

Variation in growth responses of neotropical pioneers to simulated forest gaps

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Summary

1. One proposed mechanism by which tree species coexist is through partitioning gradients of light availability. We performed a pot experiment in which seedlings of 12 pioneer species were established in 30% light, then transplanted to six light treatments designed to simulate natural gaps ranging from 25 m² (≈10% full sun) to 800 m² (60% full sun). Plants were harvested after 56–117 days, and comparisons were made of allocation patterns and growth and carbon assimilation rates.

2. Species varied strongly in their maximum relative growth rate (RGR, range 15.4–83.6 mg g⁻¹ day⁻¹). However, we found little evidence for gap-size partitioning based on growth rate, as species RGR in large and small simulated gaps was strongly correlated ($r = 0.83$, $P < 0.001$).

3. Species differences in growth reflected variation in both physiology and allocation. Net assimilation rate was a strong determinant of RGR across all simulated gap sizes ($r^2 = 0.60$ – 0.71 , $P < 0.001$). Leaf area ratio was a poor predictor of growth rate under all gap sizes ($r^2 = 0.04$ – 0.08 , NS).

4. The maximum rate of net C assimilation (A_{\max}) increased significantly with simulated gap size for all but one pioneer species, but only when measured on a per area basis. Among species variation in A_{\max} was only weakly related to RGR. Foliar nitrogen concentration varied widely among species (range 2.2–4.7% dry mass), but was only weakly correlated with RGR ($r^2 = 0.04$ – 0.30).

5. Previous growth analyses of tropical seedlings have identified both specific leaf area (SLA) and seed mass as key traits correlated with growth rate. Although SLA varied twofold and seed mass more than a thousand-fold among the pioneer species in this study, neither trait was significantly correlated with among-species variation in RGR. Although these traits underlie major differences in life history between shade-tolerant and pioneer species, they contribute little to variation in growth performance within the pioneer functional group.

Key-words: allocation patterns, gap partitioning, growth analysis, light requirements, tropical forest

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Introduction

Pioneer species dependent on canopy gaps for successful recruitment may comprise 15% or more of tree diversity in old-growth tropical forests (Brokaw 1985; Brandani *et al.* 1988; Popma *et al.* 1992; Davies *et al.* 1998; Molino & Sabatier 2001). Individual gaps in these forests are frequently initially colonized by a significant fraction of these species. For example, recently formed natural tree-fall gaps on Barro Colorado Island (BCI), Panama contained, on average, seedlings

of seven of the 24 common pioneer species in the community (Dalling *et al.* 1998). Likewise, in South-East Asia Davies *et al.* (1998) report that it is common to find five to eight *Macaranga* pioneer species present in a single gap. Interspecific differences in the timing of seedling emergence, and in susceptibility to physical and biotic hazards during establishment, may contribute to the coexistence of these species (Garwood 1986; Dalling & Hubbell 2002). Alternatively, direct competitive interactions among individuals might determine recruitment patterns. If the relative growth performance of pioneers shifts according to resource availability, then variation in gap characteristics that influence resource levels may play an important role in the maintenance of diversity within this functional group.

Growth performance may be influenced by the ability to acquire nutrients and water (Turner 1991; Burslem 1996; Denslow *et al.* 1998; Tyree *et al.* 1998). However, as yet there is little evidence to suggest that either of these resources varies at sufficiently fine scale to promote diversity strongly within a local community. In contrast, light availability varies strongly within gaps (Smith *et al.* 1992; Brown 1993; Van der Meer *et al.* 1998), and scales with gap size (Barton *et al.* 1989). Furthermore, pioneer sapling recruitment success has been shown to be gap size-dependent. Brokaw (1987) observed that three species of pioneer differed in the minimum gap size that they could successfully colonize, and that gap size requirements were proportional to the species' mean height growth rate.

In this study we re-examine gap size partitioning among BCI's pioneers, and evaluate whether it might result from changes in the rank order of species' relative growth rates (RGR) under different light conditions. Evidence for this outcome, described as a 'rank reversal' in growth performance, remains equivocal (Sack & Grubb 2001). However, to date most tests for rank reversals among tropical tree species have included both shade-tolerant and pioneer species, and have focused on differences in growth performance under light regimes characteristic of the forest understorey and gaps (Kitajima 1994; Boot 1996; Agyeman *et al.* 1999; Poorter 1999; but see Bloor & Grubb 2003). Differences in growth performance between shade-tolerant and pioneer species, however, reflect a strong divergence in life history. This results from the contrasting selective pressures that favour either traits enhancing plastic growth response to light in gaps, or traits favouring long-term survival in the understorey. Here we concentrate on pioneer species with limited capacity for survival in deep shade. We examine growth response to light under irradiance conditions characteristic of the range of sizes of natural gaps that form in the BCI forest (Dalling *et al.* 1998).

Attempts to characterize growth performance in response to gap light conditions are hampered by the spatial and temporal heterogeneity in irradiance within gaps (Brokaw 1982; Popma *et al.* 1988; Brown 1993; Sipe & Bazzaz 1994). As a consequence, light responses of seedlings have mostly been determined from pot experiments conducted in a growing house (Fetcher *et al.* 1983; Strauss-Debenedetti & Bazzaz 1991; Poorter 1999). In these experiments, artificial shade is used that typically exposes plants to relatively uniform irradiance. However, uniform conditions fail to simulate the diurnal variation in light quality and irradiance observed in natural gaps as the sun passes from peripheral shade to the canopy opening above. Simulation of the diurnal fluctuation in irradiance characteristic of gaps is important because plant biomass (Watling *et al.* 1997), and plant morphology and allocation, may be influenced by the distribution, as well as the total daily irradiance received.

We use simulated gaps to characterize the growth response to irradiance variation for young seedlings of a representative sample of BCI's pioneer species, and to determine whether species rank shifts in growth rate occur under different irradiance conditions. In addition, we use measurements of photosynthetic carbon gain, foliar nitrogen concentrations and growth analyses to determine which physiological and allocational traits underlie variation in growth performance among species. Finally, we examine whether the relative growth performance of pioneers is predicted from their seed mass, a key life-history characteristic thought to correlate with low light survival and inherent RGR (Boot 1996; Cornelissen *et al.* 1996; Rose & Poorter 2002).

