

Growth responses of seedlings of two neotropical pioneer species to simulated forest gap environments

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ABSTRACT. Traditional shade house experiments that expose plants to relatively uniform irradiance and light quality are inadequate to characterize the morphological, allocational and physiological plasticity that seedlings show to different gap environments. Here the design of a pot experiment is described that simulates the daily time course of irradiance and light quality in idealized gaps of six different sizes. Differences in response to gap size are illustrated using data from two pioneer species, *Ochroma pyramidale*, which recruits exclusively in large gaps and clearings, and *Luehea seemannii*, which colonizes small branchfall gaps as well as large gaps. *Ochroma* outperformed *Luehea* in relative growth rate in all except the smallest simulated gap size. *Ochroma*'s superior performance in the larger gaps could be attributed to a larger proportional investment in leaf biomass (i.e. a higher leaf area ratio, LAR), and higher photosynthetic rates both on a leaf area and leaf mass basis. In the smallest simulated gaps LAR was not significantly different between the species, but *Ochroma* maintained a higher net assimilation rate. These results fail to support the suggestion that gap partitioning among pioneer species arises directly from morphological and biochemical specialization to particular gap light environments. Instead, it is suggested that partitioning may result from a trade-off between seedling growth and mortality determined by species allocational patterns and mediated by interactions with herbivores and pathogens.

KEY WORDS: allocation patterns, gap partitioning, growth analysis, light quality, *Luehea*, *Ochroma*, pioneer, simulated gap, tropical rain forest

INTRODUCTION

A common explanation for the coexistence of apparently ecologically similar plant species has been the fine-scale differentiation of requirements for light

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and other resources for successful seedling establishment and early growth (Denslow 1980, 1987; Grubb 1977). Although evidence for this view remains equivocal for shade-tolerant tree species (Ashton 1995, Brokaw & Scheiner 1989, Brown & Whitmore 1992, Hubbell *et al.* 1999, Welden *et al.* 1991), convincing evidence exists of different gap size requirements among pioneer trees (Brokaw 1987) that suggests that some resource partitioning may occur.

However, little progress has been made in understanding the mechanistic basis for such partitioning. Comparative studies of seedling characteristics in natural gaps are hampered by problems of gap definition, and of extreme spatial and temporal heterogeneity in resource availability within gaps (Brokaw 1982, Brown 1993, Popma *et al.* 1988), as well as factors such as limited seed dispersal (Dalling *et al.* 1998) and variation in substrate conditions (Brandani *et al.* 1988, Riera 1985) that can also influence local distribution of seedlings. An alternative approach is to examine the response of seedlings to variation in resource availability using pot experiments (e.g. Fetcher *et al.* 1983, Huante *et al.* 1995, Strauss-Debenedetti & Bazzaz 1991).

Although light availability is likely to be the resource that shows the most variation across gaps of different sizes (Brown 1993, Grace 1991, Vitousek & Denslow 1986), traditional shade-house experiments in which plants are exposed to relatively constant light environments are unlikely to capture this variation in a realistic way. Natural gaps in forest receive prolonged periods of mostly diffuse radiation while the sun is obscured by canopy, and periods of direct radiation when the sun is above the gap. The duration of this pulse of direct radiation is dependent upon many factors (gap size, geometry, orientation, latitude, season, slope and aspect of terrain, cloudiness, atmospheric turbidity and the height of the surrounding canopy). The effects of pulses of direct radiation on seedling growth have been shown clearly in temperate (Wayne & Bazzaz 1993) and tropical forest species (Watling *et al.* 1997). In both experiments, seedlings received treatments of equal total daily irradiance either at a constant flux in shade houses, or in simulated gaps with periods of saturating light during the day. Both sets of species showed differences in morphological and allocational patterns between the treatments.

