

# Growth and mortality in high and low light: trends among 15 shade-tolerant tropical rain forest tree species

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## Summary

**1** Past work on tropical rain forest tree seedlings has been dominated by contrasts between strongly light-demanding and strongly shade-tolerant species. We examined patterns of growth and mortality among shade-tolerant tree seedlings in response to light, and investigated the morphological and physiological correlates of high seedling growth and survival rates across species.

**2** Seedlings of 15 tree species from Australian tropical lowland forest were grown for up to 1 year in neutral-density shadehouses at three light levels (10%, 0.8% and 0.2% full daylight). All species showed negligible mortality in the 10% and 0.8% shadehouses, but survival was significantly reduced in 0.2% daylight.

**3** Seedling survival rate in 0.2% daylight showed no significant relationship with either the dry mass of seed reserves (embryo plus endosperm), or relative growth rates in dry mass ( $RGR_M$ ) in 0.8% and 10% light.

**4** The  $RGR_M$  values in 0.8% and 10% daylight were strongly positively correlated, and showed a strong negative correlation with the dry mass of seed reserves. Interspecific variation in low-light  $RGR_M$  was driven by unit leaf rate (rate of accumulation of dry mass per unit area of leaf), whereas interspecific variation in high-light  $RGR_M$  was most closely correlated with leaf area ratio (leaf area per total plant dry mass).

**5** Variation in seedling characters in response to light may have important implications for the coexistence of shade-tolerant tropical tree species.

*Key-words:* Australia, relative growth rate, trade-off, tree seedlings, tropical rain forest

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## Introduction

Species-specific differences in survival and growth play a key role in plant competition and community composition. Theoretical work has shown that a trade-off between high-light growth rate and low-light survival is critical to long-term community dynamics and species coexistence in the northern temperate conifer-hardwood forests of North America (Pacala *et al.* 1996). However, the idea that such a trade-off may underpin coexistence of tree species in species-rich tropical rain forest communities is more controversial.

There are several reasons for expecting a trade-off between high relative growth rate in mass ( $RGR_M$ ) in high light and survival in low light. High growth rates are generally coupled with high respiration rates, which

will lead to starvation in low light conditions unless species are capable of marked physiological flexibility (Bazzaz 1979). High growth rates are also associated with shorter leaf life spans (Reich *et al.* 1992; Reich 1998); in limiting light shorter-lived leaves may fail to cover their production costs (Givnish 1988; King 1994). Plant carbon balance in low light conditions is further reduced by herbivory or physical damage that removes plant tissue. As high growth rates often depend on minimal allocation to reserves (Kobe 1997) or defence (Herms & Mattson 1992), faster-growing species may be more vulnerable to herbivory or disease in low light.

Many studies of seedlings and saplings, both temperate and tropical, have yielded evidence for a trade-off between  $RGR_M$  in high light and survival in low light across species (Kitajima 1994; Kobe *et al.* 1995; Grubb *et al.* 1996; Pacala *et al.* 1996; Walters & Reich 2000; Davies 2001). However, all of these studies have incorporated both shade-tolerant and light-demanding species. To date no study has explicitly tested for a

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relationship between high-light growth and low-light survival among shade-tolerant species alone, despite the fact that the majority of species in lowland tropical rain forests are shade-tolerant. It is important to recognize that contrasts observed between species at the two extremes of the shade-tolerance continuum may not be mirrored by all species along the continuum. This point is illustrated by work on the leaves of tropical tree species on Barro Colorado Island, Panama (Coley 1988). Coley noted significant positive correlations between leaf life span, leaf tannin and leaf fibre concentrations when using a data set comprising both strongly shade-tolerant and light demanding species, but no correlation was apparent within either of the groups when considered alone.

Understanding any trade-off between growth rate and survival in either functional group must involve an analysis of the morphological and physiological traits associated with high  $RGR_M$  or survival. When plants are grown in low levels of light (< 1% daylight), seedling survival often shows a positive relationship with mass of seed reserves (Leishman & Westoby 1994; Boot 1996), although this relationship may break down with age (Saverimuttu & Westoby 1996; Walters & Reich 2000). Seed size may also be an important correlate of  $RGR_M$  and numerous studies report a negative relationship between seed size and seedling  $RGR_M$  for both woody and herbaceous species (Fenner 1983; Shipley & Peters 1990; Marañón & Grubb 1993; Cornelissen *et al.* 1996).

