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Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees

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Abstract Among 13 tropical tree species on Barro Colorado Island, species with high seedling mortality rates during the first year in shade had higher relative growth rates (RGR) from germination to 2 months in both sun (23% full sun) and shade [2%, with and without lowered red: far red (R:FR) ratio] than shade tolerant species. Species with higher RGR in sun also had higher RGR in shade. These interspecific trends could be explained by differences in morphological traits and allocation patterns among species. Within each light regime, seedlings of shade-intolerant species had lower root: shoot ratios, higher leaf mass per unit area, and higher leaf area ratios (LAR) than shade tolerant species. In contrast, leaf gas exchange characteristics, or acclimation potential in these traits, had no relationship with seedling mortality rates in shade. In both shade tolerant and intolerant species, light saturated photosynthesis rates, dark respiration, and light compensation points were higher for sun-grown seedlings than for shade-grown seedlings. Differences in R:FR ratio in shade did not affect gas exchange, allocation patterns, or growth rates of any species. Survival of young tree seedlings in shade did not depend on higher net photosynthesis or biomass accumulation rates in shade. Rather, species with higher RGR died faster in shade than species with lower RGR. This trend could be explained if survival depends on morphological characteristics likely to enhance defense against herbivores and pathogens, such as dense and tough leaves, a well-established root system, and high wood density. High construction costs for these traits, and low LAR as a consequence of these traits, should result in lower rates of whole-plant carbon gain and RGR for shade tolerant species than shade-intolerant species in shade as well as in sun.

Key words Shade tolerance · Leaf photosynthesis · Seedling morphology · Growth analysis · Light acclimation

Introduction

In studying adaptation of plants to sunny and shady habitats, physiological ecologists have assumed that, all being equal, “natural selection favours plants whose form and physiology tend to maximize their net rate of energy capture” (Givnish 1988; also Loach 1967; Boardman 1977; Bazzaz 1979; Björkman 1981). More complexity could arise, however, if there was a trade-off between energy capture and susceptibility to herbivores, pathogens, or other sources of mortality. In such cases, survival of plants would not be determined by carbon balance alone. In this paper, I explore the relationship between seedling survival in shade and various morphological and physiological traits related to the maximization of carbon gain.

First-year survivorship of seedlings in shade varies widely and continuously among tropical tree species (Augspurger 1984a,b). Seedling survival in shade closely reflects light requirements for regeneration and successional status (Augspurger 1984a,b; Brokaw 1985; Denslow 1987; Swaine and Whitmore 1988). Seedlings of pioneers and light-gap species survive and grow only in high light environments, while seedlings of shade tolerant species can survive for years in the shaded understory where they typically receive 1–2% of full sunlight. In the study reported here, I quantified several traits central to the carbon balance of seedlings for 13 tropical canopy tree species whose shade tolerance had previously been quantified as the first-year survivorship in shade by Augspurger (1984b). Then, I examined directly how traits influencing the carbon balance of seedlings were correlated with their survivorship in shade, not just with the reputed successional class of the species.

The first objective of the current study was to compare the photosynthetic traits of the first set of leaves developed under controlled sun and shade environments for

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shade-tolerant and -intolerant species. Although the carbon demand for seedling development is met initially by seed reserves alone, seedlings start utilizing light as an energy source as soon as leaves or photosynthetic cotyledons expand (Kitajima 1992a). Light acclimation responses of leaf photosynthetic traits are crucial for optimization of the net carbon gain of a plant, and should be exhibited by the first seedling leaves. Leaves of plants raised in shade often have lower light-saturated net photosynthetic rates, lower light compensation points, and lower dark respiration rates than those of the same species grown under higher photosynthetic photon flux density (PPFD) (Boardman 1977; Björkman 1981). Thus, it is important to use plants grown under identical conditions for comparison among species. Also, it is important that traits are compared for plants at the same developmental stage in order to avoid possible ontogenic variation (Hoflacher and Bauer 1982; Koike 1988; Walters et al. 1993).

With regard to the interspecific differences in sun-shade responses, I made the following two predictions prior to the experiment. First, phenotypic plasticity in response to light environment should be greater for light demanding species than for shade tolerant species (Bazzaz and Carlson 1982). This was found in several other studies of tropical tree seedlings (Oberbauer and Strain 1984; Kwesiga et al. 1986; Strauss-Debenedetti and Bazzaz 1991), but was not supported in other studies (Langenheim et al. 1984; Fetcher et al. 1987; Ramos and Grace 1990; Turnbull 1991). Second, light-saturated photosynthetic rates of leaves developed in sun should be higher for light-demanding species than for shade-tolerant species, while light compensation points and dark respiration rates that influence net carbon gain in low light should be lower for shade-tolerant than for light-demanding species (Fetcher et al. 1983; Mulkey 1986; Sims and Pearcy 1989; Fredeen and Field 1991; but see Walters and Field 1987; Chazdon 1992).