Methods

STUDY SITE AND SPECIES

Seeds of 14 species were collected on Barro Colorado Nature Monument (BCNM) in central Panama (9°05' N, 79°45' W; Table 1). Eleven of these species are designated 'pioneers', with relatively small seeds (<40 mg), in most cases a persistent seed bank, high growth and mortality rates, and a strong tendency to recruit into gaps (Condit *et al.* 1996; Dalling *et al.* 1998). Two of these species are in the genus *Trema*, and represent sister species formerly grouped as *Trema micrantha*. These species were recently distinguished on the basis of morphological and molecular data (Silvera *et al.* 2003; Yesson *et al.* 2004). Here we refer to them as two morphospecies, *Trema* 'black' and *Trema* 'brown'. In addition we classify *Cavanillesia platanifolia*, a large-seeded emergent tree species, as a pioneer based on its low juvenile population density and rapid growth rate (Condit *et al.* 1993), and include an 'intermediate' species, *Alseis blackiana*, which requires gaps for seedling establishment but becomes shade-tolerant as a large seedling (Dalling *et al.* 2001). As a reference we also grew seedlings of a true 'shade-tolerant' species, *Tetragastris panamensis*. Data for *Tetragastris* are included in figures and the Appendix, but are excluded from interspecific analyses of allocation patterns and growth performance.

To ensure seedlings were of sufficient size to survive transplantation, and that seedlings used in the experiment were in a similar developmental stage, we initially raised seedlings in germination trays under ≈30% full sun in a screened growing house on BCI for 21–80 days. Seedlings were transferred to pots when they had 3 cm² true-leaf area (except *Cavanillesia* and *Tetragastris*; Table 1). Initial dry mass and leaf area of plants was determined at this time from five representative seedlings. With the exception of *Tetragastris*, all the species used have epigeal germination and foliaceous cotyledons.

Seedlings were individually transplanted into 8 l, 30 cm tall tree pots (Stuewe and Sons Inc., Corvallis, OR, USA) in an open field at Summit Botanic Gardens, 15 km south of BCI. To ensure adequate drainage, pots

Table 1. Species, air-dry seed mass, mean initial seedling dry mass ($n = 5$), growth period and harvest date for 14 species

Species	Seed mass (mg)	Initial dry mass (mg)	Growth period (days)	Harvest date
<i>Alchornea costaricensis</i>	38.5	33.2	86	November 1998
<i>Alseis blackiana</i> *	0.12	9.0	112	September 1997
<i>Apeiba membranacea</i>	14.2	4.6	110	January 1997
<i>Cavanillesia platanifolia</i>	910.0	510.8	56	July 1997
<i>Cecropia insignis</i>	0.5	3.7	86	August 1997
<i>Cordia alliodora</i>	12.5	10.1	56	August 1997
<i>Croton billbergianus</i>	24.0	28.7	73	November 1998
<i>Luehea seemannii</i>	1.9	3.5	96	November 1998
<i>Miconia argentea</i>	0.08	9.7	117	December 1997
<i>Ochroma pyramidale</i>	6.6	6.1	63	September 1996
<i>Trema micrantha</i> 'black'†	3.8	6.9	60	August 1998
<i>Trema micrantha</i> 'brown'†	1.4	4.6	68	November 1997
<i>Tetragastris panamensis</i> ‡	587.0	237.6	110	November 1998
<i>Trichospermum mexicanum</i>	2.0	9.8	87	September 1998

*Intermediate between pioneer and shade-tolerant (Dalling *et al.* 2001).

†Two morphospecies described by Silvera *et al.* (2003).

‡Shade-tolerant.

contained a 30 : 70 mixture of sand and forest soil passed through a 0.5 cm mesh sieve. Plants received natural rainfall, supplemented by hand-watering during dry periods (>2 days without rain). We grew eight seedlings of each species under each of six different light conditions simulating the irradiance conditions in natural canopy gaps on BCI ranging between 25 and 800 m². This represents the full range of gap sizes successfully colonized by pioneer species on BCI (Brokaw 1985, 1987; Dalling *et al.* 1998; Hubbell *et al.* 1999).

LIGHT TREATMENTS

Plants were grown by suspending the tree pots within growing frames aligned in a North–South direction. The sides of each frame were draped with one layer of black plastic neutral shade cloth (rated as 70% light interception), and one layer of a dye-impregnated energy film (Gold Point ST7 SLT-60, Panama City, Panama; R : FR transmittance = 0.15), used to simulate the total radiation and red : far-red light ratio found in forest gaps (R : FR defined as the ratio of quanta at 655–665 nm to quanta at 725–735 nm).

Different light treatments were obtained by varying the width of a central open aperture in the roof of the frame, which exposed seedlings to direct sunlight for varying periods and to differing amounts of diffuse light and light quality. Four replicate benches, with two seedlings of each species grown in each bench, were used to create six treatments. Treatments consisted of apertures in the roof of the bench 5.6, 8.0, 11.3, 16, 22.3 and 31.9 cm wide. The apex of transplanted seedlings was maintained 30 cm beneath the aperture. Assuming a circular gap, and a 30 m tall canopy, these aperture widths would represent gap sizes of 25, 50, 100, 200, 400 and 800 m², and daily irradiance of 4.8, 8.2, 11.8, 14.9, 19.4 and 26.2 mol m⁻² day⁻¹, respectively. Pots remained at ambient temperatures

(28–32 °C) and relative humidity (>80%) throughout the day as air could circulate freely from the base of the frames up through the central aperture. Details of the construction of the frames and of diurnal and annual variation in irradiance and light quality are provided by Dalling *et al.* (1999).

We did not include a closed aperture (shade) treatment in this experiment as the additional heat load on seedlings would not adequately simulate understory conditions. As seedlings grew, they were progressively lowered so that newly expanded seedling leaves were always maintained in the same light environment. Seedlings were grown under these conditions for between 56 and 117 days (Table 1), depending on seedling growth rate. Due to space constraints within the benches different species were grown in different years. To ensure comparability of growing conditions, seedlings were grown only during the wet season (May–early January; Table 1). To minimize tissue loss to herbivores, seedlings were sprayed every 2 weeks with a synthetic pyrethroid insecticide, Fenvalerate (Shell Chemical Co., Painesville, OH, USA). Seedlings were harvested when mean seedling leaf area in the highest light treatments was ≈200 cm².