In a review of seedling experiments that considers the whole range of light-demanding and shade-tolerant rain forest species, Veneklaas & Poorter (1998) suggest that  $RGR_M$  in low light is determined primarily by leaf area ratio (LAR; leaf area per unit whole-plant mass), which in turn is closely linked to specific leaf area (SLA; leaf area per unit leaf mass). However, the percentage daylight in the low-light treatments reviewed by Veneklaas & Poorter was appreciably higher than the percentage daylight found in the forest understorey (1.6–4% rather than 0.5–2%), so their conclusions must be regarded as provisional. These authors further propose that  $RGR_M$  in high light is driven by unit leaf rate (ULR; rate of accumulation of dry mass per unit area of leaf), which is consistent with the findings of Grubb *et al.* (1996) for temperate woody plants. The degree to which shade-tolerant tropical seedlings conform to these trends has not been addressed.

We report here a replicated shadehouse experiment involving only tropical tree species that are shade-tolerant at the seedling stage. Our low-light treatment (0.8% light) provided a better simulation of light conditions in the forest understorey than most previous shadehouse studies, and we also examined the survival of plants in a very low light treatment (0.2% light). The hypotheses tested were as follows: (i) high-light  $RGR_M$  is negatively correlated with survival in very low light across species; (ii) survival in very low light is positively correlated with the mass of seed reserves (endosperm

plus embryo); (iii)  $RGR_M$  in both low- and high-light is negatively correlated with seed mass; and (iv) low-light  $RGR_M$  is correlated closely with leaf area ratio whereas high-light  $RGR_M$  is correlated closely with unit leaf rate.

## Materials and methods

### STUDY SITE AND SPECIES

The present study was carried out at the CSIRO Tropical Forest Research Centre (TFRC), Atherton in North Queensland, Australia (17°17' S, 145°34' E). The Centre is situated at an altitude of *c.* 700 m, at the western margin of a tropical lowland rain forest region. Rainfall in Atherton averages 1400 mm per year, with a low rainfall period between May and October. Mean monthly temperatures range from 22 to 28 °C in the wet season, and from 16 to 22 °C in the dry season (Tracey 1982).

Fifteen rain forest tree species were used, six epigeal and nine hypogeal, the seed reserve dry mass varying from 0.0032 to 11.0 g (Table 1). Seeds were collected beneath parent trees in various rain forest locations on the Atherton Tablelands (at *c.* 600–700 m altitude) between December 1997 and February 1998. All 15 species establish and persist in the understorey where the diffuse site factor (dsf) *sensu* Anderson (1964) is usually in the range 0.4–2.0% but sometimes as low as 0.2% full daylight. The species differ in the amount of light needed to reach 2 m in height. In extensive studies the *Flindersia*, *Gillbeea*, *Guioa* and *Prunus* have not been found growing healthily and 2 m tall in less than 2–3% dsf (P.J. Grubb & D.J. Metcalfe, unpublished observations), and our subjective observations suggest that the *Athertonia* and *Cryptocarya triplinervis* will prove to be similarly demanding. The remaining species can be found 2 m tall in 1.0–1.5% dsf.

### LIGHT TREATMENTS

Replicate experimental light treatments were set up in neutral-density shadehouses (2 × 3 × 2.5 m) at TFRC. Three houses were established as a low-light treatment (three layers of 90% shade cloth), and three houses were established as a high-light treatment (one layer of 90% and one layer of 70% shade cloth). Clear plastic was attached to the sides of the high-light houses to ensure comparable airflow in both high- and low-light shadehouses. In addition, a very low light treatment was set up under the benches in the low-light shadehouses. The bench tops were covered with a layer of 70% shade cloth and trays of plants (which occupied 75% of the bench). This very low light treatment was designed to examine species differences and plant performance under extreme conditions, with the plants kept close to or below their natural light compensation point for a prolonged period of time.

Maximum/minimum thermometers and thermo-hygrographs set up in the shadehouses indicated that

**Table 1** Study species, species code, seed reserve dry mass (g), germination type and number of months grown in experimental treatments. Mean seed reserve dry mass data are from Grubb & Metcalfe (1996) except for species marked \*, which were obtained by J.M.G. Bloor. Germination categories are epigeal (E) and hypogeal (H). Nomenclature follows Henderson (1997) and assignment to families follows Stevens (2002)

