including all species (see also Vanclay 1991*b*), and for four individual species' models (*M. winkleri*, *M. hypoleuca*, *M. beccariana*, and *M. trachyphylla*). A significant positive deviation from zero of the additional untransformed dbh coefficient (using Wald's test) indicated a significant increase in the probability of mortality at larger tree sizes. *Macaranga hypoleuca* was excluded from this analysis due to limited sample sizes. Analyses were conducted using JMP (SAS Institute, Cary, North Carolina) and SYSTAT (Wilkinson 1990) software packages.

The first analyses involved a single explanatory variable: species, dbh, $\log_e$(dbh), light, soil texture, or one of the ten possible two-way interaction terms. Then, an analysis involving all five main effects was conducted. Adding interaction terms to the five main effects model proved difficult due to limited sample sizes in some cells. Nevertheless, significant species by size and microenvironment interactions necessitated finer scale analyses for each species. Within-species stepwise analyses were conducted by starting with variables with significant effects, and adding additional variables and interaction terms to test for their independent effects on the probability of mortality. Goodness of fit measures, $R^2(M)$, for logistic regression models including only signficant variables were calculated from log-likelihood ratios following Magee (1990).

Growth.—Tree diameter at breast height (dbh) and tree height were measured at the start and end of the 32-mo study period. Diameter, basal area, and height increments were calculated on an annual basis for each tree. Least squares multiple regression analyses were used to test for independent effects of species, tree size, light, and soil on growth rates. Analyses including all variables found significant effects of species and all interactions involving species, so analyses were conducted separately for each species, and only the latter results are presented. In several species the inclusion of a $(\text{dbh})^2$ term led to significantly improved model fit. Due to limited sample sizes it was not possible to include soil, light, and size in multiple regression models for each species. Since soil texture was not significantly correlated with light levels ($P > 0.05$, $n = 409$) or tree size ($P > 0.05$, $n = 2177$) for all trees pooled; single factor nonparametric analyses of soil effects on diameter growth are presented. Analyses of the size dependence of basal area and diameter growth rates found qualitatively similar results, and only the basal area growth rates are shown. Results of single factor and multiple regression analyses for the effects of light and tree size on growth are presented. r_s refers to the Spearman rank correlation.

RESULTS

Interspecific patterns of mortality and growth

Rates of tree mortality differed significantly among the 11 *Macaranga* species, and ranged along a continuum from 0.9–20.6%/yr (Table 1). Species more commonly associated with high-light microsites had higher mortality rates (Fig. 1A). These species were also less shade tolerant, as mortality rates in low light (CI = 1 and 2) were strongly positively correlated with species' mean CI index (Fig. 1B). The more shade-tolerant species had lower mortality rates in all light environments (Fig. 2).

Annual diameter and height growth rates were significantly greater in species typically associated with high-light microsites (Table 1). Diameter growth was significantly positively correlated with species' mean CI index, and with mortality in low light (Fig. 3). The more shade-tolerant species (*M. kingii*, *M. lamellata*, *M. havilandii*, and *M. hullettii*) had lower median (<1.2 mm/yr) and maximum diameter growth rates (<11.0 mm/yr), and virtually no fast-growing trees. Whereas species associated with high-light microsites had higher median (>2.0 mm/yr) and maximum diameter growth rates (>19.0 mm/yr), and more fast growing trees. Nevertheless, all species had >10% of trees surviving with essentially no diameter growth (≤1.0 mm/yr; Table 1). Several species typically associated with high-light microsites had substantial proportions of suppressed trees (e.g., *M. triloba* 34% and *M. beccariana* 22%). Height growth was strongly positively correlated with diameter growth in all species ($r_s = 0.41$–0.90, $P < 0.01$), except *M. hypoleuca* ($r_s = 0.24$, $P > 0.1$).

Mortality and growth in relation to tree size and microenvironment

Mortality.—Logistic regression models including the four main effects separately, found that the probability of mortality was significantly related to species, tree size, light levels (all $P < 0.005$), and to soil texture ($P = 0.012$). When these effects were included in a single model (without interactions) species, tree size and light levels contributed significantly to the model (all $P < 0.001$), but soil texture did not ($P = 0.80$). Interactions between species, tree size and light levels were also all significant when added to the combined model (all $P < 0.001$), reflecting species-specific patterns of mortality with respect to tree size and light availability (Table 2).

Nine species had significantly higher mortality rates for smaller trees independent of changes in light levels, and in three species (*M. winkleri*, *M. beccariana*, and *M. trachyphylla*) the probability of mortality also increased significantly in larger size classes (Table 2, Fig. 4). Four species (*M. hosei*, *M. hypoleuca*, *M. triloba*, and *M. trachyphylla*) had significantly greater mortality rates in lower light environments independent of the effects of tree size (Table 2, Fig. 2). In *M. havilandii* there was no independent effect of light levels on the probability of mortality, but the interaction between tree size and light levels was significant. In four species, tree size, but not light levels, significantly influenced the probability of mortality: For *M. winkleri* and *M. beccariana* mortality was not significantly increased in low light as mortality rates were high in all CI classes; for *M. gigantea* sample sizes were probably too small to detect a light effect; and for the shade tolerant *M. kingii* mortality was consistently low in all light levels (Fig. 2). In two relatively shade-tolerant species (*M. hullettii* and *M. lamellata*) neither tree size, nor light levels significantly affected the probability of mortality (Table 2).