HARVEST MEASUREMENTS

In the morning of the day that seedlings were harvested (09 : 00–11 : 30 h), seedlings of 12 species were removed from the benches and exposed to saturating light conditions (>800 μmol m⁻² s⁻¹) for ≈10 min before maximum rates of net C assimilation (A_{\max}) were measured. Rates of net CO₂ uptake of one leaf per plant were measured using a portable open gas-exchange system (LI-COR 6400, LI-COR, Lincoln, NE, USA). The environment within the leaf cuvette was controlled to be similar to ambient conditions. Leaf temperatures during the measurements were between 28 and 35 °C.

The leaf area of harvested seedlings was measured using an automated leaf area meter (LI-3000A, LICOR). The mass of foliar, stem and root fractions was measured after drying for 72 h at 70 °C. Foliar N concentrations were determined for a subset of 11 species using an elemental analyser at the University California-Davis (Appendix).

Relative growth rate (RGR, units $\text{mg g}^{-1} \text{day}^{-1}$) was calculated as the slope of the relationship between \ln total biomass and time between transplantation and harvest for each species in each gap treatment. Net assimilation rate (NAR; biomass increment per unit leaf area, units $\text{g m}^{-2} \text{day}^{-1}$) was calculated for individual plants according to the following equation:

$$\text{NAR} = [(W_f - W_i)X(t)] / [(A_f - A_i) / (\ln A_f - \ln A_i)] \quad \text{eqn 1}$$

where W_f and W_i are the final and initial dry mass (g), respectively, A_f and A_i are the final and initial leaf area (m^2), respectively, and t is the duration of the experiment (days). Leaf mass fraction (LMF, leaf mass per unit whole plant mass, units g g^{-1}); stem mass fraction (SMF, stem and petiole mass per unit whole plant mass, units g g^{-1}); root mass fraction (RMF, root mass per unit whole plant mass, units g g^{-1}); leaf area ratio (LAR, leaf area per unit whole plant mass, units $\text{cm}^{-2} \text{g}^{-1}$); and specific leaf area (SLA, leaf area per unit leaf mass, units $\text{cm}^{-2} \text{g}^{-1}$) were calculated from the final harvest data. Photosynthetic potential N-use efficiency (PNUE, net C assimilation per unit leaf N, units $\mu\text{mol CO}_2 \text{mmol}^{-1} \text{N s}^{-1}$) was calculated from maximum net assimilation rate and foliar N concentration measured on the same leaves.

Table 2. *F* values from ANOVA conducted on mean values from two seedlings grown within each of 24 simulated gaps. Six light levels and 14 species are considered as fixed factors. All dependent variables were \ln -transformed prior to analysis. Photosynthesis data were available for a subset of 12 species and nitrogen data for a subset of 10 species (see Appendix)

Attribute	Light	Species	Light \times Species
Biomass	30.9***	21.9***	1.4**
Leaf area	10.1***	11.8***	1.5*
Specific leaf area ($\text{cm}^{-2} \text{g}^{-1}$)	80.0***	76.1***	1.2
Leaf area ratio ($\text{cm}^{-2} \text{g}^{-1}$)	71.0***	43.5***	1.3
Relative growth rate ($\text{mg g}^{-1} \text{day}^{-1}$)	24.7***	124.3***	1.3
Net assimilation rate ($\text{g m}^{-2} \text{day}^{-1}$)	46.5***	66.4***	2.0***
Root mass fraction (g g^{-1})	9.2***	22.9***	1.7*
Stem mass fraction (g g^{-1})	11.6***	76.9***	1.9***
Leaf mass fraction (g g^{-1})	1.8	27.2***	2.5***
$N_{(\text{mass})}$	6.5***	60.5***	1.5*
$N_{(\text{area})}$	17.1***	26.7***	1.4
$A_{\text{max}(\text{area})}$	48.8***	45.7***	1.8**
$A_{\text{max}(\text{mass})}$	3.9**	55.8***	1.8**
PNUE ($\mu\text{mol CO}_2 \text{mmol}^{-1} \text{N s}^{-1}$)†	4.7**	19.3***	2.1**

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

†PNUE, photosynthetic potential N-use efficiency.

DATA ANALYSIS

Patterns of variation among species and simulated gap sizes in seedling allocation pattern and physiology, and their contribution to growth, were explored using regression and ANOVA models. Analyses were performed on the means of the two seedlings of each species grown on each replicate bench ($n = 4$ per species per treatment). All dependent variables were \ln -transformed prior to analysis to evaluate whether all species show a proportional response to irradiance (Poorter & Garnier 1996; Poorter 1999). Data were analysed as a fixed-factor rather than split-plot ANOVA because both seedlings planted in some benches died before harvest, resulting in an unbalanced design. Here we assume that variation in growth conditions among benches is small compared to variation among gap sizes, as has been found in analyses restricted to smaller subsets of these species (Dalling *et al.* 1999, 2001; Silveira *et al.* 2003). Multiple regression was used to identify which traits contributed significantly to among species variation in relative growth rate. Condition indices were used to remove predictor variables from regression models that contributed strongly to collinearity (Belsley *et al.* 1980). Individual species' responses to variation in light availability were analysed as regressions of dependent variables against \log (simulated gap size). The slope of these regressions was used as an index of plasticity of response to gap size.

Results

With the exception of LMF, all seedling attributes measured responded to variation in simulated gap size (Table 2). The most responsive variables were SLA, followed by LAR, $A_{\text{max}(\text{area})}$ and NAR, reflecting a strong plastic response of leaf morphology to irradiance. Species also varied significantly for all attributes measured, and in many cases, including RGR, inherent differences among species accounted for more variation than did light responses (Table 2). In contrast, interactions between species and simulated gap size were not significant for SLA, LAR and RGR, indicating that rank growth performance was maintained across simulated gap treatments.