Species	Family	Species code	Seed reserve dry mass	Germination type	Months grown
<i>Gillbeea adenopetala</i>	Cunoniaceae	ga	0.0032	E	9
<i>Cryptocarya murrayi</i>	Lauraceae	cm	0.379*	H	9
<i>Cryptocarya aff. triplinervis</i>	Lauraceae	ct	0.139*	H	7
<i>Cryptocarya mackinnoniana</i>	Lauraceae	ml	0.332*	H	8
<i>Argyrodendron trifoliolatum</i>	Malvaceae	at	0.061	H	11
<i>Aglaia sapindina</i>	Meliaceae	as	0.297	H	9
<i>Athertonia diversifolia</i>	Proteaceae	ad	11.0	E	9
<i>Cardwellia sublimis</i>	Proteaceae	cs	0.66	E	10
<i>Darlingia darlingiana</i>	Proteaceae	dd	0.15	E	7
<i>Prunus turneriana</i>	Rosaceae	pt	1.8	H	8
<i>Flindersia bourjotiana</i>	Rutaceae	fb	0.08*	E	11
<i>Castanospora alphanthii</i>	Sapindaceae	ca	1.7	H	11
<i>Cupaniopsis flagelliformis</i>	Sapindaceae	cf	0.22	H	11
<i>Guioa lasioneura</i>	Sapindaceae	gl	0.026	E	12
<i>Synima macrophylla</i>	Sapindaceae	sm	0.25	H	11

they did not differ significantly from each other in their temperature/relative humidity during the experimental period. Over the course of the experimental period, weekly maximum temperatures in the shadehouses ranged from 20 to 36 °C. Photosynthetically active radiation (PAR) measurements in the high- and low-light shadehouses were  $9.9 \pm 0.89\%$  and  $0.8 \pm 0.09\%$  full daylight (based on comparisons of treatment vs. outdoor instantaneous readings made throughout the day at plant level using LI-190SA Quantum sensors: Li-Cor, Lincoln, NE, USA). These light levels are comparable with those found in the centres of single-treefall gaps and in the forest understorey, respectively (Bloor 2003). PAR recorded in the very low light treatment was  $0.21 \pm 0.06\%$  full daylight, which corresponds to the lowest mean light levels previously recorded in the understorey of Australian rain forests (Bjorkman & Ludlow 1972; Connell & Green 2000).

#### GROWTH EXPERIMENT

Seeds were germinated in shallow trays filled with forest topsoil in a 'nursery' shadehouse (4% full daylight) at TFRC. The soil came from a depth of 0–15 cm and was derived from basalt; chemical analyses for this soil are presented elsewhere (Metcalfe *et al.* 2002). Once the first pair of leaves or photosynthetic cotyledons was fully expanded, seedlings were carefully dug up, washed, measured and weighed. Seedlings were then planted individually into plastic pots (16 cm high, 6 cm diameter) containing a mixture of 50 : 50 forest soil and washed river sand (derived from granite), and randomly allocated to a light treatment. Nine to 15 plants of each species were assigned to each treatment in each shadehouse, except for the *Flindersia* and *Gillbeea*, where five seedlings were used in each treatment. 'Setting up' dates varied among species due to different

seed collection times, and to the time-consuming nature of potting; species were allocated to light treatments over a period of 4 months and all species were set up by 30 June 1998.

Once the plants were set up in the shadehouses, initial harvests were taken for a subsample of each species (6–10 plants per species). These initial harvests recorded stem height, root length, leaf length, leaf area (using an area meter, Delta-T Devices, Burwell, UK) and seedling dry mass (seedlings were oven-dried at 70 °C for 48 h). Regression equations based on fresh and dry masses of the harvested seedlings were used to estimate the initial dry masses of the remaining seedlings (mean  $r^2 = 89.1 \pm 2.2$ ). Additionally, leaf length and area of the harvested seedlings were used to estimate the initial leaf areas of the unharvested seedlings (mean  $r^2 = 72.9 \pm 2.6$ ). Plants allocated to each shadehouse were watered regularly. Any seedlings dying in the first 2 weeks after potting were replaced. Following seedling transfer into the shadehouses, survival censuses were initiated and carried out monthly throughout the experiment. Plants were regularly relocated within the shadehouses during the experimental period to reduce possible positioning effects.

The mean growing period between initial and final harvest was 9.5 months (range 7–12 depending on species' germination dates, Table 1). The start of the growth experiment coincided with the end of the wet season and a period of cooler temperatures and limited growth; increased growth coincided with increasing temperatures from September onwards. Species with longer growth periods experienced a longer period of cool temperatures at the start of the experiment but all species had experienced 6 months of favourable growing conditions by the end of the experiment. No leaf abscission was observed in the high- or low-light treatments during the study period.