Shade houses constructed out of neutral shade filters (e.g. plastic or wire mesh) may also fail to capture morphological and allocational responses attributable to variation in light quality or spectral composition (Schmitt & Wulff 1993). Sunlight has a relatively uniform spectral distribution of quanta from 400–800 nm, whereas shade light that has passed through a forest canopy is depleted of quanta in the red and blue wavelengths, reducing the red:far red light ratio (measured at 655–665 nm and 725–735 nm respectively) from *c.* 1.2 under open sky to *c.* 0.2 under dense shade (Lee 1987, Stoutjestijk 1972). Seedlings, particularly of pioneer or early successional species, may be quite sensitive to variation in R:FR, responding through changes in internode elongation, biomass allocation to shoots and roots, specific leaf area, and consequently,

relative growth rates (Kwesiga & Grace 1986, Morgan & Smith 1979). Indeed, Lee *et al.* (1996) found that variation in growth and morphology of seedlings of the Asian tropical pioneer tree *Endospermum malaccense* M. A. could be attributed primarily to variation in R : FR (0.23 and 1.25) rather than to variation in irradiance (3–11% full sun).

Here, we describe the design of a pot experiment that simulates both the daily variation in irradiance and light quality of idealized forest gaps of different sizes. We illustrate some of the patterns of morphological and physiological plasticity of seedlings grown under these conditions by reporting results for the growth analysis of *Ochroma pyramidale*, a pioneer species restricted to large gaps and clearings in central Panama, and for *Luehea seemannii*, a pioneer capable of recruiting in small treefall and branchfall gaps.

METHODS

Plant material and study site

The study was carried out in an open field at the Summit Botanical Gardens in central Panama (9°05'N, 79°45'W). Seeds of the two species studied were collected on nearby Barro Colorado Island (BCI). *Ochroma pyramidale* (Cav. ex Lam.) Urban, is a very fast growing pioneer tree, common in large disturbances, and in young secondary forest, but which rarely colonizes treefall gaps in old forest (Croat 1978, Dalling *et al.* 1998). Wind-dispersed seeds (6.6 mg) are produced year-round. *Luehea seemannii* Tr. & Planch., is a pioneer tree capable of colonizing gaps caused by smaller disturbances, and seedlings and saplings are frequently found in treefall or large branchfall gaps in old growth forest (Croat 1978, Dalling *et al.* 1998). Wind-dispersed seeds (1.9 mg) are released in the late dry season (March to May).

Construction of simulated gaps

Six different light environments simulating gaps of different sizes were created by suspending tree pots within growing frames aligned in a north–south direction (Figures 1 and 2). The frames were constructed out of lightweight steel girders bolted together to support two vertical sheets of steel mesh. Eight-litre capacity, 30-cm tall tree pots (Stuewe Sons Inc., Corvallis, Oregon) were sandwiched between these mesh sheets and supported at adjustable heights using sections of steel reinforcing rod threaded between the mesh. The frames 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; R : FR transmittance = 0.15) used both to reduce total irradiance incident on the plants and to reduce the red : far red light ratio to simulate transmission through a dense forest canopy. Different light treatments were created by varying the width of a central open aperture in the roof of the frame (Figure 2) which exposed seedlings to variable periods of direct sunlight, differing intensities of diffuse light and variable light quality. Plant pots



Figure 1. The array of simulated gaps in place in Summit Botanical Gardens, Republic of Panama.

remained at ambient temperatures (28–32 °C) and relative humidity (80–90%) throughout the day, as air could circulate freely from the base of the benches up through the central aperture (Figure 2).

Light treatments

Four replicate benches, with two seedlings of each species grown within each bench, were used for each of six light treatments consisting of bench roof apertures: 5.6, 8.0, 11.3, 16.0, 22.3 and 31.9 cm. Benches were separated 3 m apart and arranged in a fully randomized array. Assuming a circular gap, and a 30-m tall canopy, we calculate that these aperture widths simulated 25, 50, 100, 200, 400 and 800 m² idealized gap sizes respectively. We did not include a closed aperture treatment in this experiment as the additional heat load on seedlings would not adequately simulate understorey conditions. Furthermore, these treatments represent the full range of sizes of natural gaps colonized by seedlings of pioneer species on BCI (Brokaw 1982, Dalling *et al.* 1998). To allow adequate drainage, pots contained a 30:70 mix of sand and forest soil passed through a sieve of 0.5-cm mesh. Plants received natural rainfall, supplemented by hand-watering during dry periods (> 2 d without rain).