My second objective was to examine how morphological traits influencing the whole-plant carbon budget might be correlated with seedling survival in shade. Quantification of biomass allocation patterns and respiratory components is necessary for estimation of whole-plant carbon budgets (Givnish 1988). If respiration per unit mass is less variable than morphological traits among species, biomass allocation patterns are largely responsible for interspecific differences in whole-plant carbon budgets. Within species, shade-grown individuals allocate relatively more biomass to shoots than roots (lower root:shoot ratio), develop thinner leaves (smaller leaf mass per unit area, LMA), and have greater ratios of total leaf area to total mass (higher leaf area ratio, LAR) than sun-grown individuals (e.g., Loach 1970; Popma and Bongers 1988; Walters et al. 1993). These are considered to be adaptive phenotypic responses to shading, because they increase the ratio of photosynthesis to respiration at the whole plant level and contribute to the maintenance of a positive carbon budget and maximization of growth in shade (Givnish 1988). If maximization

of carbon gain and growth rate in shade is an adaptive evolutionary strategy for survival in shade, then shade tolerant species should have a lower root to shoot ratio, lower LMA, and higher LAR than those of light demanding species under the same light environment. As a result, this hypothesis predicts a negative correlation between seedling mortality rates and relative growth rates. The opposite trend is predicted, if natural selection favors a high defense and storage allocation in the shaded environment, where the relative cost of carbon loss to herbivores and pathogens is high and recovery from tissue loss is difficult due to energy limitation (Coley et al. 1985; Coley 1993). If survival in shade requires construction of durable leaves with thick cuticles, durable woody stems with high lignin contents, well-developed roots for secure support, and storage of carbohydrates in roots and stems, shade tolerant species should have higher LMA, higher root to shoot ratio, lower LAR, and lower RGR. These two alternative hypotheses were central to this study.

Materials and methods

Study site and study species

The ecology of the study site, the semideciduous lowland forest on Barro Colorado Island (BCI), Panama, has been described in Leigh, et al. (1982). Nomenclature of the study species follows Croat (1978). All 15 study species (Table 1) are canopy trees as adults, reproducing by seeds dispersed by wind between the end of dry season and early rainy season. All species naturally germinate in both understory and light gaps during the early rainy season (mid-May to early June), except for *Ochroma pyramidale* which requires high temperatures or mechanical scarification. The mortality rate of 13 of the 15 species had been quantified in a separate study as the negative value of the regression slope of \log_e [number surviving + 1] plotted against time (germination - 1 year) under controlled sun and shade conditions in a growth house (Augspurger 1984b; Kitajima and Augspurger 1989; Table 1). This mortality rate (number/number/week) is the equivalent of the average killing power (or k -value) in a life-table analysis (Begon and Mortimer 1981). The species ranks for this mortality rate generally paralleled the mortality ranks of naturally occurring seedlings in the understory among 9 species (Augspurger 1984a) and skewness of sapling distribution towards light gaps (Hubbel and Foster 1986), and reflect their successional status (Table 1).

I determined the morphological and photosynthetic traits of these species at 2 months after germination for two reasons. First, the survivorship curves were relatively linear (log-scale) from germination through the first year, and the trends of relatively constant mortality rates were already set within the initial 2-month period. Second, at 2 months after germination, all species had exhausted seed reserve, had at least two true leaves, and had completed the initial construction of the autotrophic organs which should influence the subsequent carbon balance and survivorship (2 months–1 year).

Growth conditions and light treatments

Seeds of each species were collected under a single large mother tree. Seedlings were grown in a screened enclosure situated in a large clearing on BCI between May and August 1986, except for *Tachigalia versicolor* which was grown and measured in 1985 with a comparable method (Kitajima and Augspurger 1989). Seeds were planted in nursery flats filled with forest soil between 23 and

Table 1 Study species listed in the order of the rank of shade tolerance. Also listed are their seed mass, mortality rate (= -slope of survivorship curves; Augspurger 1984b), and wood density of 1-year old saplings. Rank of seedling tolerance is based on both field and growth house experiment (Augspurger 1984 a,b). (no data available for those ranked as NA). These species can be

classified into commonly used regeneration classes as follows. 1,2 shade-tolerant with equal survival in gaps and shade; 3–6 and VAT: medium shade-tolerant and small gap-dependent; 7–12 (and TRI): large gap-dependent or early successional; 13: pioneer, prevented from germination in shade. For Leguminosae, subfamily is indicated by -C: Caesalpinioideae, and -P: Papilionoideae