**Table 2** Plant variables derived for growth and morphological analysis in this paper. Abbreviations and units are shown. W is seedling dry mass (g), H is seedling height (cm), A is seedling leaf area (cm<sup>2</sup>) and T is time (mo). Subscripts refer to initial (1) or final (2) harvest

Variable	Abbreviation	Units
Relative growth rate ( $\ln W_2 - \ln W_1 / (T_2 - T_1)$ )	RGR <sub>M</sub>	g g <sup>-1</sup> mo <sup>-1</sup>
Relative height growth rate ( $\ln H_2 - \ln H_1 / (T_2 - T_1)$ )	RGR <sub>H</sub>	cm cm <sup>-1</sup> mo <sup>-1</sup>
Unit leaf rate ( $(W_2 - W_1) / (\ln A_2 - \ln A_1) / (T_2 - T_1)$ , ( $A_2 - A_1$ )	ULR	g cm <sup>-2</sup> mo <sup>-1</sup>
Leaf area ratio (total leaf area/total seedling dry mass)	LAR	cm <sup>2</sup> /g
Leaf mass fraction (leaf dry mass/total seedling dry mass)	LMF	g/g
Stem mass fraction (stem dry mass/total seedling dry mass)	SMF	g/g
Root mass fraction (root dry mass/total seedling dry mass)	RMF	g/g
Specific leaf area (total leaf area/total leaf dry mass)	SLA	cm <sup>2</sup> /g
Specific stem length (stem length/stem dry mass)	SSL	cm/g
Specific root length (total root length/root dry mass)	SRL	cm/g
Root branching index (root tips/total root length)	RBI	tips/cm

In February 1999, three to five randomly selected individuals of each species from each shadehouse were harvested. Each of the harvested seedlings was measured to determine stem length, maximum root length, leaf number and leaf area. In addition, a subsample of roots was taken for each species and scanned to determine total root length and number of root tips (WINRhizo package 3.9, Regent Instrument Inc., Quebec, Canada). Seedlings showed no signs of being pot-bound when removed from their pots, even in the high-light treatment. All plants were then oven-dried (70 °C for 48 h) to obtain dry mass values for the roots, leaves and stems. Plant dry mass values did not include cotyledon remains or testas as in all cases these had dropped off.

Based on the harvest data, several plant variables were derived (Table 2). Relative growth rate in mass (RGR<sub>M</sub>) was calculated for each plant individually using estimates of initial dry mass. Unit leaf rate (ULR) was also calculated for each plant using estimates of initial leaf area. Calculation of ULR is valid only when seedling dry mass and leaf area are linearly related over a period of observations (Hunt 1982), a condition that could not be tested in this study. However, previous work has found this relationship to hold for a number of the species used in this study (Osunkoya & Ash 1991), and the relationship was assumed to hold for all the study species. Leaf area ratio (LAR) and specific leaf area (SLA) were calculated both as mean values over the growth period (using initial and final harvest data) and also as final harvest values for comparison.

#### STATISTICAL ANALYSIS

Each shadehouse in this study represents a true replicate of one light treatment. Analyses were performed on the means of individuals from each replicate, and all means quoted in the text are derived from three mean values per light treatment.

Many phenotypic traits of plants change over the course of plant growth as a function of plant size, and

these ontogenetic responses may confound functional responses to a particular environment (Gedroc *et al.* 1996). In this study, it was not possible to compare plants of different species at a common biomass and examine plant functional responses to light. Instead, correlation analysis and regressions were used to investigate relationships between values for plant characteristics in a given light treatment. Analyses based on mean values of LAR and SLA over the growth period generated identical trends to analyses based on final harvest values for LAR and SLA. Consequently we present only the analyses based on final harvest values.

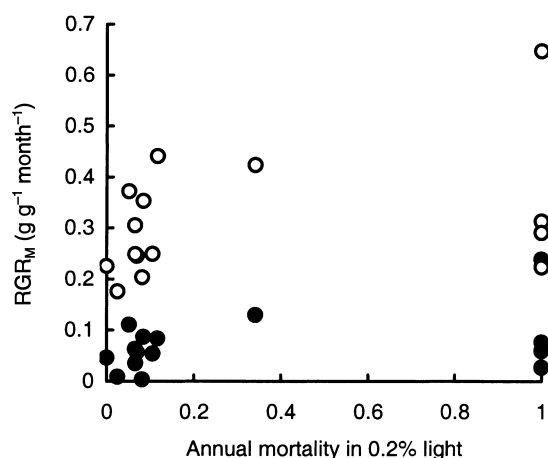
Annual mortality estimates were calculated for each species in each shadehouse according to Sheil *et al.* (1995), and examined using the non-parametric Kruskal–Wallis test. Data were transformed where necessary to conform to assumptions of normality and homogeneity of variance. All statistical analysis was carried out using the MINITAB 12.0 package.

## Results

### SEEDLING SURVIVAL

Seedling mortality was negligible for all species in both high (10%) and low (0.8%) light treatments during the experimental period. Four seedlings died from *c.* 1050 seedlings that were set up in these two light treatments. However, considerable losses occurred in the 0.2% light treatment, and a number of species suffered 100% mortality by the end of the study period (Fig. 1). The cause of mortality in 0.2% light was not generally apparent; only in a few cases was fungal infection observed.