The significant effect of soil texture in the single variable model was due to the clay-soil species having

PLATE 1. A stand of *Macaranga hosei* in a large forest opening that resulted from a landslide in the 1960s in the Lambir forest. The trees are easily recognized by their pale slender trunks, small leaves, and distinctive shallow crowns. *Macaranga hosei* is one of several large-statured high-light demanding *Macaranga* species that persist in forest openings well after the smaller statured species have died (photograph by the author).

TABLE 1. Annual mortality and growth rates for 11 species of *Macaranga* over 32 months in Lambir, Sarawak, Malaysia.

				Growth							
		Mortality		Diameter					Height		
Macaranga species	Soil	%	*N*	Med.	Max.	% Slow	% Fast	*N*	Med.	Max.	*N*
gigantea	SC	5.5	58	4.0	(38.9)	26	22	46	0.67	(4.3)	24
winkleri	C	16.7	168	6.9	(30.5)	12	41	100	1.80	(4.1)	47
hosei	C	15.1	252	2.8	(22.1)	18	13	159	0.66	(2.9)	45
hypoleuca	C	9.0	72	3.1	(21.3)	25	16	57	0.62	(2.2)	22
triloba	C	20.6	417	2.1	(19.4)	34	9	225	0.44	(2.0)	92
beccariana	C	17.9	666	2.4	(23.8)	22	10	398	0.60	(2.4)	82
trachyphylla	C	7.2	861	2.1	(29.9)	28	8	693	0.69	(2.8)	131
havilandii	S	6.8	129	0.8	(8.7)	59	0	102	0.21	(1.0)	57
hullettii	SC	2.3	402	1.1	(10.9)	47	1	366	0.40	(1.5)	20
lamellata	S	0.9	346	1.0	(6.7)	49	0	329	0.18	(1.1)	44
kingii	C	2.3	107	0.4	(6.7)	77	0	90	0.23	(0.9)	33
P		<0.001		<0.001						<0.001	

Notes: Mortality rates for all trees (%/yr), median and maximum diameter growth rates (mm/yr), the percentage of slow- (≤ 1.0 mm/yr) and fast- (>10.0 mm/yr) growing trees, and median and maximum height growth rates (m/yr) are listed for each species. Biases in spatial distributions with respect to soil texture indicated as sandy (S), clay (C), or evenly distributed (SC). *P* values refer to significance levels from among-species comparisons using chi-square tests for mortality and Kruskall-Wallis nonparametric tests for growth. Species are arranged in order of increasing shade tolerance as in Fig. 1. Mortality rates of *M. havilandii* are listed on a per-stem basis as the species is clonal.

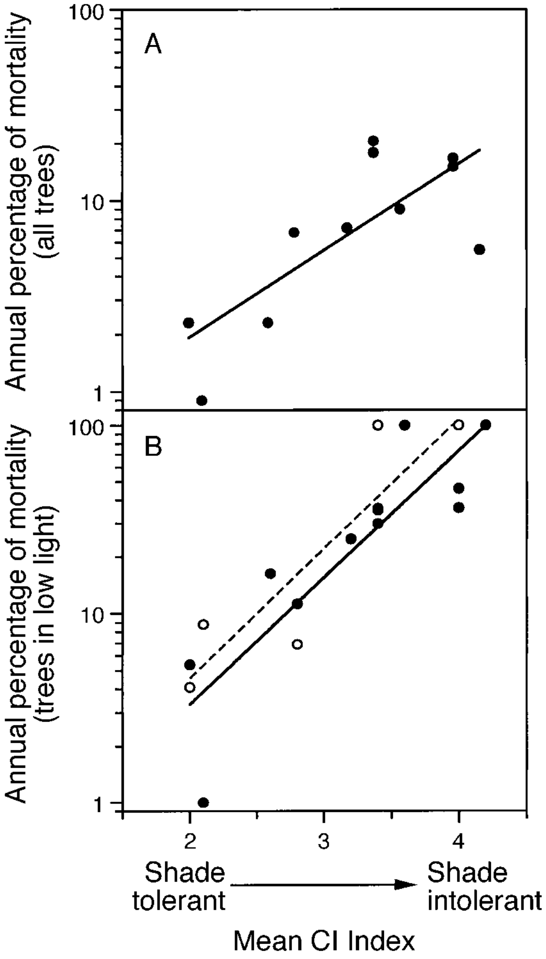

FIG. 1. Annual mortality rates (%/year) in relation to the degree of association with high-light microsites (mean CI index) among 11 species of *Macaranga.* (A) Mortality of all trees vs. mean CI index, $r^2 = 0.41$, $P < 0.01$. (B) Mortality of trees in low light (CI = 2, solid circles and solid line, $r^2 = 0.57$, $P < 0.01$) and very low light (CI = 1, open circles and dashed line, $r^2 = 0.66$, $P < 0.01$) vs. mean CI index. Three species were absent from CI = 1 microsites.

higher mortality rates than the sandy-soil species (Table 1). Soil texture added no explanatory power to the combined regression model that included the species effect. Soil texture did not significantly influence mortality rates in any of the 11 *Macaranga* species (Table 2).