Rank	Code	Species (Family)	Seed Mass ^a (mg)	Mortality Rate (week ⁻¹)	Sapling Wood Density (g cm ⁻³)
1	ASP	<i>Aspidosperma cruenta</i> (Apocynaceae)	492	0.0047	0.51
2	TAC	<i>Tachigalia versicolor</i> (Leguminosae-C)	427	0.00049	0.58
3	BOM	<i>Bombacopsis sessilis</i> (Bombacaceae)	330	0.00033	0.57
4	PLA	<i>Platypodium elegans</i> (Leguminosae-P)	327	0.0018	–
5	LON	<i>Lonchocarpus latifolius</i> (Leguminosae-P)	55.3	0.021	–
6	LAF	<i>Lafoensia panicifolia</i> (Lythraceae)	6.0	0.0053	–
7	TER	<i>Terminalia amazonica</i> (Combretaceae)	2.6	0.018	0.63
8	COR	<i>Cordia alliodora</i> (Boraginaceae)	7.7	0.024	0.55
9	PSE	<i>Pseudobombax septenatum</i> (Bombacaceae)	50.0	0.029	0.37
10	LUE	<i>Luehea seemannii</i> (Tiliaceae)	0.91	0.043	0.37
11	CEI	<i>Ceiba pentandra</i> (Bombacaceae)	31.8	0.045	0.36
12	CAV	<i>Cavanillesia platanifolia</i> (Bombacaceae)	441	0.12	–
13	OCH	<i>Ochroma pyramidale</i> (Bombacaceae)	3.4	0.15	0.24
NA	VAT	<i>Vatairea erythrocarpa</i> (Leguminosae-P)	(482)	–	–
NA	TRI	<i>Trichospermum mexicanum</i> (Tiliaceae)	(2.5)	–	–

^a Mass of seed excluding seed coat except those in parentheses

29 May 1986 under moderate shade (10% of full sun). Immediately following germination, seedlings were singly transplanted to plastic pots (1 or 3.5 l, depending on the seed size) filled with topsoil taken from the forest edge. Slow-release fertilizer (Osmocote 20–20–20) was applied once 6 weeks after planting.

At transplanting, seedlings were randomly assigned to sun (23%) and shade (2%) treatments ($n = 10$ in sun, and $n = 20$ in each type of shade). Two kinds of shading treatments different only in red:far red (R:FR) ratio were created in order to examine the possible effect of light quality under canopy (Smith 1982; Kwesiga and Grace 1986; Kwesiga et al. 1986; Turnbull 1991). Neutral shade (R:FR = 1.33) was created with shade cloth, while canopy-mimic shade (R:FR = 0.23) was created with a filter following Lee (1985). Mean daily total PPFD (and% PPFD) measured for 10 days during the experiment was $6.3 \text{ mol m}^{-2} \text{ day}^{-1}$ (23%) for sun treatment, and $0.5 \text{ mol m}^{-2} \text{ day}^{-1}$ (1.9%) for both shade treatments. Statistical difference in each photosynthetic, morphological, or growth measurement among light treatments were tested by two models of statistical contrast (GLM procedure, SAS). The first model tested the effect of light quality, by contrasting neutral shade to canopy-mimic shade. The second model tested the effect of light intensity by contrasting sun treatment with the average effect of two shade treatments with sun treatment by an orthogonal contrast vector $\{1, -0.5, -0.5\}$. These are *a priori* tests and did not require adjustment of *P* values. There was no significant statistical difference in any photosynthetic, morphological, or biomass measurement between the two shade treatments at $p = 0.05$. The only exception was that hypocotyls at 7 weeks were significantly longer under canopy-mimic shade than in neutral shade for three light-demanding species of Bombacaceae (OCH, CEI, and PSE, see Table 1 for abbreviations). Thus, for simplicity of presentation, data for the two shade treatments were pooled to calculate the means and standard errors given in the results section below.

Measurements of leaf photosynthetic parameters

CO₂ exchange rates of fully-expanded leaves of three seedlings per treatment per species were measured between 7 and 10 weeks after germination with an open-system infrared gas analyzer (ADC model 225) in a configuration similar to the open system of Ehler-

ringer (1983). CO₂ concentration of ambient air in the chamber (= efflux air) was monitored and maintained at $350 \pm 10 \text{ ppm}$ using a mass-flow controller (Tylan model FC260). The air was humidified to approximately 80% at 25 °C. The leaf chamber (180 ml) was made of nickel-plated brass, equipped with a water jacket and heat fins at the bottom, and covered with a clear teflon sheet. Leaf temperature was $26 \pm 2^\circ \text{C}$ during measurements. Two metal halide lamps were used as the light source. The light intensity in the leaf chamber was monitored by a silicon photodiode inside the chamber and adjusted to the desired values by placing layers of neutral shade cloth above the chamber. After an induction period of 20–30 min at $500 \mu\text{mol m}^{-2} \text{ s}^{-1}$ PPFD, steady-state CO₂ exchange rates of leaves were at $800 \mu\text{mol m}^{-2} \text{ s}^{-1}$ PPFD for light saturated net photosynthetic rate (A_{max}), then at 100, 50, and $0 \mu\text{mol m}^{-2} \text{ s}^{-1}$. The apparent light compensation point was calculated using the two points at 0 and $50 \mu\text{mol m}^{-2} \text{ s}^{-1}$ PPFD. All species developed at least two true leaves by 2 months after germination. However, the leaf size of some species was extremely small in shade. Thin photosynthetic cotyledons were used for PSE and the whole shoot, including two cotyledons and small first leaf, was enclosed in the chamber for OCH and COR grown in shade. The photosynthetic oxygen evolution rates of such thin cotyledons are equivalent of true leaves (Kitajima 1992b). No measurements were taken for several shade-grown plants that did not develop large enough leaves or cotyledons (LUE, TER, TRI).