Light measurements and R:FR ratio within the benches were measured on a sunny day in the early wet season in May 1998. These values are representative for the experiment because solar azimuth, latitude and photosynthetically

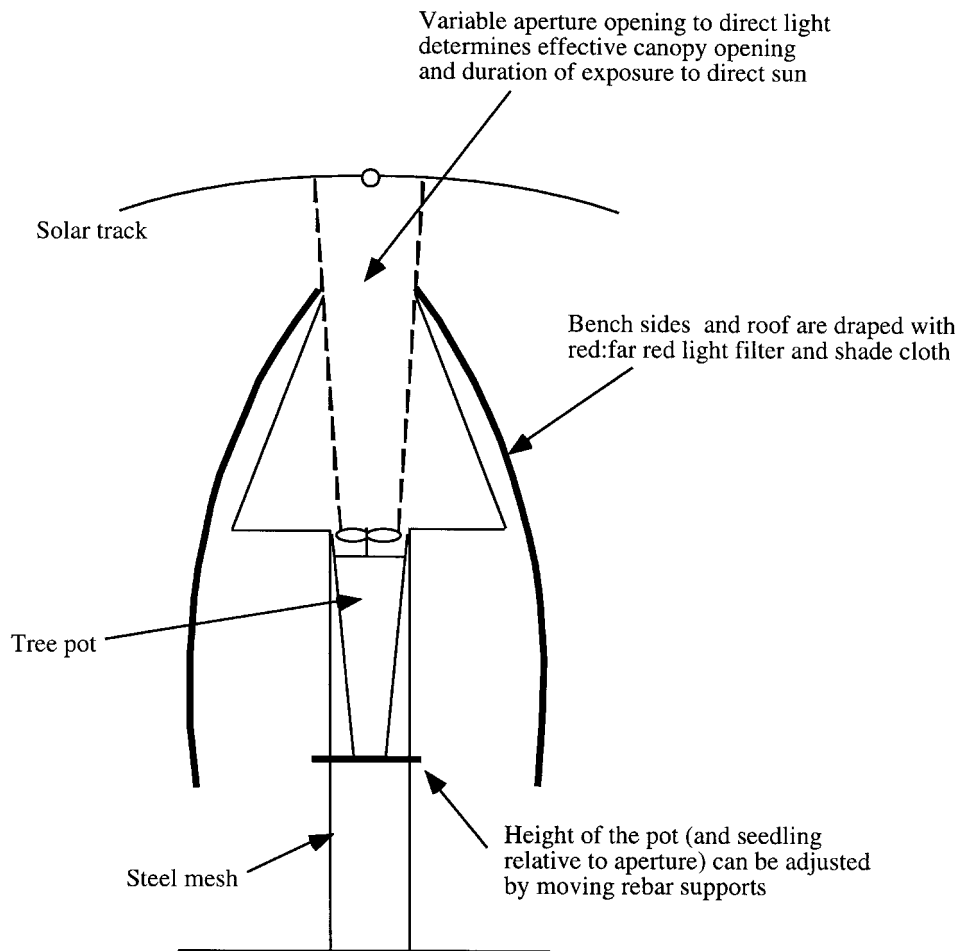


Figure 2. Schematic representation of the design of simulated gaps.

active radiation (PAR) do not vary markedly through the wet season (May–November) when measurements were made (Table 1). Photon flux density (PFD) was measured using a LI-COR quantum sensor (LI-COR Inc., Lincoln, NE, USA). Measurements were made at one randomly chosen bench for each light treatment at 10-min intervals in the early morning and late afternoon, and at 3–5-min intervals during the middle of the day while the plants were

Table 1. Solar altitude at 12h00, and solar azimuth at 08h00 at Summit Botanic Gardens, and mean monthly solar radiation (1983–1998; $GJ\ m^{-2}\ d^{-1}$) measured above the canopy at nearby Barro Colorado Island (reprinted from Paton 1998).