Growth.—In eight species, growth rates varied significantly with tree size (Fig. 5), independent of the strong positive correlation between light availability and tree size ($P < 0.001$, $n = 732$; Table 3). Four species, including the three small-statured, shade-intolerant species *M. winkleri*, *M. triloba*, and *M. beccariana*, had highest growth rates in intermediate size classes and significant reductions in growth at larger sizes (Fig. 5). In contrast, growth in the large-statured, shade-intolerant species, *M. gigantea* and *M. hosei*, increased across all size classes with light levels held constant (Table 3). Due to differences in the size-dependence of growth among species, the rank order of species' growth rates changed with increasing tree size (Fig. 6). *Macaranga winkleri* had the highest growth rates up to 6 cm dbh, after which *M. gigantea*, *M. hosei*, and/or *M. hypoleuca* had higher growth rates (see Plate 1). The more shade-tolerant species had significantly lower growth rates than the other species across all size classes. Despite reductions in growth with tree size in several species, light availability had a significant positive effect on growth in four of the 11 species (Table 3, Fig. 7).

Soil textural variation in the 52-ha plot significantly influenced diameter growth in six species (Table 3). In five of these species, growth rates were significantly higher on clay-rich (texture class 1) than on sand-rich soils (texture class 4; data not shown), and for all trees pooled, growth rates on clay soils (class 1; mean = 4.6 mm/yr, $n = 376$) were almost double those on sandy soils (class 4; mean = 2.4 mm/yr, $n = 1201$).

Diameter growth rates were rather weakly correlated with CI index ($r_s < 0.35$ for all species, except *M. hypoleuca*, $r_s = 0.55$). At lower light levels, growth of all trees pooled was strongly limited by both light and soil resource availability (Fig. 8). Whereas in high to very high light levels, growth was significantly lower on sand-rich than on clay-rich soils, but not different among light levels (Fig. 8). Due to limited sample sizes

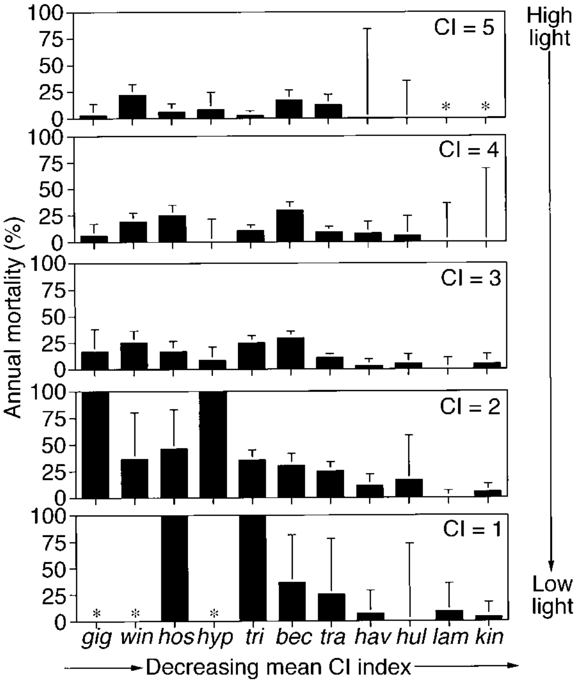

FIG. 2. Annual mortality rates (%/year) for 11 species of *Macaranga* growing in five crown illumination classes (5 = high light, 1 = low light) in Lambir. Asymmetric 95% confidence intervals were derived from the *F* distribution (Alder 1995). Species are listed by their first three letters, in order of decreasing mean CI index for trees living in the forest. An asterisk indicates there are no trees in that light level.

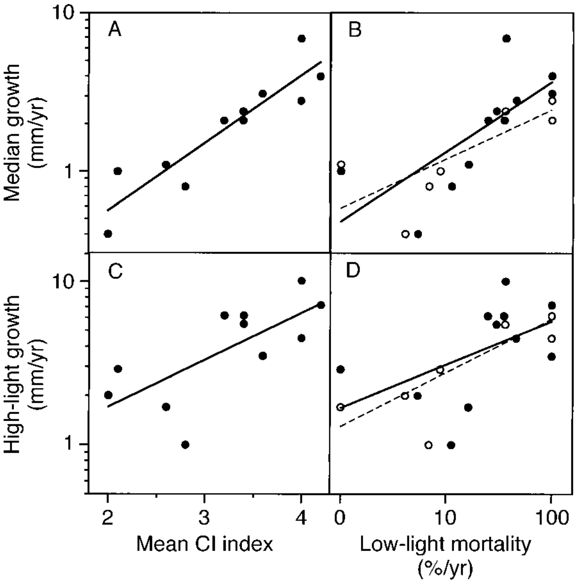

FIG. 3. Relationships between diameter growth and degree of association with high-light microsites (mean CI index), and between growth and low-light mortality rates among 11 species of *Macaranga.* (A) Median diameter growth (mm/yr) vs. mean CI index, $r^2 = 0.84$, $P < 0.01$. (B) Median diameter growth vs. low-light mortality (low light, CI = 2, solid circles and solid line, $r^2 = 0.53$, $P = 0.01$; very low light, CI = 1, open circles and dashed line, $r^2 = 0.56$, $P = 0.03$). (C) Median high-light diameter growth (mm/yr; CI = 4) vs. mean CI index, $r^2 = 0.51$, $P = 0.01$. (D) Median high-light diameter growth vs. low-light mortality (low light, CI = 2, solid circles and solid line, $r^2 = 0.26$, $P = 0.11$; very low light, CI = 1, open circles and dashed line, $r^2 = 0.61$, $P = 0.03$). In (B) and (D), three species were absent from CI = 1 microsite.