Growth analysis

Immediately after gas exchange rates were measured, seedlings were harvested and the leaf mass per unit area (LMA) of the leaves used for gas exchange measurements, total plant dry mass, root:shoot ratio (root mass divided by shoot mass), and leaf area ratio (LAR, total leaf area divided by the total seedling mass) were determined. Seed mass was determined after removing the seed coat. All mass values were determined after drying at 60 °C.

Mean relative growth rate (RGR, Hunt 1982, eq. 2.7) between germination and harvest was calculated as follows

$$\text{RGR} = \frac{\ln(\text{seedling mass}) - \ln(\text{mean seed mass})}{\text{seedling age at harvest}} (\text{g g}^{-1} \text{ week}^{-1}).$$

The goal here was not to estimate the instantaneous growth rate, but rather to examine the relative change in mass between seed and seedling standardized for the differences in seedling mass and age at harvest (7–10 weeks old). Variation in harvest date itself did not cause a systematic bias in RGR, since there was no significant interspecific correlation between harvest date and calculated RGR. The photosynthetic epigeal cotyledons of eight species (OCH, CAV, CEL, LUE, PSE, COR, TFR, LAF, TAC, TRI; Table 1) were treated as leaves in calculation of leaf area ratio. In separate comparative studies of 50 species, I found that these thin cotyledons were equivalent to true seedling leaves in terms of photosynthetic rates, LMA, and life-span (Kitajima 1992a,b). Non- or semi-photosynthetic thick cotyledons of the remaining species (ASP, BOM, PLA) had naturally abscised before the harvests and were not included in seedling mass. Remaining seedlings in sun treatment were kept growing for another year, and then their wood density was measured for the stem near the base.

Correlation analysis

Species means of response variables of sun-grown and shade-grown plants were used as units for the correlation analyses. Their ratios (= sun mean divided by shade mean) or differences (= sun mean – shade mean) were used as indicators of the degree of phenotypic plasticity. Spearman's rank correlation coefficients (r_s) were used for conservative tests of correlations, because this non-parametric approach is robust to sample distribution problems. For significant relationships, parametric relationships were also examined (e.g., Pearson's correlation coefficients and simple regressions). Seedling mortality rates were log-transformed before plotting in order to correct for their skewed distribution.

Results

Effects of light intensity and species as well as their interactions on gas exchange and morphological traits were all highly significant (two-way analysis of variance, $P < 0.0001$), except for dark respiration rates per unit mass of leaf (species effect was significant at $P < 0.05$).

Gas exchange characteristics

Although significant interspecific variation existed in all CO_2 exchange characteristics, none had a significant correlation with the seedling mortality rates in shade, except for A_{max} per unit mass of sun-grown plants ($P < 0.07$) (Table 2). Light saturated net photosynthetic rate, A_{max} per unit area (Fig. 1A) and per unit mass (Fig. 1B) varied widely among species within a given light treatment. In all but one species (ASP), sun-grown seedlings had significantly higher A_{max} per unit area than shade-grown seedlings (Fig. 1A). Per unit mass, fewer species (8 out of 12 species) had significantly different A_{max} between sun and shade (Fig. 1-B); significant differences on an area basis in three species (BOM, PSE, VAT) disappeared with the concurrent changes in leaf mass per unit area (Fig. 1C). Dark respiration rates (R_d) and light compensation points (LCP) were lower for most species in shade than in sun (Fig. 2). However, as a result of larger proportional errors, these differences were significant in only four species for R_d per unit area and LCP (CAV, BOM, TAC, VAT), and in only two species for R_d per unit mass (CAV, VAT).

Table 2 Spearman's rank correlation tests among seedling mortality rates in shade and various morphological and physiological traits for 13 tropical tree species (n : number of species, r_s : correlation coefficient, P : level of significance, NS if $P > 0.1$). A positive r_s indicates that the value of the variable is higher for shade intolerant species with high mortality