Month	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Altitude (°)	60.9	69.8	80.6	87.4	78.9	75.5	78.6	87.3	80.8	69.3	60.6	57.6
Azimuth (°)	63.0	72.4	84.4	98.1	108.2	112.0	108.5	98.4	84.6	71.9	62.7	59.7
Radiation	18.1	19.6	21.8	19.5	15.4	13.7	14.0	14.4	14.2	13.3	12.3	14.8

exposed to direct illumination. We also checked for consistency between benches in the same light treatment by comparing proportional light transmittance (calculated from PFD measurements made above and within the bench) several times during the day. The R:FR ratio within the benches was measured periodically through the day using a Skye Instruments SKR 110 R:FR quantum sensor (Skye Instruments, Powys, Wales).

Growth analyses

Seeds of *Ochroma* and *Luehea* were germinated in a growing house under 50% full sun, and were transplanted into individual pots 1 and 3 wk after seedling emergence when they had total dry masses of 7.0 and 3.5 mg respectively. As seedlings grew, the pots were lowered progressively deeper into the bench so as to ensure that newly expanded seedling leaves were always maintained at an equal distance from the aperture (Figure 2). To minimize tissue loss to herbivores, seedlings were sprayed every 2 wk with Fenvalerate insecticide. Seedlings were grown under these conditions for 63 d (*Ochroma*) and 96 d (*Luehea*) before harvesting in November and December 1996. The harvest date was determined by the time taken for the first seedlings of each species to develop *c.* 200 cm² of leaf area. The leaf area of harvested seedlings was measured using an automated leaf area meter (LI-3000A, attached to a transparent belt conveyer LI-3050A, LI-COR Inc., Lincoln, NE, USA) and the mass of foliar, shoot and root fractions was measured after drying for 72 h at 70 °C. Relative growth rates were calculated as the difference in log_e seedling dry mass between transplanting and harvest.

Photosynthesis measurements

During the morning of the day that seedlings were harvested (09h00–11h30), seedlings were exposed to direct sunlight (900–1700 μmol m⁻² s⁻¹) for *c.* 30 min before maximum rates of photosynthesis were measured. Net photosynthesis of one leaf per plant was measured using a portable open gas exchange system (LI-COR 6400, LI-COR Inc., 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.

Statistical analysis

Effects of gap size and species on seedling size, allocational patterns, growth and photosynthesis were analysed using a split-plot analysis of variance with 'species' effect nested within the plot term (Multivariate General Linear Hypothesis procedure, SYSTAT 5.2). Analyses were performed on the means of the two seedlings of each species grown in each simulated gap.

RESULTS

Light environments of simulated gaps

The benches were designed to simulate gaps ranging from 25 to 800 m², based on a 30-m canopy height. On a sunny day in May 1998, these