Seedling survival in very low light differed significantly amongst species (Kruskal–Wallis statistic = 30.9,  $P < 0.01$ ), but showed no significant relationship with either high- or low-light RGR<sub>M</sub> (Fig. 1), thus falsifying our first hypothesis. Our second hypothesis was also falsified because seedling survival in 0.2% light showed no significant correlation with the dry mass of seed reserves (Pearson's  $R = -0.31$ ,  $P > 0.20$ ).



**Fig. 1** Relationship between seedling relative growth rates ( $RGR_M$  in either 10% or 0.8% of full daylight) and estimated annual mortality in deep shade (0.2% light) for 15 shade-tolerant tree species. Open circles represent species in 10% light; dark circles represent species in 0.8% light.

#### RELATIVE GROWTH RATES IN LOW AND HIGH LIGHT

All species attained the highest biomass and seedling heights in the high-light treatment (Fig. 2). Species' growth rates in the low-light treatment were generally very low, but showed a wide spread of values (Fig. 3). The  $RGR_M$  value of the fastest growing species, *Gill-beea adenopetala*, was 30 times greater than that of the slowest growing species, *Cryptocarya murrayi*. In high light the difference between the highest and lowest

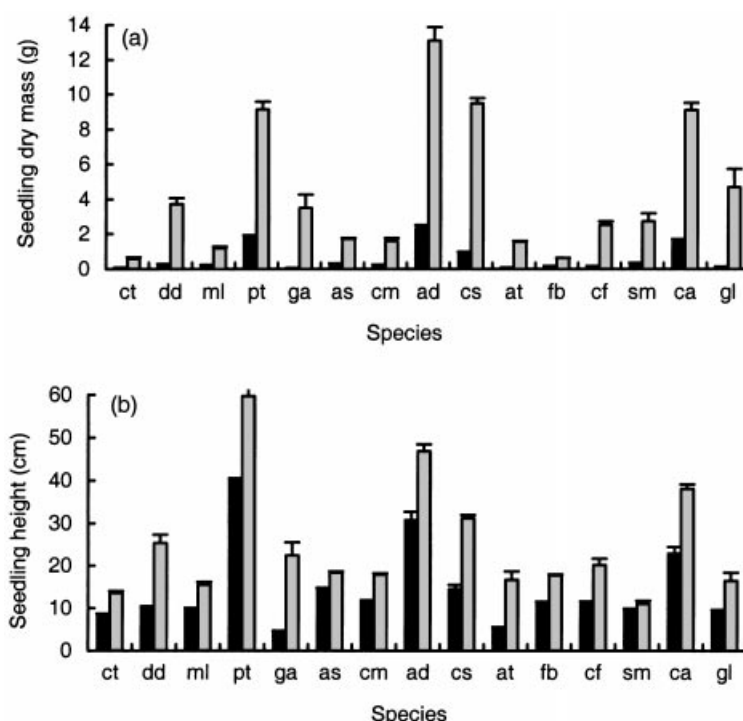
**Table 3** Rank order of species according to seedling height for 15 species grown in 0.8% or 10% daylight. Species are ranked according to their mean seedling height at the start ( $t_0$ ) and end of the experimental period; species' codes and growth periods are given in Table 1

Species rank														
Harvest	pt	ad	ca	cs	as	cm	ml	cf	dd	fb	ct	sm	gl	at
$t_0$	1	2	3	4	5	6	7	8	9	10	11	12	13	14
0.8%	1	2	3	4	5	6	10	8	9	7	13	11	12	14
10%	1	2	3	4	8	9	13	7	5	10	14	15	12	11

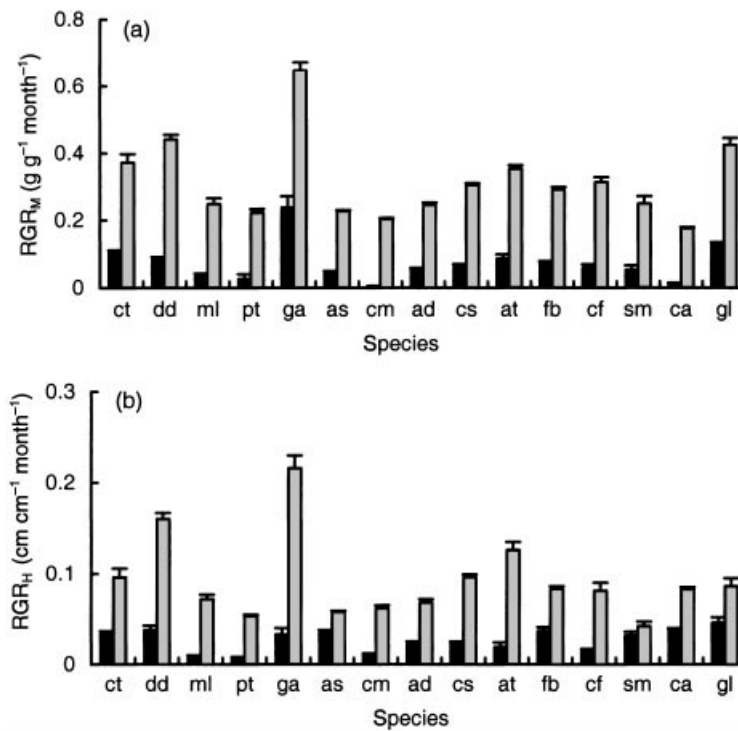
$RGR_M$  values was an order of magnitude smaller (Fig. 3). No relationship was found between  $RGR_M$  values and growth period in either low or high light (Pearson's  $R = 0.02$  and  $-0.09$ , respectively,  $P > 0.80$  in both cases).