	n	r_s	P
Seed size			
Seed mass (without seed coat)	13	-0.42	NS
Seedling traits expressed in shade			
A_{max} per unit area	11	-0.35	NS
R_d per unit area	10	0.13	NS
R_d per unit mass	10	0.25	NS
Light compensation point	10	0.27	NS
Leaf mass per unit area	13	-0.63	0.03
LAR	13	0.73	0.005
Root: shoot ratio	13	-0.61	0.03
RGR	13	0.53	0.07
Total seedling mass	13	-0.34	NS
Seedling traits expressed in sun			
A_{max} per unit area	13	0.25	NS
A_{max} per unit mass	13	0.52	0.07
LAR	13	0.54	0.06
RGR	13	0.63	0.02
Total seedling mass	13	-0.18	NS
Ratio of sun phenotype to shade phenotype			
A_{max} per unit area	11	0.32	NS
A_{max} per unit mass	11	0.30	NS
Leaf mass per unit area	13	-0.12	NS
LAR	13	-0.27	NS
Root: shoot ratio	11	0.31	NS
Total seedling mass	13	0.58	0.04
Difference between sun phenotype and shade phenotype			
RGR	13	0.67	0.02

Light compensation points were strongly correlated with the R_d per unit area ($r^2 = 0.90$, $P < 0.0002$) and R_d per unit mass ($r^2 = 0.85$, $P < 0.0009$) in shade, but not in sun.

Growth and morphological traits

In both sun and shade, the relative growth rates from seeds to seedlings (RGR) were significantly higher for species with higher mortality rates in shade (Table 2, Figs. 3, 4). The four most shade tolerant species had negative RGR in shade. Abscission of exhausted storage cotyledons in three shade tolerant species (ASP, BOM, PLA) had little influence on RGR. Their RGR in shade would be still negative even if the mass of lost cotyledons were added to the seedling mass. Species with higher RGR in sun had higher RGR in shade as well ($r_s = 0.91$, $P < 0.0001$; Fig. 5). In all species, RGR was significantly higher for sun-grown plants than for shade-grown plants (Fig. 3). The lower the shade tolerance of the species, the greater was its RGR enhancement from shade to sun (= difference between sun and shade) (Table 2). Neither seed mass nor seedling mass in shade had a significant correlation with seedling shade tolerance of the species

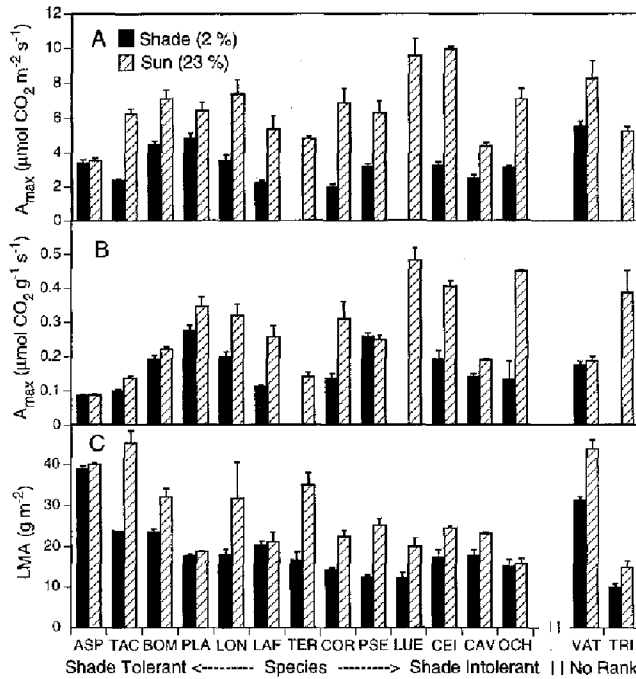


Fig. 1 Light saturated net photosynthetic rates **A** per unit leaf area, and **B** per unit leaf mass, and **C** leaf mass per unit area of fully expanded leaves of 2 month-old seedlings raised in shade (2% full sun) and sun (23% full sun) for 15 tropical tree species with known degrees of seedling shade tolerance. See Table 1 for the full names of the species. Mean and 1 SEM for $n = 3$ to 6 seedlings

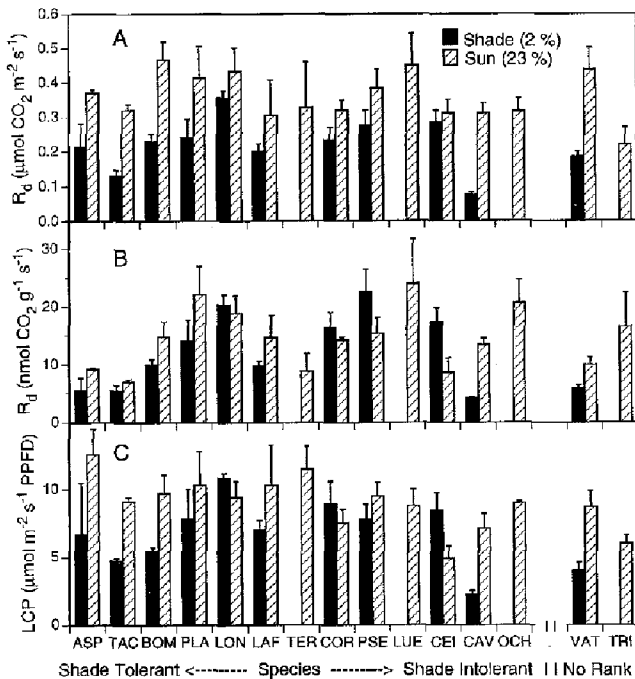


Fig. 2 Dark respiration rates **A** per unit leaf area, and **B** per unit leaf mass, and **C** light compensation points of fully expanded leaves of 2 month-old seedlings raised under shade and sun. Mean and SEM for $n = 3$ to 6 seedlings. See Table 1 for the full names of the species