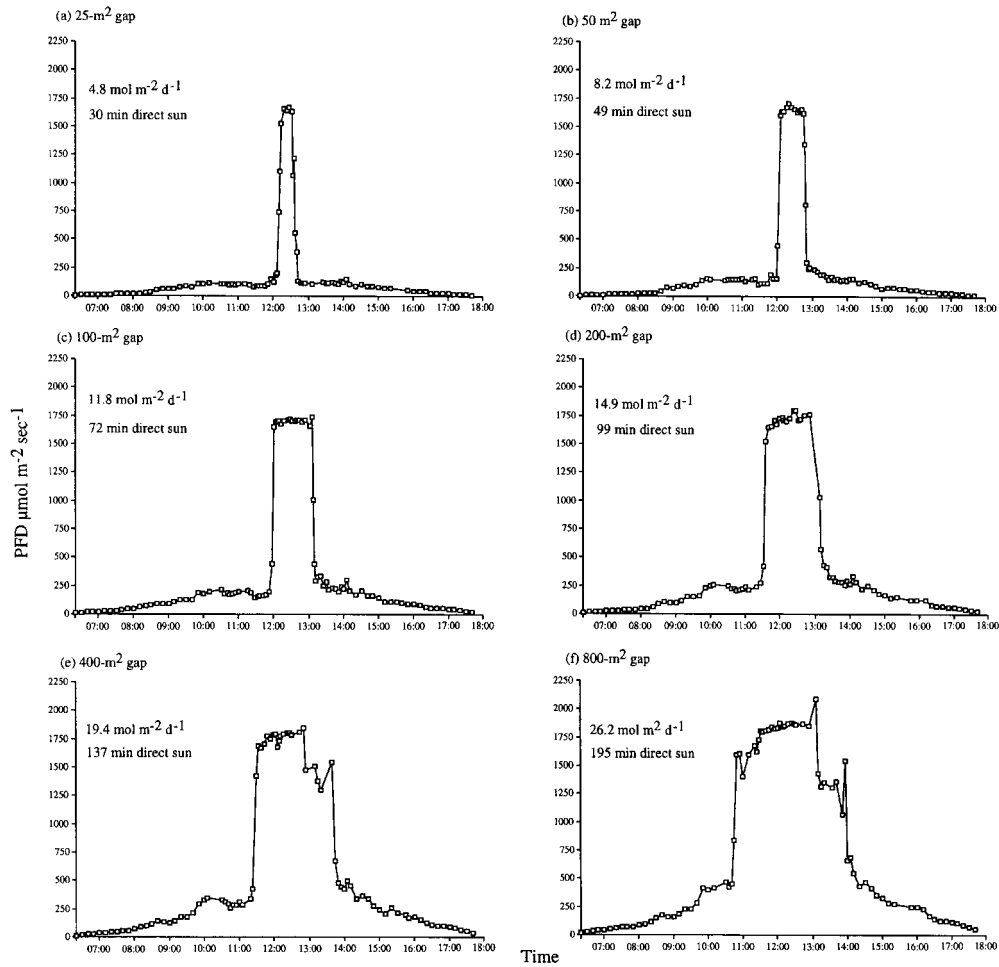


Figure 3. Daily time courses of photon flux density (PFD) made under sunny conditions on 2 May 1998. PFD values were depressed somewhat after 13h00 by intermittent clouds. Above canopy PFD was 45.6 mol m⁻² d⁻¹.

treatments corresponded to total radiation values of between 4.8 mol m⁻² d⁻¹ (11% full sun) and 26.2 mol m⁻² d⁻¹ (57% full sun), and exposure to direct solar radiation of between 30 and 195 min in the 25 m² and 800 m² simulated gaps respectively (Figure 3). Light measurements made in replicate benches of the same gap size treatment were very similar; values of light transmittance, calculated from paired PFD measurements made above and within the benches generally varied by < 0.2%. Values of R:FR were lowest in the smallest gap treatments, and for all treatments during the mid-morning (Figure 4), when the highest proportion of total PFD was filtered through the energy film. R:FR did not decline as markedly during the afternoon after 15h00 because increased cloud cover resulted in higher diffuse radiation inputs through the roof aperture.