VARIATION IN GROWTH RATES AMONG PIONEERS

Maximum relative growth rates (RGR) varied eight-fold among species, from a minimum of $10.3 \text{ mg g}^{-1} \text{day}^{-1}$ for the shade-tolerant species *Tetragastris* and $13 \text{ mg g}^{-1} \text{day}^{-1}$ for *Cavanillesia* in the smallest simulated gaps, to $83.6 \text{ mg g}^{-1} \text{day}^{-1}$ for the 'brown' morphospecies of *Trema* in the largest simulated gaps (Fig. 1; Appendix). However, while a few pioneers had very fast RGRs, many species had slower but similar rates; for six species maximum RGR varied by $\leq 7 \text{ mg g}^{-1} \text{day}^{-1}$ (Appendix; Fig. 1). Although gap size

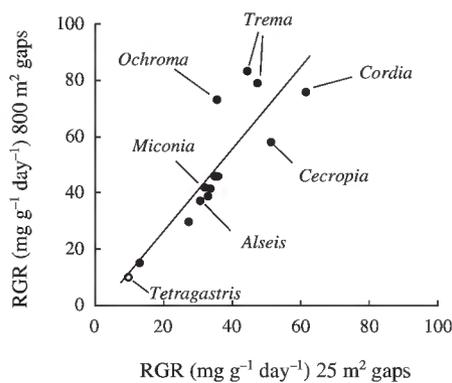


Fig. 1. Correlation of species' mean relative growth rate (RGR) measured in the largest (800 m²) simulated gaps against mean RGR measured in the smallest (25 m²) simulated gaps.

did influence RGR for all species combined (Table 2), not all species responded to variations in light availability (Fig. 2). We found a significant positive effect of $\log(\text{simulated gap size})$ on RGR for only nine of 14 species (Appendix). In general, faster-growing species showed greater plasticity of RGR in response to light, indicated by a positive correlation (Pearson's $r = 0.59$, $P < 0.05$) between maximum RGR and the slope of $\ln(\text{RGR})$ vs $\ln(\text{gap size})$.

Overall, the relative growth performance of species was not dependent on gap size. Species with high RGR in the largest simulated gaps also maintained high RGR in the smallest simulated gaps (Pearson's $r = 0.83$, $P < 0.001$; Fig. 1). Cross-overs in rank growth rate between gap sizes were therefore rare. Some exceptions, however, were found for the fastest-growing species.

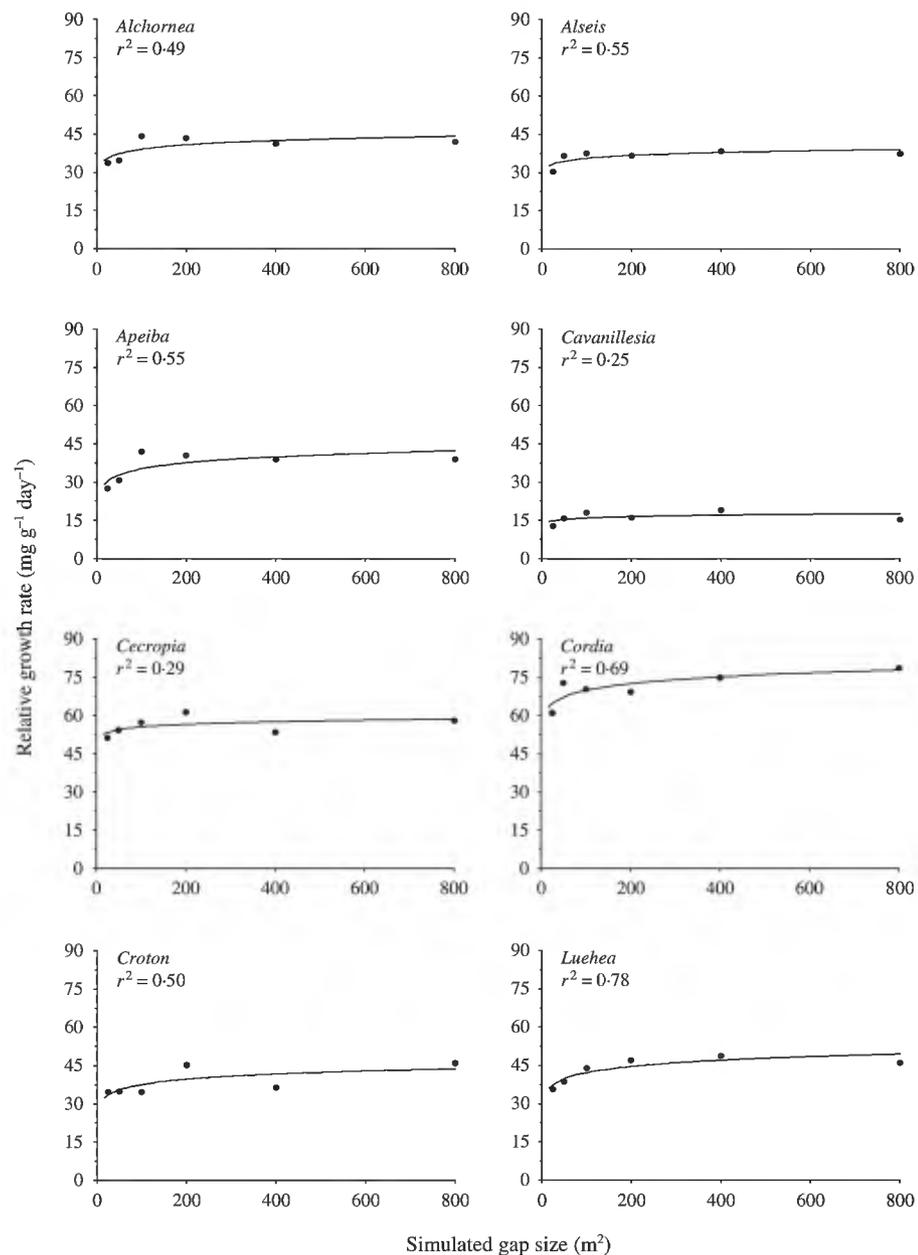


Fig. 2. Regressions of species' mean relative growth rate vs $\log(\text{simulated gap size})$.