for some species, it was not possible to test whether this pattern of resource-limited growth occurred in all species. However, in no species was diameter growth significantly greater in the highest compared to the second highest light level (Fig. 7), and in *M. hosei*, *M. triloba*, *M. beccariana*, and *M. trachyphylla* mean growth rates were 15–29% lower in CI = 5 than in CI = 4. In *M. beccariana* and *M. trachyphylla* growth of high-light trees (CI $\geq$ 4) was significantly lower in sandy than in clay soils ($P < 0.01$). Several other species (e.g., *M. hosei*) had significant soil texture effects but no light effects on growth (Table 3).

Discussion

Interspecific variation in mortality and growth

Mortality and growth rates varied by over an order of magnitude among the 11 *Macaranga* species, and encompassed the typically high rates reported for pioneer species, as well as the low rates reported for many shade-tolerant understorey species (Lang and Knight 1983, Alvarez-Buylla and Martinez-Ramos 1992, Condit et al. 1993, 1995, Lugo and Scatena 1996). Pioneer species are thought to either grow well or die, and consequently to have high average growth rates with low variance (Lieberman and Lieberman 1987), however, most species in this study had high percentages of suppressed individuals. Further monitoring will assess whether the probability of mortality for the slow growing trees is increased, as is found at the community level (Swaine et al. 1987*a*, Hall 1991, Manokaran and Swaine 1994).

The wide range of low-light mortality rates reflected a wide range of shade tolerance in *Macaranga.* This variation was strongly correlated with the species' spa-

TABLE 2. Summary of stepwise logistic regression results for the effect of soil texture (T), tree diameter (D; $\log_e$[dbh]), crown light levels (L; CI index), and the dbh × light interaction (D × L), on the probability of mortality over 32 months in 11 species of *Macaranga.*

Macaranga species	N_{LD}	N_T	Single variable				Stepwise addition						$R^2(M)$
			T	D	L	D × L	D + L	L + D	D + D × L	D × L + D	L + D × L	D × L + L	
gigantea	36	29	NS	<0.001	NS	NS	NS	···	NS	···	···	···	0.178
winkleri	103	105	NS	<0.001	NS	NS	NS	···	NS	···	···	···	0.080
hosei	100	147	NS	<0.001	0.002	NS	0.049	0.004	NS	···	0.008	···	0.226
hypoleuca	34	60	NS	<0.001	0.001	0.001	0.043	0.001	0.012	<0.001	0.002	0.002	0.643
triloba	215	127	NS	<0.001	<0.001	<0.001	0.027	<0.001	NS	<0.001	<0.001	<0.001	0.375
beccariana	221	499	NS	<0.001	NS	NS	NS	···	NS	···	···	···	0.083
trachyphylla	228	775	NS	<0.001	0.008	<0.001	0.005	<0.001	0.048	<0.001	<0.001	0.001	0.227
havilandii	102	77	NS	0.042	NS	0.006	NS	···	0.035	NS	···	NS	0.169
hullettii	34	399	NS	NS	NS	NS	···	···	···	···	···	···	···
lamellata	52	347	NS	NS	NS	NS	···	···	···	···	···	···	···
kingii	51	105	NS	0.032	NS	NS	NS	···	NS	···	···	···	0.042

Notes: Numbers are P values from log-likelihood ratio chi-square tests of the significance of inclusion of each explanatory variable in each species' model. Initial single-variable analyses included T, D, L, and D × L separately. Addition sequences proceeded only following the significance of the first variable, and P values indicate the significance of adding the extra variable. Models for *M. winkleri, M. hypoleuca, M. beccariana,* and *M. trachyphylla* also included untransformed dbh. Species are arranged in order of increasing shade tolerance as in Fig. 1. Sample sizes were: for models with light alone and with light and diameter (N_{LD}), for soil texture alone (N_T), and for tree diameter alone as in Table 1. NS indicates no significant effect. $R^2(M)$ measures were calculated as described in *Methods: Data analysis* for regression models including significant variables only and are not directly comparable among species.