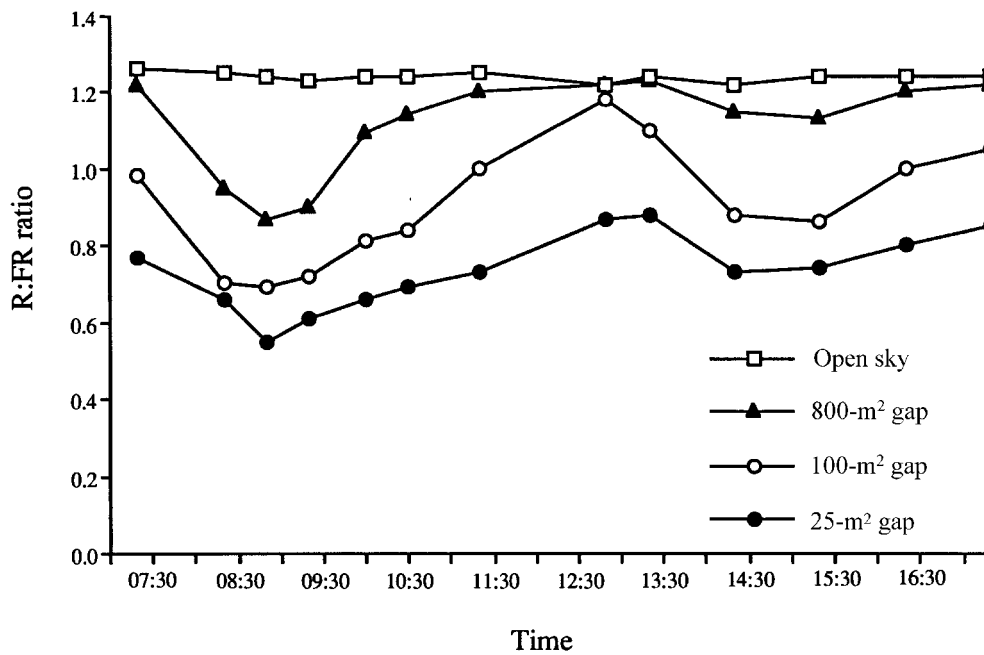


Figure 4. Red : far red light measurements made on 2 May 1998. For clarity, values are only presented for three of six simulated gap treatments, and for measurements made above the benches (open sky) measurements.

Seedling responses to gap environments

Both the large-gap 'specialist' pioneer *Ochroma pyramidale*, and the 'generalist' pioneer *Luehea seemanii* showed strong plastic responses in growth and allocation to differences in gap size (Table 2; Figure 5). Relative growth rate of both species increased with increasing gap size (Figure 5a), but growth of *Ochroma* was more sensitive to gap size than was *Luehea* (100% variation in RGR versus 30% variation). Higher RGR in *Ochroma* can be attributed to both differences in carbon allocation and biochemical factors (cf. Poorter *et al.* 1990). Net assimilation rate (NAR, the efficiency with which leaf area is used to assimilate

Table 2. *F*-values from split-plot analyses of variance conducted on the mean values from two seedlings grown within each simulated gap. *Luehea* and *Ochroma* seedlings were grown for 63 and 96 days respectively under six simulated gap sizes. Degrees of freedom (df) for growth and morphology measurements: species = 1,18; gap = 5,18; species \times gap = 5,18. For photosynthesis measurements the smallest gap size treatment was excluded (df species = 1,13; gap = 4,13; species \times gap = 4,13).

Attribute	Species	Gap	Species \times gap
Leaf weight ratio (g g^{-1})	116.1***	2.2	9.1***
Root weight ratio (g g^{-1})	65.3***	1.9	7.1***
Specific leaf area ($\text{cm}^2 \text{g}^{-1}$)	25.1***	33.9***	1.4
Leaf area ratio ($\text{cm}^2 \text{g}^{-1}$)	10.7***	11.8***	3.8**
Net assimilation rate ($\text{g m}^{-2} \text{d}^{-1}$)	49.8***	42.7***	0.9
Relative growth rate ($\text{g g}^{-1} \text{d}^{-1}$)	47.5***	21.2***	4.0*
Photosynthesis ($\mu \text{mol m}^{-2} \text{s}^{-1}$)	54.5***	13.7***	3.3
Photosynthesis ($\mu \text{mol g}^{-1} \text{d}^{-1}$)	31.7**	2.6	2.3