Relative growth rates in height ( $RGR_H$ ) showed comparable variation in the two treatments; the highest and lowest  $RGR_H$  values across species differed by a factor of seven and five in the low- and high-light treatments, respectively (Fig. 3). Species differed in initial seedling height, but differences in  $RGR_H$  led to a number of crossovers in the rank order of species according to height, particularly in the high-light treatment (Table 3).

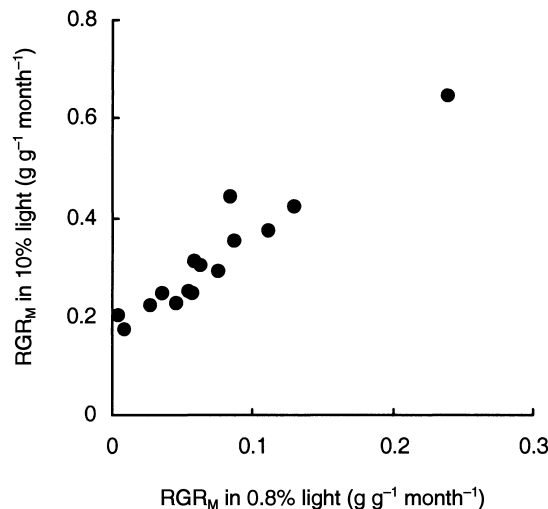
There was a strong positive relationship between low-light and high-light  $RGR_M$  across species (Fig. 4), and the rank order of species' growth rates did not differ significantly between the two treatments (Kendal's  $\tau = 0.81$ ). In contrast, no significant relationship was found between  $RGR_H$  values in high and low light.



**Fig. 2** Final harvest values of (a) seedling dry mass and (b) seedling height for 15 shade-tolerant species grown in either 10% or 0.8% of full daylight. Pale bars represent species in 10% light; dark bars represent species in 0.8% light. Means ( $\pm$  SE) are shown;  $n = 3$ . Species are arranged according to increasing growth period (species' codes and growth periods are given in Table 1).



**Fig. 3** Relative growth rates on (a) biomass ( $RGR_M$ ) and height ( $RGR_H$ ) basis for 15 shade-tolerant species grown in either 10% or 0.8% of full daylight. Means ( $\pm$  SE) are shown;  $n = 3$ . Species are arranged according to increasing growth period (species' codes and growth periods are given in Table 1).

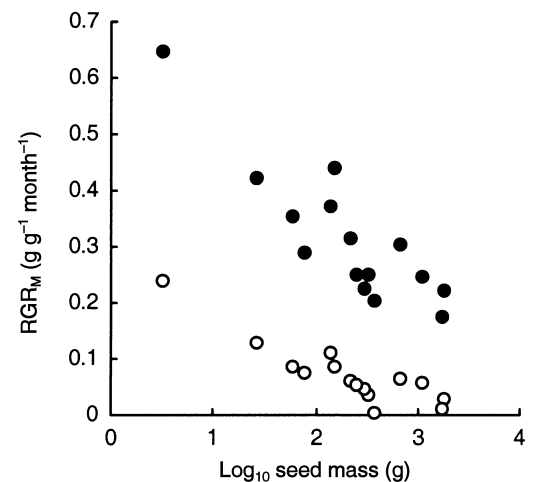


**Fig. 4** Relationship between relative growth rates ( $RGR_M$ ) of seedlings grown in 10% light and  $RGR_M$  of seedlings grown in 0.8% light for 15 shade-tolerant tropical species ( $r^2 = 0.68$ ,  $P < 0.0001$ ). Each point is a species mean.

Values for  $RGR_H$  in low light were not significantly correlated with  $RGR_M$  in low light across species. However,  $RGR_H$  in high light showed a strong positive relationship with  $RGR_M$  in high light across species (Pearson's  $R = 0.81$ ,  $P < 0.001$ ).