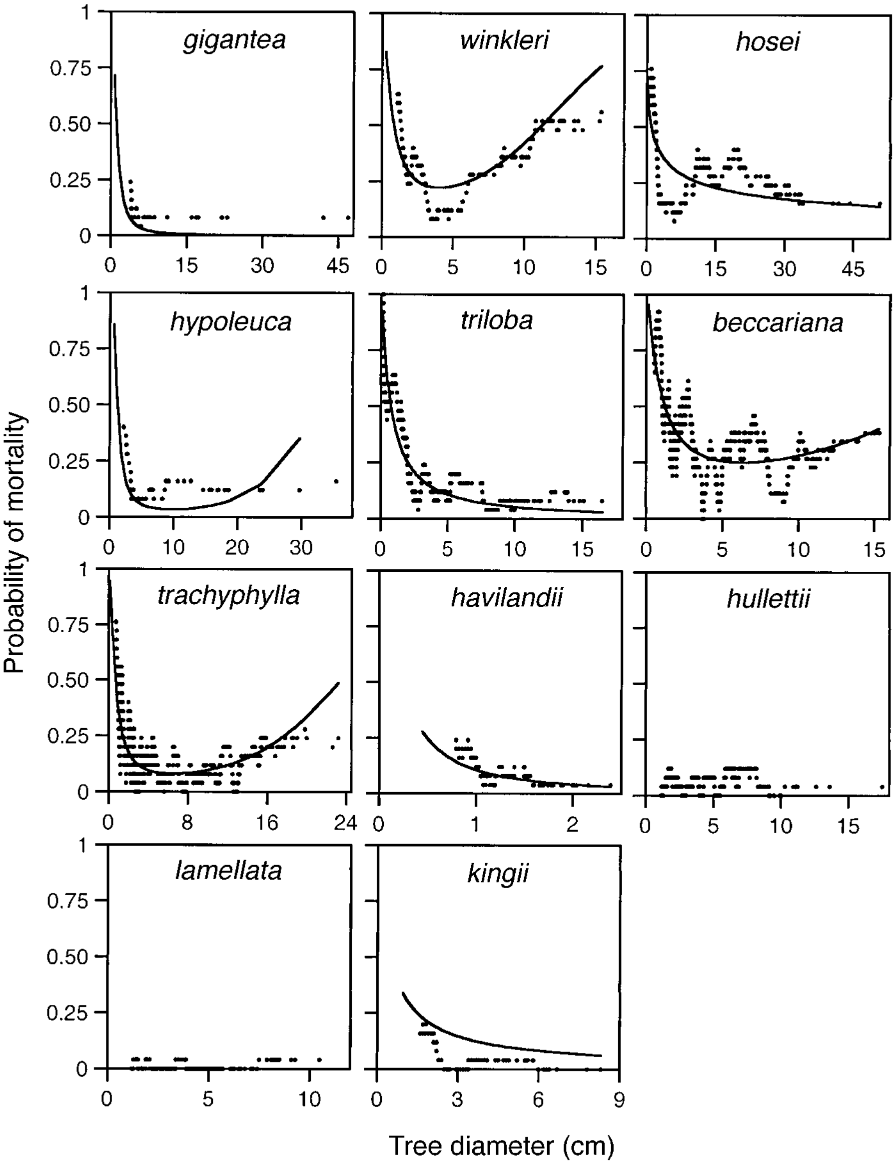

FIG. 4. Logistic regression models of the probability of mortality over 32 mo as a function of tree diameter for 11 species of *Macaranga* in Lambir. Points indicate sliding 25-point averages of the proportion of trees dying to illustrate the approximate fit of the models. Models were fit only for species in which the probability of mortality was significantly related to tree size. For *M. winkleri*, *M. hypoleuca*, *M. beccariana*, and *M. trachyphylla*, models included both dbh and $\log_e$(dbh) variables; other models included only $\log_e$(dbh).

tial distributions in the forest with respect to light availability, and with seedling photosynthesis and biomass allocation patterns (Davies 1998). Strong positive relationships between growth and mortality in *Macaranga* support the view that variation in shade tolerance among species involves a trade-off between high-light growth and low-light survivorship (Pacala et al. 1994, Kobe et al. 1995, Walters and Reich 1996). Walters and Reich (1996) suggest that higher low-light growth may also be an important component of shade tolerance in tree species, as higher growth is often linked to higher survival (see also Denslow et al. 1990). This advantage may not be evident except in very low light levels where growth of less shade-tolerant species may be lower than growth of more shade-tolerant species. For *Macaranga*, the large sample of trees studied encompassed their natural distributions with respect to light levels. Although seedlings were undersampled, the very high low-light mortality rates in the more shade-intolerant species appeared to preclude them from persisting in light levels where growth rankings might otherwise reverse.