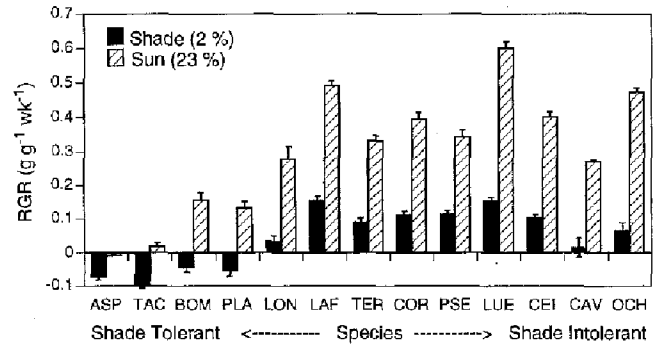


Fig. 3 Relative growth rates (RGR) of seedlings from germination to 2 months under controlled shade and sun for 13 tropical tree species with known degrees of seedling shade tolerance. See Table 1 for the full names of the species

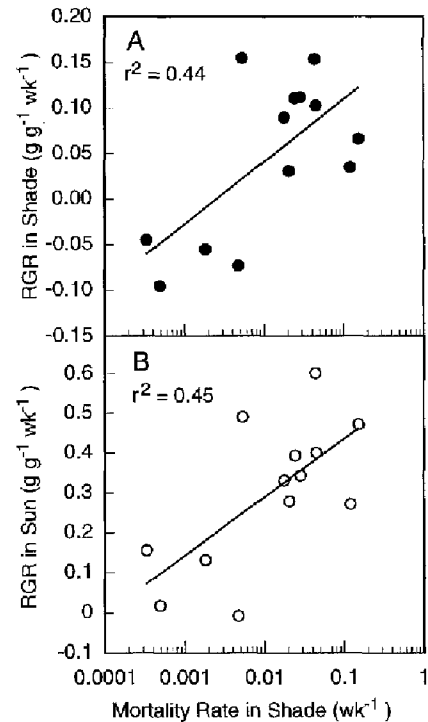


Fig. 4 Relative growth rates (RGR) of seedlings raised **A** in shade and **B** in sun, regressed against the first-year mortality rates of seedlings in shade for 13 tropical tree species ($P < 0.02$ for both relationships). Each point is a species mean

(Table 2). The whole plant mass at 2 months was still largely influenced by seed mass in both sun and shade ($r_s = 0.73$, $P < 0.005$ in sun, $r_s = 0.95$, $P < 0.001$ in shade) and to a much lesser extent by RGR ($r_s = -0.48$, $P < 0.1$ in sun, $r_s = -0.62$, $P < 0.03$ in shade). Thus, the larger the seed, the larger the seedling and the smaller the RGR. The negative correlation between RGR and seed mass was stronger in sun ($r_s = 0.87$, $P < 0.0001$) than in shade ($r_s = 0.76$, $P < 0.003$). The fact that correlation was stronger in sun where biomass gain was greater indicates that this relationship was not a mere autocorrelation, but was a result of the association of seed mass with

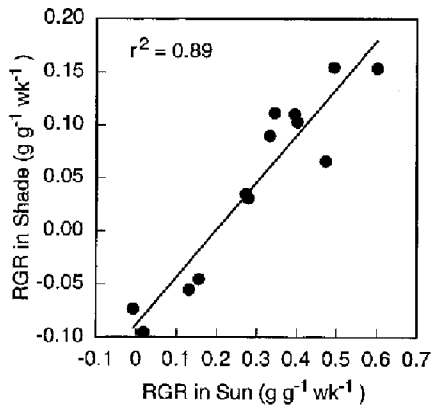


Fig. 5 Relationship between relative growth rates (RGR) of seedlings grown in shade and RGR of seedlings grown in sun for 13 tropical tree species ($P < 0.0001$). Each point is a species mean