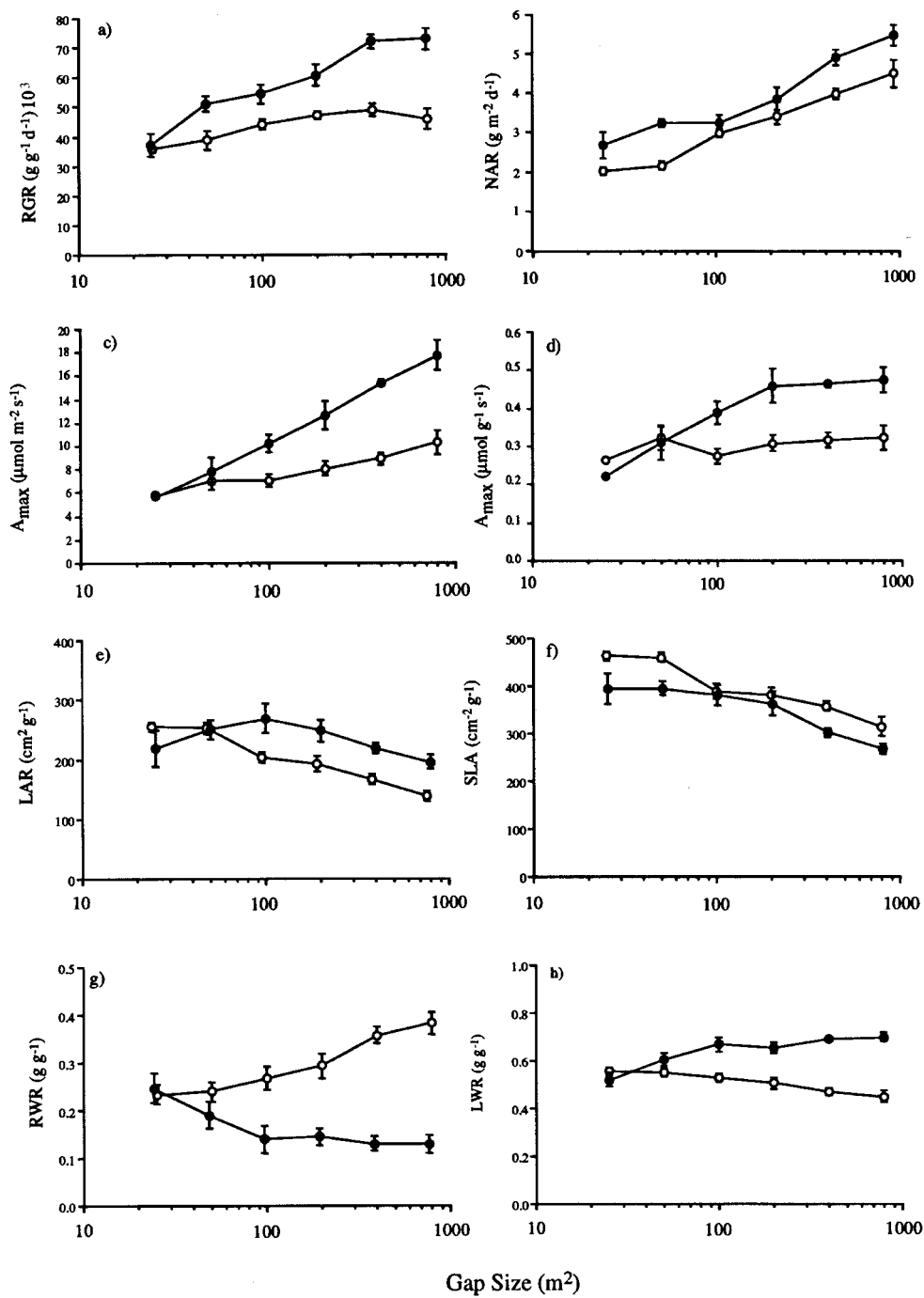


Figure 5. Variation in (a) relative growth rate (RGR), (b) net assimilation rate (NAR), (c) maximal photosynthetic rate (A_{max}) per unit leaf area, (d) maximal photosynthetic rate (A_{max}) per unit leaf mass, (e) leaf area ratio (LAR), (f) specific leaf area (SLA), (g) root weight ratio (RWR). Measurements made on seedlings of *Luehea seemannii* (open circles) and *Ochroma pyramidale* (closed circles) grown in each of six simulated gap sizes. Note the logarithmic scale on the x-axis.

carbon) of *Ochroma* was greater than that of *Luehea* over all the gap sizes, but increases in NAR with gap size were similar in both species (Figure 5b). Net assimilation is in part determined by the rate of photosynthetic carbon gain of plants. Maximum rates of photosynthetic carbon gain expressed on a leaf area basis were enhanced as gap size increased, particularly in *Ochroma* (Figure 5c). On a dry weight basis, maximum photosynthetic rates of *Luehea* were insensitive to increases in gap size (Figure 5d). Thus, *Ochroma* appears to have a greater capacity to use prolonged exposure to high light levels for photosynthetic carbon gain than does *Luehea*.