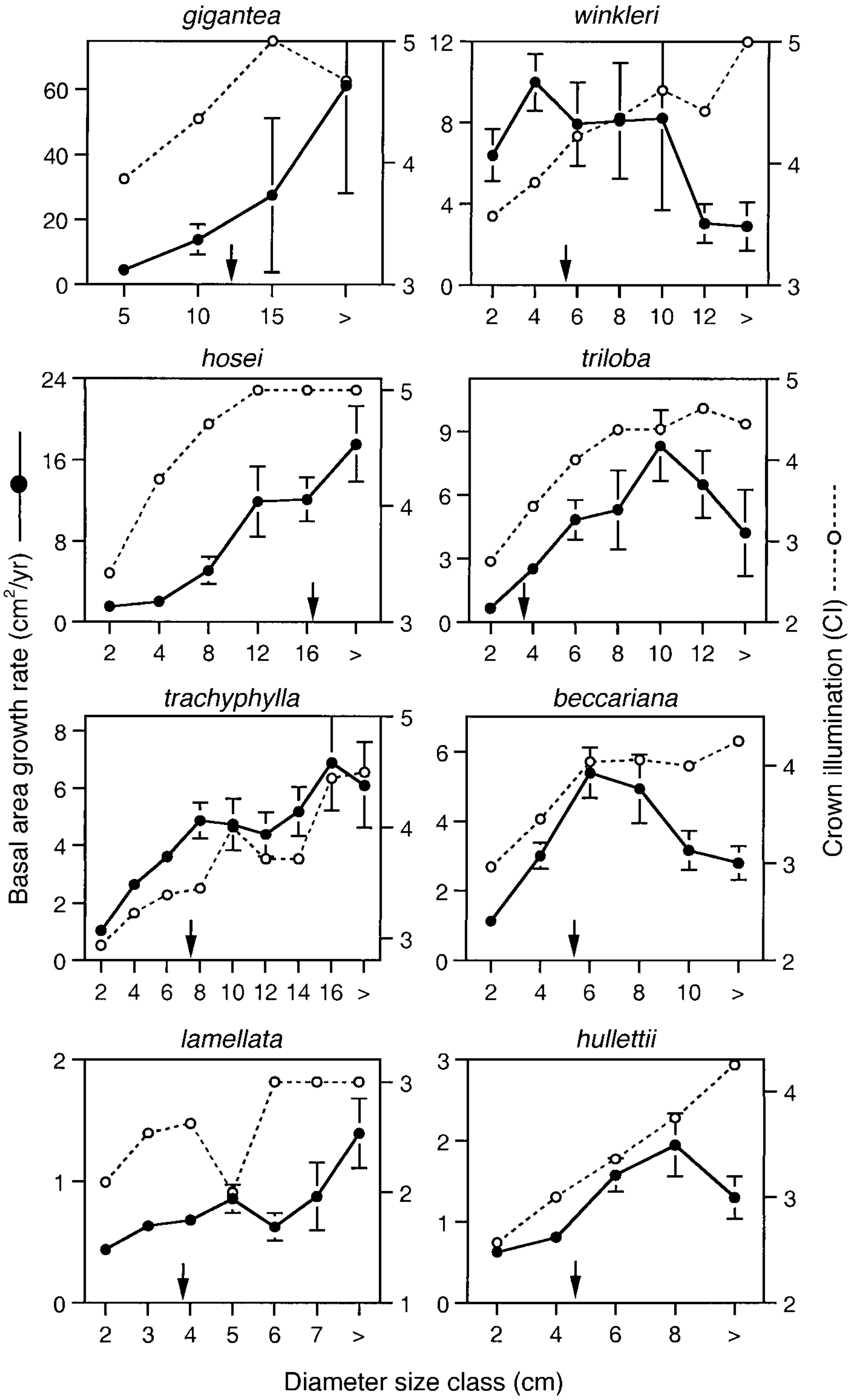

FIG. 5. Relationships between basal area growth rates and tree size in the eight *Macaranga* species with significant size-dependent growth. Values are mean growth (cm^2/yr, mean ± 1 SE) for increasing size classes (e.g., 2 is <2 cm dbh, 4 is 2–4 cm dbh, etc.). Note the different scales used for each species. Sample sizes for growth are as in Table 1. Mean crown illumination levels for each size class are also shown. Right-hand panels show the four species with significant decreases in growth at larger size classes. Arrows indicate the estimated size threshold above which most trees in each species reproduced (from Davies and Ashton 1999).

TABLE 3. Summary of analyses of the effects of tree size and light levels, and of soil texture on growth rates in 11 *Macaranga* species.

Species	Tree size	Light	$r^2_{\rm L}$	$N_{\rm L}$	Soil texture	$N_{\rm T}$
gigantea	<0.01 (0.01)	NS	0.88	26	NS	26
winkleri	0.02	NS	0.06	51	NS	75
hosei	<0.01	NS	0.32	53	<0.01	107
hypoleuca	0.04 (NS)	<0.01 (NS)	0.42	25	NS	49
triloba	<0.01	<0.01	0.25	123	0.07	103
beccariana	<0.01	<0.01 (0.03)	0.29	98	<0.01	339
trachyphylla	<0.01	<0.01	0.26	158	<0.01	641
havilandii	NS	NS	NS	80	<0.01	62
hullettii	<0.01 (0.03)	NS	0.16	29	0.03	361
lamellata	<0.01	NS (0.02)	0.25	49	0.04	329
kingii	<0.01 (NS)	NS	0.19	40	NS	88

Notes: For tree size, light, and soil texture P values are from single-factor Kruskall-Wallis tests are given. Multiple regression analyses assessed the effects of tree size and light on basal area increment as represented in Fig. 5, with sample size $N_{\rm L}$ and $r^2_{\rm L}$; P values are given in parentheses only where they differ from single-factor results. Sample sizes are for single-factor analyses of tree size as in Table 1. NS indicates no significant effect.