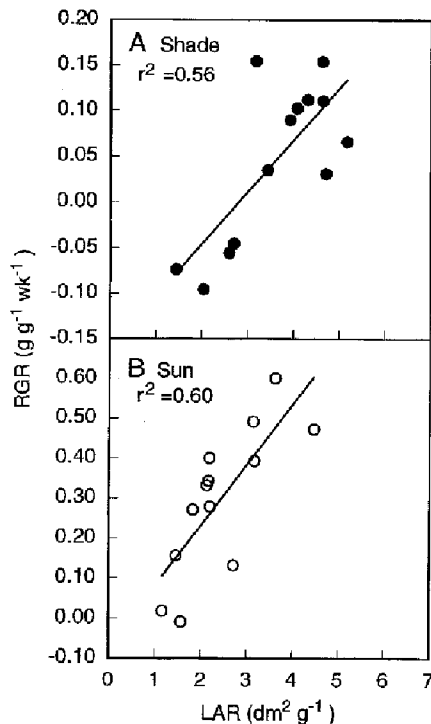


Fig. 6A,B Relative growth rate (RGR) regressed against their leaf area ratio (LAR) for seedlings of 13 tropical tree species, raised under A shade ($P < 0.004$) and B sun ($P < 0.002$) for 2 months. Each point is a species mean

morphological and physiological traits of seedlings. Among the allocation variables examined, LAR was the best predictor of RGR (Fig. 6). LMA and root:shoot ratio were also correlated with RGR, but to a lesser degree (Pearson's correlation coefficient, $r = -0.64$ and -0.48 in shade, -0.73 and -0.43 in sun, respectively). A_{max} was correlated with RGR in sun ($r = 0.71$ and 0.59 on mass and area basis, respectively), but not in shade. Thus, morphological traits that influence LAR were the general basis for the negative relationship between shade tolerance and RGR.

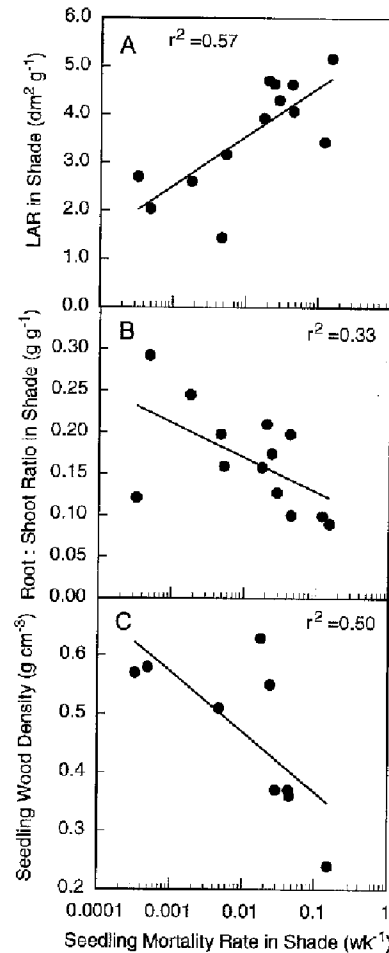


Fig. 7A,B Morphological traits of 2 month-old seedlings developed under shade and C wood density of 1 year-old seedlings, regressed against first-year mortality rates of seedlings in shade, for 13 tropical tree species. Each point is a species mean. $P < 0.003$ (A), $P < 0.04$ (B), and $P < 0.03$ (C)

Both in sun and shade, shade-tolerant species had a suite of morphological traits that lead to lower rates of carbon gain and growth than shade intolerant species. Shade tolerant species had greater leaf mass per unit area (LMA), higher root:shoot ratio, and lower LAR in shade than shade intolerant species (Table 2, Figs. 2, 7A,B). Also, shade tolerant species had higher wood density (Fig. 7C), another trait that leads to lower RGR. Shade tolerant and intolerant species exhibited similar degrees of morphological acclimation responses to light. Ratios of sun-phenotype to shade-phenotype in LMA, LAR, and root:shoot ratio were not correlated with shade mortality rate (Table 2). In 12 out of 15 species, shade-grown plants had significantly lower LMA than sun-grown plants (Fig. 1C). Fewer species showed significant light acclimation in root:shoot ratios (lower in shade than in sun) and LAR (greater in shade than in sun).

Discussion

Negative correlation between growth rate and shade tolerance

Species that failed to survive in shade exhibited a higher RGR in both sun and shade (Fig. 4). RGR in sun and shade were strongly correlated; species that grew faster in sun also grew faster in shade. Such correlation has also been found for seven Melastomataceae species (Ellison et al. 1993). The high inherent growth rates of shade intolerant species probably reflect strong natural selection for faster growth in light gaps where competition is the key selective force. This negative relationship between RGR and survivorship would not disappear even if relative growth rates were calculated using two seedling harvests. In a separate study of growth analyses of 50 tree species (Kitajima 1992b), RGR at three different developmental stages of seedlings (germination - cotyledon expansion, cotyledon - expansion of first true leaves, first-leaf -cotyledon abscission) were significantly correlated with each other. The results in Table 2 and Figs. 3 and 4 support the prediction that pioneer species have higher growth potential than mature forest species, as well as a greater degree of growth enhancement in sun relative to shade (Bazzaz and Pickett 1980). The species examined here were canopy tree species that eventually experience full sun. Thus, the shade-tolerant species here were facultatively adapted to shade and different from obligate shade species that grow and reproduce in the understory. Seedlings of shade tolerant species may survive in the shaded understory for years without significant growth, and simply resume growth when a light gap opens (Brokaw 1985; Canham 1988; Kitajima and Augspurger 1989; Turner 1990). Thus, lack of positive correlation between growth and survival is not surprising, especially in the short term ($\ll 1$ year).