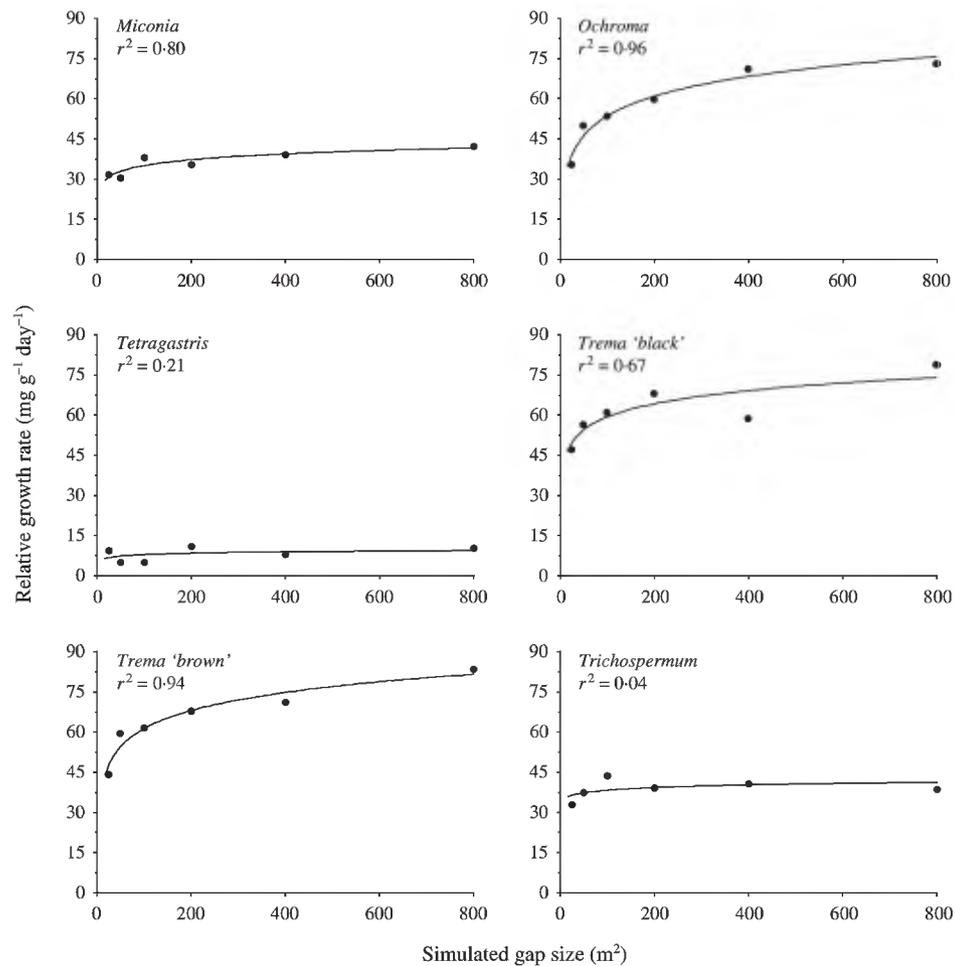
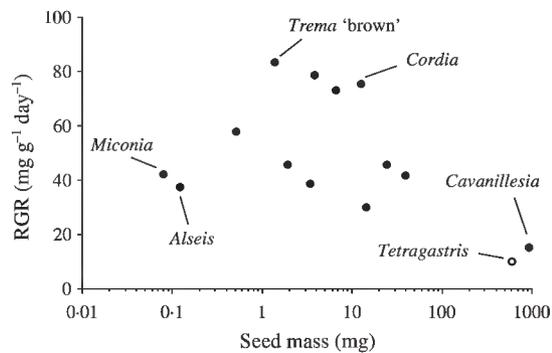


Fig. 2. Continued

Fig. 3. Regression of species' mean relative growth rate (RGR) in simulated 800 m^2 gaps against seed mass (log scale).

Cecropia and *Cordia* grew more quickly than *Ochroma* and *Trema* in the smallest gaps, whereas the two *Trema* morphospecies (which had very similar RGR) and *Ochroma* grew most quickly in the largest gaps (Fig. 1). Relative growth rate was independent of seed size. Both the largest-seeded species, *Cavanillesia* and *Tetragastris*, and the smallest seeded species, *Alseis* and *Miconia*, had comparatively low RGR (Fig. 3).

VARIATION IN ALLOCATION IN RESPONSE TO LIGHT

Most variation in patterns of C allocation among species and light conditions was observed in investment in support tissues. The biomass fraction allocated to leaves (LMF) did not differ significantly among the simulated gap-size treatments, but did vary significantly among species (Table 2; mean = 0.57, SD = 0.06) and showed a slight tendency to decrease with seed mass for all gap sizes combined ($r^2 = 0.28$, $F = 4.2$, $P = 0.07$). The SMF and RMF, however, did vary with simulated gap size (Table 2). In general, investment was made in stem biomass in small simulated gaps at the cost of investment of root biomass representing an elongation response to low light levels. The degree and direction to which SMF varied in response to irradiance, however, was species-specific (Appendix). The steepest declines in SMF with increasing irradiance were recorded for two species with among the highest and lowest RGR (*Ochroma* and *Miconia*). For two slower-growing species, *Alseis* and *Cavanillesia*, SMF increased significantly with irradiance. Mean SMF for all gap sizes combined was positively correlated with seed mass ($r^2 = 0.56$, $F = 14.0$, $P = 0.003$), and was significant at

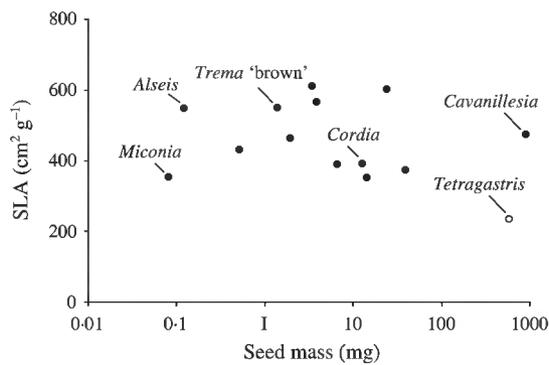


Fig. 4. Regression of mean specific leaf area (SLA) in 25 m² gaps with seed mass (log scale).

all except the smallest simulated gap sizes. The RMF of most species did increase significantly with gap size (Appendix; Table 2), from an overall mean of 0.19 (SD = 0.05) in the smallest simulated gap size to 0.23 (SD = 0.07) in the largest gap. However, variation in RMF was not related to seed mass ($r^2 = 0.10$, $F = 1.3$, NS).