#### RELATIVE GROWTH RATES AND SEED RESERVES

Our third hypothesis was supported:  $RGR_M$  was negatively correlated with seed reserve dry mass (Fig. 5).



**Fig. 5** Relationship between seedling relative growth rates ( $RGR_M$  in either 10% or 0.8% of full daylight) and dry mass seed reserve ( $lg_1EE$ ) for 15 shade-tolerant tree species. Open circles represent species in 10% light; solid circles represent species in 0.8% light.

The correlation was stronger in high light than in low light (Pearson's  $R = -0.87$  vs.  $-0.67$ ,  $P < 0.001$  and  $P < 0.01$ , respectively).

Initial seedling height was correlated with seed reserve mass (Pearson's  $R = 0.88$ ,  $P < 0.001$ ), but final seedling height showed the correlation only in low light (Pearson's  $R = 0.86$ ,  $P < 0.001$ ). In high light, initial differences in height were overcome by differences in  $RGR_H$ .

**Table 4** Correlation matrix for seedling traits of 15 species grown in 0.8% or 10% daylight. Values in the table are Pearson's correlation coefficients; numbers below the diagonal refer to plants grown in 0.8% daylight, whereas values above the diagonal refer to plants grown in 10% daylight. Numbers shown in bold are significant at the 0.05 level following Bonferroni adjustments (Rice 1989)

	RGR <sub>M</sub>	ULR	LAR	SLA	LMF	SMF	RMF	SSL	RBI	SRL
RGR <sub>M</sub>	*	0.13	0.55	0.34	0.43	-0.65	0.05	0.23	0.43	0.55
ULR	<b>0.90</b>	*	-0.45	-0.40	-0.35	0.38	-0.01	-0.48	0.11	-0.18
LAR	0.63	0.33	*	<b>0.83</b>	<b>0.80</b>	-0.75	-0.35	0.76	-0.06	<b>0.78</b>
SLA	0.64	0.53	<b>0.96</b>	*	0.16	-0.32	0.24	0.57	0.09	0.62
LMF	0.38	0.18	0.76	0.49	*	<b>-0.83</b>	-0.67	0.56	-0.18	0.49
SMF	-0.51	-0.22	<b>-0.82</b>	-0.66	<b>-0.85</b>	*	0.23	-0.39	-0.23	-0.42
RMF	0.08	0.00	-0.06	0.08	-0.51	-0.01	*	-0.43	0.49	-0.31
SSL	0.63	0.52	<b>0.77</b>	<b>0.79</b>	0.25	-0.59	0.44	*	-0.42	<b>0.88</b>
RBI	0.41	0.27	0.38	0.36	0.25	-0.48	0.27	0.48	*	-0.20
SRL	0.41	0.38	0.49	0.58	0.15	-0.33	0.20	<b>0.78</b>	0.35	*

#### RELATIVE GROWTH RATES AND SEEDLING TRAITS

Interspecific variation in RGR<sub>M</sub> was associated with different plant traits in low and high light (Table 4), but in neither case did the results match our predictions. In low light, RGR<sub>M</sub> was most closely correlated with ULR across species (Pearson's  $R = 0.90$ ,  $P < 0.05$ ). Positive correlations between RGR<sub>M</sub> and either LAR or SLA were not significant. LMF was significantly negatively correlated with SMF (Pearson's  $R = -0.85$ ,  $P < 0.05$ ), indicating that greater allocation to leaves occurred at the expense of allocation to stems.

In high light RGR<sub>M</sub> was not correlated with ULR across species (Table 4). The strongest correlation was with LAR, though this did not reach significance. The LAR values were significantly correlated with both SLA and LMF (Pearson's  $R = 0.83$  and  $0.80$ , respectively,  $P < 0.05$ ), and showed a non-significant negative correlation with ULR. Again LMF was significantly negatively correlated with SMF (Pearson's  $R = -0.83$ ,  $P < 0.05$ ).

#### Discussion

##### INTERSPECIFIC VARIATION IN MORTALITY

All species in this study showed equally high survival in the 0.8% light treatment, consistent with their persistence in the understorey as seedlings in 0.4–2.0% dsf. However, species' differences became apparent when seedlings were grown in 0.2% light. Mortality rates recorded in 0.2% light showed significant interspecific variation, but were not significantly related to the mass of seed reserves. Although seed mass may increase seedling longevity in the short term due to extra resources available for metabolism, this advantage lasts only while there are seed reserves to be deployed (Saverimuttu & Westoby 1996).