In addition to higher NAR, *Ochroma* also had significantly more of its biomass allocated to leaf area (higher LAR) than *Luehea* in the large gap sizes (Figure 5e). Higher LAR in *Ochroma* compared to *Luehea* was not achieved through decreasing leaf thickness, as specific leaf area (SLA) of *Ochroma* was generally lower than that of *Luehea* (Figure 5f). Instead, higher LAR in *Ochroma* was in part maintained by an exceptionally low investment in root biomass (RWR) and correspondingly higher investment in leaf biomass (LWR) in the large gap treatments (Figure 5g).

DISCUSSION

Natural canopy gaps clearly vary in many important attributes other than size, and gaps of the same size may have quite different light regimes (Brown 1993, Whitmore *et al.* 1993). The use of standardized conditions that provide repeatable simulations of gap light environments are therefore of considerable utility for growth analyses and ecophysiological studies. This bench experiment provides good simulations of gaps exposed to some period of direct solar radiation during the day, with daily inputs of direct and indirect solar radiation, and R:FR increasing with gap size (Figures 3 & 4; Brown 1993, *c.f.* Lee 1987). It does not simulate gaps, or gap microsites which are not exposed to direct solar radiation, even though this may commonly occur seasonally at high latitudes, and at low latitudes in narrow gaps that are oriented east–west.

Seedlings of both species responded morphologically and physiologically to variation in gap size. Although growth rates of the two species were comparable in the smallest gap treatment, *Ochroma* out-performed *Luehea* in larger simulated gaps through a combination of higher photosynthetic rates, and higher proportional allocation to leaf tissue (Figure 5). A striking result for *Ochroma* is the finding of decreasing RWR with increasing light. This appears to be very unusual for a tropical tree (e.g. Ashton 1995, Bongers & Popma 1990, Fetcher *et al.* 1983, Popma & Bongers 1988), and may result in greater susceptibility to drought stress than in other pioneers. Since *Ochroma* is also highly mycotrophic (more so than *Luehea*; E. Kiers *et al.* unpubl. data), it might possibly invest carbon in its mycorrhizae rather than in root tissue under high light conditions.

Results from this experiment also point to the potential value of specific leaf area (SLA) as a comparative measure of the light conditions experienced

among plants within a species. Variance in SLA within light treatments for these and other species is quite low despite high variance in total leaf area among plants (Figure 5f; J. Dalling, unpubl. data). Specific leaf area has been shown to be the most important component in determining growth potential using a series of phylogenetic contrasts across many species (Saverimuttu & Westoby 1996, but see Poorter & Remkes 1990). Since SLA can be measured in the field by extracting small leaf discs, and among pioneers is often correlated with leaf thickness measured using a micrometer (J. Dalling, unpubl. data), results for species grown in the simulated gaps might readily be compared with growth and allocation patterns of seedlings grown in natural gaps.

Interestingly, although *Ochroma* is absent from small gaps in central Panama, it performed as well, or better than *Luehea* in simulated small gap environments in terms of its relative growth rate (Figure 5a), net assimilation rate (Figure 5b) and photosynthetic rate (Figure 5c,d). If observed patterns of gap partitioning among pioneer species are largely the consequence of different morphological and physiological optima adopted by different species then we would have expected to have seen much more dramatic differences in relative growth performance between the species across the gap size gradient. Gap partitioning may arise however, as a result of trade-offs between growth and mortality (Dalling *et al.* 1998), with differences in allocational patterns among species favouring either growth in high light conditions or survival in relatively low light conditions (Kitajima 1994). Results using these simulated gaps suggest that while high growth and resource acquisition rates may be important in determining the success of species in large gaps, low growth rates caused by conservative carbon allocation patterns (Kitajima 1994), and the ability to withstand pathogens (Augspurger & Kelly 1984), herbivores (Coley 1983) and other hazards (Clark & Clark 1989) are possibly important for success in small gaps and in the deep shade of the understorey (Kitajima 1996 and references therein).

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