Mortality and growth in relation to ontogeny

High mortality and low growth rates are typical for juvenile rain forest trees due to low understorey light levels, exposure to physical and biotic disturbances, and the potential for short-term water deficits (Augspurger 1984*a*, *b*, Kobe 1999). Increases in mortality and declines in growth in larger tree size classes are less well understood, even though they have been reported in a range of species (Vanclay 1991*a*, *b*, Alvarez-Buylla and Martinez-Ramos 1992, Milton et al. 1994, Alder 1995, Condit et al. 1995, Clark and Clark 1996). In *Macaranga*, growth rates declined for four species, and mortality rates increased for three species in larger size classes, despite increasing light availability through ontogeny. Harcombe (1987) suggested that size-dependent increases in tree mortality may be common as overmature trees tend to grow slowly, and are therefore more susceptible to death. But why do large trees grow slowly in only some *Macaranga* species? Reductions in diameter growth in larger size classes were particularly strong for the smaller statured, shade-intolerant species (*M. winkleri*, *M. beccariana*, and *M. triloba*). Peak growth approximately coincided with size at first reproduction in the first two of these species (Fig. 5), and two species had significantly higher growth rates in nonreproductive than reproductive trees (Davies and Ashton 1999). Reduced diameter growth may therefore have reflected a reallocation of resources to reproduction rather than a reduction in overall biomass growth rates. Resources other than light also change through pioneer tree ontogeny, and may influence patterns of mortality and growth. Soil nutrient and water availability may initially increase and later decrease through the gap-phase cycle (Becker et al. 1988, Denslow et al. 1998). However, there was no evidence that changes in soil resources affected the large and small shade-intolerant species differently. Soil texture had a significant effect on growth independent of tree size, and the larger statured species were no less sensitive to soil resource variation than the smaller species.

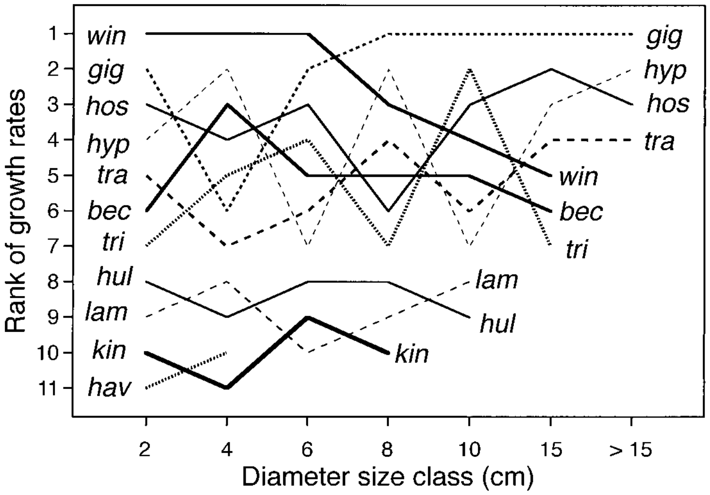

FIG. 6. Changes in the rank order (from highest to lowest) of median annual basal area growth rates with increasing tree size among the 11 *Macaranga* species. Sample sizes are given in Table 1. Species are indicated by their first three letters.

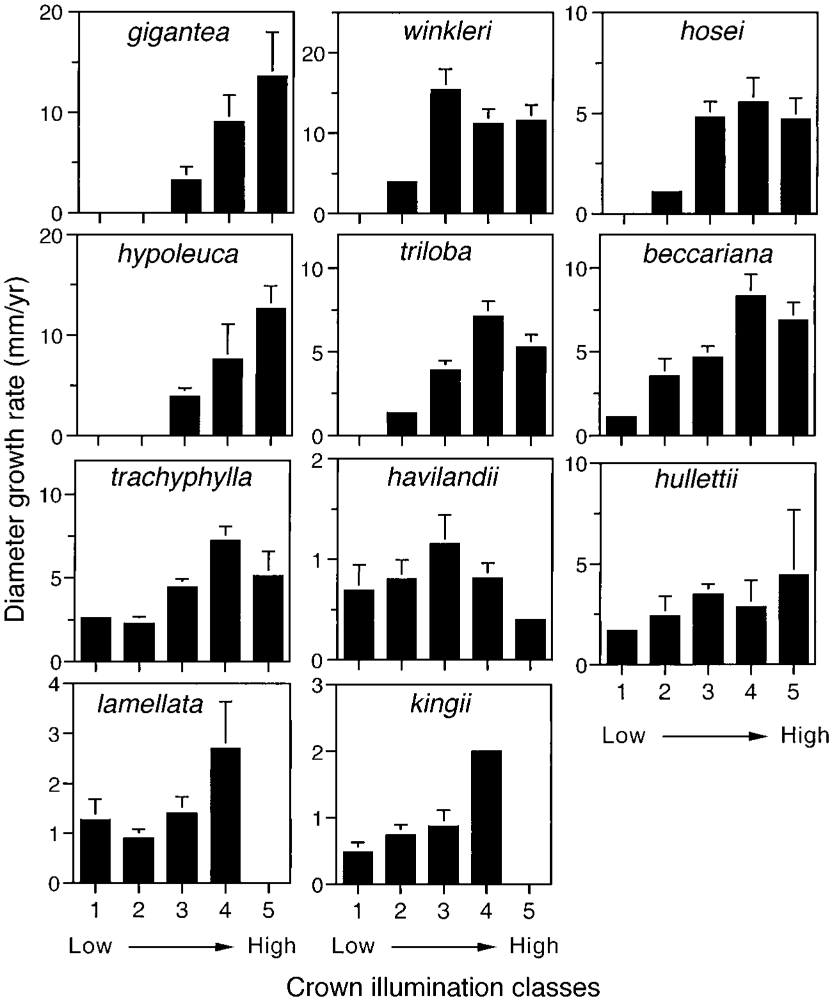

FIG. 7. Mean annual diameter growth rates (mm/yr, mean + 1 SE) of trees in five crown illumination classes (1 = low light to 5 = high light) for 11 species of *Macaranga*. Significance of differences in growth among light levels and sample sizes are given in Table 3. Note the different scales used for each species. Species are arranged from top to bottom as in Table 1.