No relationship was found between high-light RGR<sub>M</sub> and survival in very low light across species. This result contrasts with the findings of seedling growth studies that included both shade-tolerant

and light-demanding species (Kitajima 1994; Walters & Reich 2000). Of course, a trade-off between low-light survival and high-light growth mediated by herbivores, pathogens or periods of water shortage may be observed in the field but will not be detected in controlled growing conditions. However, in a parallel field study of six shade-tolerant tree species (a subset of the 15 species studied here), Bloor (2001) found no evidence of a relationship between high-light growth and low-light survival across species. Uncoupling of the relationship between high-light growth and low-light survival in shade-tolerant species may hinge on differences in light response and plant flexibility among shade-tolerant species.

##### INTERSPECIFIC VARIATION IN GROWTH

The RGR<sub>M</sub> values obtained in the low light treatment for each species ranged between 0.004 and 0.24 g g<sup>-1</sup> mo<sup>-1</sup>, and were generally lower than those reported elsewhere for other shade-tolerant tropical tree species (Walters & Reich 1999). This finding must reflect the lower light level imposed on the seedlings (0.8% light as opposed to 2–4% light imposed in previous studies). Species' RGR<sub>M</sub> values observed in the high-light treatment were comparable to, if not greater than, previously recorded values for shade-tolerant tropical species grown in 8–12% daylight (Walters & Reich 1999).

Across species, low-light RGR<sub>M</sub> showed a strong positive relationship with high-light RGR<sub>M</sub>. This finding is consistent with the results of tropical seedling studies that included both shade-tolerant and light-demanding species (Ellison *et al.* 1993; Kitajima 1994; Poorter 1999; but see Agyeman *et al.* 1999), and mirrors the trend found among forest-grown shade-tolerant tropical seedlings (Bloor 2003). The results of this study indicate that the positive relationship between species' RGR<sub>M</sub> values in low and high light is not driven simply by differences between shade-tolerant and light-demanding species, but may be determined by intrinsic plant constraints unrelated to shade-tolerance.

$RGR_M$  is conventionally regarded as the product of ULR and LAR (Briggs *et al.* 1920). It seems reasonable to assume that LAR may underlie interspecific variation in  $RGR_M$  in a low-light environment as it determines light interception, whereas variation in ULR can become important only when there is adequate light and plants can realize high photosynthetic rates. However, we found that ULR rather than LAR or SLA drove interspecific variation in low-light  $RGR_M$ . In high light, variation in  $RGR_M$  was more strongly correlated with LAR than with ULR. These data corroborate work by Osunkoya *et al.* (1994), who also showed that  $RGR_M$  was more strongly correlated with LAR than ULR in 'high light' (10% daylight) for Australian rain forest seedlings.

Poorter (1999) has neatly demonstrated that the relative contributions of LAR and ULR to interspecific variation in  $RGR_M$  may change along a light gradient (3% to 100% light) in tropical tree seedlings. His results indicated that for plants grown in up to 15% light, LAR was the stronger determinant of  $RGR_M$ . In our study the high-light treatment was 10% light, and LAR was indeed the stronger determinant of plant growth across species. The low-light treatment in our study was 0.8% light, and therefore considerably lower than Poorter's lowest light level. As Poorter might expect, increased LAR (and hence enhanced capacity for light interception) was correlated with increased  $RGR_M$  for the plants grown in 0.8% light. However, ULR was even more strongly related to  $RGR_M$  in these deep shade conditions. This is perhaps not altogether surprising as leaf respiration rates become increasingly important components of  $RGR_M$  in environments where carbon gain is minimal (Givnish 1988; Boot 1996; Reich 1998).

#### IMPLICATIONS FOR SPECIES COEXISTENCE

It is often difficult to accept that niche differentiation plays an important role in maintaining species diversity in tropical rain forests when faced with the large numbers of shade-tolerant tree species that commonly coexist in such communities (Hubbell 1979). However, the results of this study reveal that shade-tolerant species are by no means a homogenous functional group in terms of seedling survival or growth. This finding is consistent with studies of shade-tolerant seedlings in the forest understorey (Zagt 1997; Bloor 2001; Montgomery & Chazdon 2002).

Interspecific variation in relative growth rates may translate into competitive differences among species if faster-growing species are able to overtop slower-growing neighbours over time (Boot 1996). Our data demonstrate changes in height ranking across shade-tolerant species over time, particularly under high-light conditions. A shifting competitive hierarchy among species in a given light regime over time may interact with species-specific responses to environmental variables, thus promoting species coexistence. In addition, species with greater survival rates in the forest

understorey will have a greater chance of outliving their neighbours and being successful when a gap forms (Brown *et al.* 1999). Different combinations of morphological and physiological characters may confer the same degree of understorey survival across species, and could help to explain why so many species can pack into the same 'shade-tolerant niche'.

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