In contrast to LMF, species varied more strongly in SLA (Table 2), ranging from 611 cm² g⁻¹ for *Trichospermum* in the smallest simulated gaps to 224 cm² g⁻¹ for *Cecropia* in the largest simulated gaps. Regressions of SLA against log(simulated gap size) were significant for every species including the shade-tolerant *Tetragastris* (Appendix). For 11 of 14 species, coefficients of determination were >0.5 indicating that SLA can be quite a fine discriminator of light availability. Despite this wide variation, SLA had only a weak positive effect on RGR at any given gap size ($r^2 < 0.14$, $P > 0.01$, all treatments). Plasticity in SLA was not correlated with RGR in any gap size ($r^2 < 0.09$, $P > 0.05$), and was not related to seed mass (e.g. 800 m² simulated gaps, $r^2 = 0.09$; 25 m² simulated gaps, $r^2 = 0.01$; Fig. 4).

For most species, variation in leaf area scaled to whole-plant mass (LAR) largely reflected variation in SLA, because proportional allocation to leaf mass tended to vary little across simulated gap sizes. As with SLA, LAR contributed relatively little to variation in RGR among species (e.g. both smallest and largest gap size, $r^2 = 0.18$, $F = 11.2$, $P < 0.001$; Fig. 5a). Variation in RGR among species, however, was strongly affected by differences in NAR (the efficiency with which leaf area is used to assimilate C). The NAR reflects both allocational and physiological responses to light, and had the largest effect on RGR in large gaps (smallest simulated gaps, $r^2 = 0.58$, $F = 16.4$, $P < 0.001$; largest simulated gaps, $r^2 = 0.74$, $F = 32.8$, $P < 0.001$; Fig. 5b).

CARBON ASSIMILATION AND NITROGEN-USE EFFICIENCY

The maximum rate of net C assimilation (A_{\max}) increased significantly with simulated gap size for most species when expressed on a per area basis, but only for

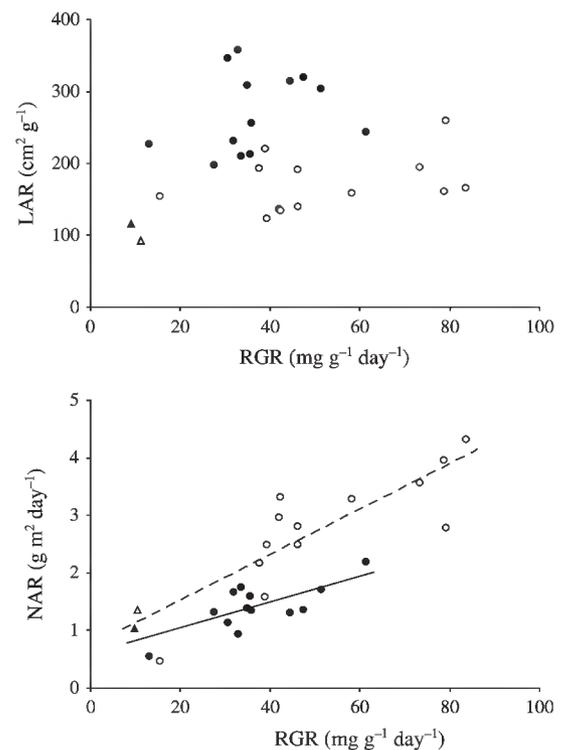


Fig. 5. Correlations of mean relative growth rate (RGR) with (a) leaf area ratio (LAR) and (b) net assimilation rate (NAR) for 14 species in 25 m² (●) and 800 m² (○) simulated gaps. Triangular symbols represent *Tetragastris*.

four (mostly fast-growing) species on a per mass basis (Appendix). Within-species variation in area-based assimilation rates could therefore be explained largely by variation in SLA. Interspecific variation in $A_{\max(\text{area})}$ or $A_{\max(\text{mass})}$ was weakly positively correlated to RGR, but was significant only for simulated gap sizes ≥ 100 m² ($r^2 = 0.1-0.26$, $P < 0.05$), corresponding to environments with more prolonged duration of saturating light levels. Similarly, NAR was only significantly positively correlated with $A_{\max(\text{area})}$ in the largest simulated gap size ($r^2 = 0.25$, $F = 13.4$, $P < 0.05$; $r^2 = 0.37$, $F = 5.8$, $P < 0.05$). $A_{\max(\text{mass})}$ was unrelated to NAR.

Foliar N concentration was quite variable among species (range 2.2–4.7%; Appendix), but did not vary consistently with gap size. Foliar N concentration decreased significantly with increasing gap size in the intermediate species *Alseis*, and increased with gap size in the fast-growing pioneers *Cordia* and *Ochroma* (Appendix). Within-species correlations of foliar N concentration with $A_{\max(\text{mass})}$ were not significant for any species, but positive correlations of foliar N per unit leaf area (N_{area}) and $A_{\max(\text{area})}$ were found in six of 10 species. Foliar N concentration was more strongly correlated with interspecific variation in C assimilation rates ($A_{\max(\text{mass})}$) in the larger simulated gaps (smallest gaps, $r^2 = 0.04$, $F = 1.2$, $P > 0.05$; largest gaps, $r^2 = 0.27$, $F = 11.4$, $P < 0.01$). In contrast, foliar N concentration was not correlated with RGR in the largest gaps, and was only weakly positively correlated with RGR in the smallest simulated gap size ($r^2 = 0.30$,

$F = 44.9$, $P < 0.001$). As a consequence of wide variation in foliar N concentration and C assimilation rates, PNUE also varied strongly among species (Table 2), from $0.08 \mu\text{mol CO}_2 \text{ mmol}^{-1} \text{ N s}^{-1}$ for *Alseis* in small simulated gaps to $0.27 \mu\text{mol CO}_2 \text{ mmol}^{-1} \text{ N s}^{-1}$ in *Ochroma* in the largest gap size. The PNUE was only very weakly (and negatively) correlated with RGR in small simulated gaps (smallest gaps, $r^2 = 0.17$, $F = 5.4$, $P < 0.05$), and was unrelated to RGR in larger gap sizes. Species mean PNUE in the largest gaps was significantly positively correlated with the slope of the $A_{\text{max(areal)}} - N_{\text{areal}}$ relationship ($r^2 = 0.55$, $F = 9.67$, $P < 0.05$).