Microenvironmental effects on tree performance

In the absence of dispersal limitation, differential mortality with respect to microenvironmental variation should correspond to observed tree distribution patterns. For light, *Macaranga* species typically associated with high-light microsites had greater low-light mortality, as has been widely reported for tropical trees (Howe 1990, Brown and Whitmore 1992, Clark and Clark 1992, Alder 1995, Ashton et al. 1995, Burslem and Whitmore 1996). Greater mortality rates in high light for the more shade-tolerant species were not found, however trees of these species rarely occurred in high-light microsites. In contrast, biases in *Macaranga* spatial distributions with respect to soil texture were not supported by differences in mortality among soils. Such differences may not have been detected if they typically occur during seedling establishment (only plants ≥1 cm dbh were monitored in the 52-ha plot), or if the occasional severe droughts in north west Borneo (Walsh 1996), lead to higher mortality of clay-soil species on the drought-prone sandy soils at Lambir.

Greater light availability results in higher growth rates for many tropical rain forest tree species (Augspurger 1984*a*, Popma and Bongers 1988, Denslow et al. 1990, King 1991, Welden et al. 1991, Clark and Clark 1992, Newell et al. 1993, Kobe 1999), suggesting that light is the main resource limiting growth in these forests. However, most studies have involved only seedlings or saplings (but see Clark and Clark 1992), and have not assessed the importance of other resources (but see Núñez-Farfan and Dirzo 1988, Uhl et al. 1988, Fisher et al. 1991). Both light and soil resource availability significantly influenced tree growth in some *Macaranga* species in this study. The effect of soil textural variation was strong, with most species, and all trees pooled, having substantially lower growth on the nu-

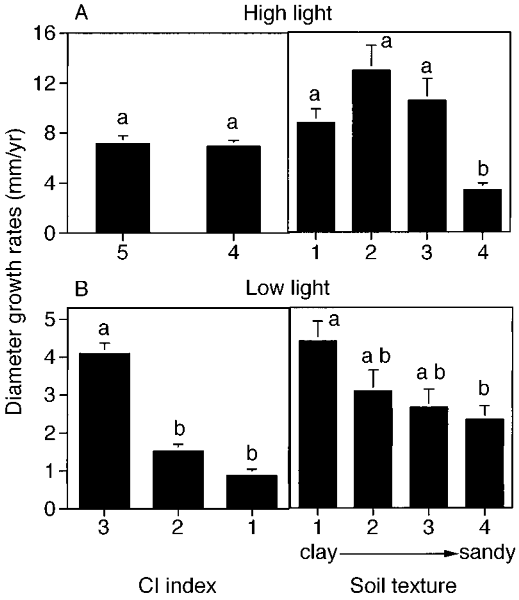

FIG. 8. Diameter growth rates (mm/yr) for trees of all species pooled in (A) high light (CI index ≥ 4) and (B) low light (CI index ≤ 3) in the four soil texture classes (class 1 = clay-rich soil to class 4 = sand-rich soil). Significant differences among means within each panel are indicated by different letters from Scheffé tests.

trient poor, well-drained sandy soils at Lambir (Ashton and Hall 1992, Palmiotto 1998). In contrast, growth was generally weakly correlated with light availability for most of the *Macaranga* species.

Light availability was not measured quantitatively for each tree in this study, and categorical indices of crown illumination may limit our ability to distinguish species' responses to light variation (Kobe 1999). However, strong spatial patterning of the *Macaranga* species with respect to CI index, and its strong correlation with independent measures of seedling ecophysiological traits (Davies 1998), suggest that the CI index was a good estimate of light availability. In several species, and for all trees pooled, light availability was found to limit growth in low light levels, but not in high to very high light levels, where growth was strongly limited by soil resources. Several forest processes may restrict pioneer trees to higher light levels, where growth may be primarily limited by resources other than light: light-induced seed germination (e.g., Vazquez-Yanes and Smith 1982), very high low-light mortality rates of seedlings and saplings, and the individuals that do survive grow into higher light environments through ontogeny (Davies et al. 1998).

This study found that the dynamics of early successional *Macaranga*-dominated tree communities are influenced by complex interactions between soil resource and light availability, coupled with species-specific ontogenetic trajectories of performance. Variation in the size dependence of performance provides an important axis of temporal successional differentiation among the species. After gap formation, a mix of *Macaranga* species are common, the smaller shade-intolerant species initially dominate while the larger, equally shade-intolerant species persist and dominate midsuccessional communities. Throughout this successional sequence species vary in response to light and soil resource availability that directly affects their spatial distributions in the forest. Further work, particularly at germination and establishment, is required to reveal the causal basis for differences in species' distribution patterns and performance with respect to soil resources (Clark et al. 1998). In general, studies that assess the roles of a greater range of potentially limiting resources on the performance of trees throughout ontogeny, will provide greater insight into the factors influencing species coexistence in diverse tropical rain forest communities.

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