Multiple regression analysis of seedling traits further highlighted the codependencies among LAR, NAR, SLA and $A_{\text{max(areal)}}$ as predictors of RGR. However, NAR and foliar N concentration alone explained a large component of interspecific variation in RGR ($r^2 = 0.82\text{--}0.89$ for different simulated gap sizes).

Discussion

VARIATION IN GROWTH PERFORMANCE AMONG PIONEER SPECIES

Brokaw's (1987) observation that co-occurring pioneer species differ in their minimum gap size requirements for successful recruitment suggested that resource partitioning among species might result from changing competitive hierarchies along a gradient of light availability. Here we tested the hypothesis that a group of coexisting pioneer species differ in the light conditions they require for optimal growth within the range of gap sizes under which they are observed to recruit in the field (Dalling *et al.* 1998). Two results, relevant to the mechanism of species coexistence among these species, are evident from this study. First, shifts among species in rank growth rate with light availability are relatively small and are restricted to the fastest-growing species. Second, many of the most abundant pioneers have very similar RGRs despite large differences in seed size and SLA (Fig. 1).

This first result is in general agreement with recent reviews of variation in seedling growth rate in response to light (Veneklaas & Poorter 1998; Sack & Grubb 2001). These report generally strong positive correlations in seedling growth between low and high light for studies including both pioneer and shade-tolerant species (Ellison *et al.* 1993; Kitajima 1994; Osunkoya *et al.* 1994; Poorter 1999; Kitajima 2002). One caveat to our study, however, is that growth responses to high irradiance conditions were rather small (Fig. 2), with little increase in growth rate recorded for most species in simulated gap sizes above 200 m^2 (33% full sun). Limited response to high irradiance may indicate that seedling growth was constrained by N availability (Latham 1992; Grubb *et al.* 1996, 1997), resulting in increased photoinhibition (Ferrar & Osmond 1986).

An exception in our study was the cross-over in growth performance seen for the very fastest-growing

pioneers. We found that *Cecropia* grew more quickly than the two *Trema* morphospecies and *Ochroma* in the smallest simulated gap sizes, but more slowly in the largest gaps (Fig. 1). This result is consistent with a recent study that showed higher growth rates of transplanted *Cecropia* seedlings than *Trema* ('black') or *Miconia* seedlings in artificially created gaps with light conditions similar to the smaller simulated gaps used in this study (Pearson *et al.* 2003).

Cecropia aside, similarities in rank growth performance across a light gradient suggest that gap partitioning may be driven primarily by variation in growth-dependent seedling mortality rates. A negative relationship between survival in low light (2%) and high light RGR is evident when both shade-tolerant and pioneer species are grown together (Kitajima 1994; Kobe 1999), but also appears to hold specifically for pioneers under much higher light conditions. In two studies conducted at BCNM, Dalling *et al.* (1999) and Dalling & Hubbell (2002) found a positive correlation between relative height growth rate and mortality rate for seedlings of 14 pioneer species growing in both natural and artificially created gaps.

Although covariation in growth and mortality rates may play a role in the coexistence of pioneers, our results indicate that other mechanisms must be important. Many of the 12 pioneer species had very similar RGRs: for six pioneers (*Alchornea*, *Apeiba*, *Croton*, *Luehea*, *Miconia* and *Trichospermum*) maximum RGR varied by $<7 \text{ mg g}^{-1} \text{ day}^{-1}$ (Appendix). These species are also among the most common pioneers in the old-growth forest, accounting for 83% of the 3310 stems $>1 \text{ cm d.b.h.}$ of the 12 pioneer species present in the 50 ha Forest Dynamics Plot on BCI (Condit *et al.* 1996). Assuming that the similarity in RGR among these species is retained through early ontogeny, then the differences in absolute size among recruiting individuals of these species are likely to be mostly determined by variation in initial seed mass and timing of seedling emergence.

PHYSIOLOGICAL AND ALLOCATIONAL RESPONSES TO VARIATION IN LIGHT AVAILABILITY

We show wide variation among pioneers in the physiological and allocational traits underlying growth. Previous studies have indicated that RGR at high light intensities tends to scale with dry mass gain per unit leaf area (NAR), while leaf area per unit whole plant dry mass (LAR) is a stronger determinant of RGR under low light conditions [reviewed by Veneklaas & Poorter (1998), but see Bloor & Grubb (2003) for an exception at very low irradiance]. Here we found that NAR, and not LAR, was correlated with RGR under all simulated gap sizes, with the strongest relationship for the largest gaps. This is consistent with results of growth analyses of 15 tropical tree seedlings grown under a range of light conditions in Bolivia, which

showed that the switch in importance between LAR and NAR occurred at 10–15% daylight (Poorter 1999).

Despite the nonsignificant effect of LAR on RGR, the major component of LAR (leaf area per unit mass, SLA) showed substantial variation among species, with almost twofold variation among the pioneer species in both small and large simulated gaps (Appendix). Within species, SLA was remarkably sensitive to variation in light availability. For 11 out of 14 species, coefficients of determination for regressions of SLA vs $\log(\text{gap size})$ were >0.5 (Appendix). Fine morphological discrimination of light availability suggests that SLA might have some utility as a rapid assay of light regimes experienced by similarly sized seedlings and saplings in the field, although effects of nutrient supply and ontogeny on SLA require more exploration (Van de Vijver *et al.* 1993, Veneklaas & Poorter 1998; Meziane & Shipley 1999; Thomas & Bazzaz 1999).

Among-species variation in NAR is, in part, determined by variation in net C assimilation rates (A_{\max}). In general we found that species with the highest $A_{\max(\text{area})}$ also had the highest RGR values, but only in the larger simulated gaps where NAR was a stronger determinant of RGR, and where light levels are potentially saturating for photosynthesis for several hours per day (Dalling *et al.* 1999). A strong effect of NAR on RGR leads to the expectation that A_{\max} would also be strongly correlated with RGR (Walters *et al.* 1993; Kitajima 1994), but here the relationship was surprisingly weak. Likewise, high assimilation rates tend to be associated with large investments in N in the photosynthetic apparatus (Field & Mooney 1986). However, relationships here between foliar N and photosynthetic capacity were poor. Species with high foliar N concentrations had the highest A_{\max} values in the largest gap sizes, although this relationship was apparent only when values were expressed on a per area basis, reflecting intraspecific variation in SLA. Within species we found no relationship between foliar N concentration and $A_{\max(\text{mass})}$, and only a weak relationship for all species combined. This is in contrast to the strong relationships found for seedlings of secondary successional species found in a more N-limited forest in the Rio Negro region of Amazonia (Reich *et al.* 1994).

Among species, foliar N concentration was positively correlated with RGR, although only in the smaller simulated gaps. This reflects greater PNUE in large gaps of some, but not all, fast-growing species, notably *Cordia* and *Ochroma* (Appendix). The PNUE in large gaps was correlated with the slope of the A_{\max} –N relationship, indicating that high PNUE among these species is achieved by high N investment to photosynthetic structures (Reich *et al.* 1994; Vincent 2001).

LIFE HISTORY AS A DETERMINANT OF GROWTH RESPONSE

To date, comparative analyses of seedling growth performance for tropical plants have used species

spanning a wide range of shade tolerance (Kitajima 1994; Osunkoya *et al.* 1994; Huante & Rincón 1998; Agyeman *et al.* 1999; Poorter 1999; but see Bloor & Grubb 2003). Correlational analyses across these species groupings have identified two key traits, SLA and seed mass, that appear to covary with relative growth rate. However, interpreting variation in seedling growth performance as being primarily influenced by one or a few underlying morphological or allocational traits may be misleading. Variation in performance is a consequence of the total life history of a plant, determined by many interacting traits that collectively describe the phenotypic response to variation in resource availability.

Although SLA has been found to correlate with RGR in several previous studies (Osunkoya *et al.* 1994; Huante & Rincón 1998; Poorter 1999), we found no evidence for an effect of SLA on RGR under the relatively high light conditions used in this experiment. Indeed, two of the fastest-growing pioneers had among the highest SLA (*Trema* ‘black’) and lowest SLA (*Ochroma*) of the species investigated. Similarly, Bloor & Grubb (2003) also failed to find a significant correlation between SLA and RGR when comparing 15 shade-tolerant species in both low (0.8% daylight) and high light (10% daylight). Significant correlations between SLA and RGR may therefore largely reflect the difference between slow-growing, shade-tolerant species with low and largely invariant SLA, and fast-growing pioneers with relatively high SLA. The contrast in SLA response to variation in irradiance is perhaps the most striking difference between these species groups. For shade-tolerant species, low SLA associated with tough, long-lived, herbivore-resistant leaves confers a survival advantage under low light (Reich *et al.* 1991; Kitajima 1994), whereas the plastic response of pioneers is to increase SLA in low light, thereby increasing the efficiency of light capture (Loach 1970).

Likewise, we caution against interpreting variation in RGR as being coupled to seed mass, despite a few strong correlations reported in the literature (Shipley & Peters 1990; Reich *et al.* 1998). Large seed mass has been suggested to constrain RGR during early seedling growth. This may arise if some seed reserves remain in storage rather than immediately being used in tissue construction (Harms & Dalling 1997), or if seedlings allocate a larger proportion of their biomass to support tissue (Walters *et al.* 1993) or producing cotyledons and initial leaves with lower SLA, with consequently lowered assimilation rates per unit tissue dry mass (Grubb 1998). However, for pioneer species which typically have foliaceous cotyledons, all seed reserves are immediately mobilized as seedlings emerge. Larger-seeded pioneers may have higher initial resource allocation to support tissue; however, at harvest time we found only a small and marginally significant effect of seed mass on the fraction of biomass allocated to leaves.

We found no effect of seed mass on RGR in this study (Fig. 3), although there is a trend towards a

negative relationship when the smallest-seeded species with low RGR (*Alseis* and *Miconia*) are excluded. We classify *Alseis* as being intermediate in its life history between pioneer and shade-tolerant species, with seed germination and seedling allocation patterns typical of pioneers, but with a low shade mortality rate of established plants (Dalling *et al.* 2001). *Miconia* is one of the most abundant pioneers at our study site and is capable of successful recruitment in relatively small gaps (Brokaw 1987; Pearson *et al.* 2003). The fastest-growing pioneers, *Cordia*, *Ochroma* and *Trema*, all had seed mass >1 mg. We suspect that extremely small seed mass may be disadvantageous for fast-growing species successful in high-irradiance microsites where very small seedlings with superficial root systems are particularly susceptible to rapid drying of surface soil layers during short, dry spells (Engelbrecht *et al.* 2001).

In conclusion, our analysis conducted within one functional group of tree species finds little evidence for direct niche partitioning along a gradient of gap sizes according to variation in growth rate. Only the fastest-growing pioneer species showed evidence for switched rankings in growth performance across the gradient of gap sizes. Furthermore, a trade-off between growth in high light and survival in low light is also unable to account for coexistence of the most abundant pioneers in this community. Interspecific differences in RGR observed over a range of simulated gap sizes for these species are likely to be masked by individual variation in growth response (Clark *et al.* 2003), and by variation in initial absolute seedling size and the timing of seedling emergence.

This study also fails to support several proposed relationships between growth performance and underlying traits. Although simple classifications of species into functional groups based on seed mass or morphology may provide some very coarse predictions, we are much less hopeful than Rose & Poorter (2004) that seed mass data will provide a more general tool for predicting plant responses to variation in the light environment.

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Supplementary material

The following material is available from <http://www.blackwellpublishing.com/products/journals/suppmat/FEC/FEC868/FEC868sm.htm>

Appendix S1. Mean seedling growth, allocation, maximum photosynthetic rates, foliar nitrogen contents and potential photosynthetic N-use efficiency (PNUE) in six simulated gap sizes (± 1 SE). Regression coefficients, *F* and *P* values are given for linear regressions of dependent variables vs log(simulated gap size).

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