Determinants of RGR

The four most shade tolerant species had negative growth rates, while less shade tolerant species achieved positive growth in shade (Fig. 3). Interspecific differences of RGR at the early seedling stage probably hinge on two aspects: seed reserve utilization and allocation patterns. Shade-tolerant species in this experiment had not recovered from the initial loss of mass during the seed reserve dependency period, although all seed reserves had been used up before the harvest. Shade intolerant species had photosynthetic cotyledons and developed photosynthetic organs earlier than shade tolerant species with storage cotyledons (Kitajima 1992a). Thus, shade-intolerant species rapidly invested all seed reserves in such a manner as to bring a rapid return in carbon gain, while shade-tolerant species kept the seed reserves as storage for longer periods at the expense of growth rate. Although seed mass and seedling size have been shown to be correlates of shade tolerance for temperate tree spe-

cies (Grime and Jeffrey 1965), neither seed mass nor total seedling mass at 2 months was directly related to the degree of shade tolerance. Nevertheless, a larger seed size is a strong correlate of cotyledon type, and is also a prerequisite for spending a large portion of the initial seed reserve for the construction of denser leaves and a large root system in shade. Thus, seed mass was indirectly related to the shade tolerance of the species; the larger the seed size, the lower the inherent growth rate, and the higher the shade tolerance of the species.

Another reason for the negative interspecific correlation between growth rate and survivorship in shade was that shade tolerant species allocated a greater portion of their seed reserves to roots, as well as for a higher LMA at the expense of leaf area expansion (Table 2). Once plants start depending on light as an energy source, RGR is influenced by a combination of photosynthetic and morphological traits. In theories of growth analysis, RGR is a product of net photosynthetic rate per unit leaf area times LAR. In sun, RGR was correlated with morphological traits, such as root:shoot ratios, LAR, and photosynthetic capacity (A_{max}). In shade, only morphological traits, but not leaf gas exchange characteristics, were related to RGR. The lack of correlation between gas exchange characteristics and RGR in shade is not surprising because respiration by non-photosynthetic organs, which was not directly measured here, increases its relative importance in the balance between respiration and photosynthesis in the shaded environment (Givnish 1988). Walters et al. (1993) found that whole-plant respiration rates were similar among three Betulaceae species; however, the most shade-tolerant *Ostrya virginiana*, respire a higher proportion of daily photosynthetic income and has a higher ratio of respiration to RGR than the other two species. Thus, contrary to the earlier prediction, shade tolerant species have lower instantaneous rates of carbon gain as well as lower RGR than shade intolerant species in shade as well as in sun. These findings for temperate tree seedlings corroborate the findings for tropical tree seedlings in this study.

Durable seedling bodies with tough leaves, high LMA, high wood density, and high allocation to roots are more common among shade tolerant species, and such traits defend seedlings against multiple hazardous agents in the understory, including herbivores, pathogens, and branch falls. Thus, shade tolerant species allocate more to defense at the expense of growth. This is in agreement with the general theory of carbon allocation among growth, defense, and storage (Mooney 1972; Coley et al. 1985; Chapin et al. 1990). The main causes of mortality of tropical tree seedlings in the shaded understory are damping-off disease and herbivory (Augspurger 1984a,b; Kitajima and Augspurger 1989). When survival is paramount, species should allocate more to defense against herbivores, pathogens, or accidental loss of tissue, as well as to storage for recovery from the loss of tissue, at the expense of growth. It is important to point out that relative growth rates measured here are not the same as the realized growth rate in the field after car-

bon loss to herbivores and pathogens have taken place. Future research on shade tolerance should address carbon loss due to biotic and physical agents, as well as the cost and benefit of defensive traits and storage of non-structural carbohydrates in stems and roots.

Morphology and shade tolerance

Evolutionary responses to enhance survivorship in shade appear to be in the opposite direction from plastic responses to shade. Both shade-tolerant and -intolerant species exhibited acclimation responses of morphological traits to optimize the whole-plant carbon balance in shade. Within species, shaded plants had smaller leaf mass per unit area (LMA), lower investment in roots (root:shoot ratio), and greater leaf area per plant mass (LAR). Among species, shade tolerant species had significantly higher LMA, relatively larger investment in roots, and lower LAR than shade intolerant species in both sun and shade (Table 2 and Fig. 7). In temperate tree species also, evolutionary responses to light environment have been found to be opposite of phenotype plasticity; within species, shaded individuals have lower LMA and chemical defenses in leaves; however, among species, shade-adapted species have higher LMA and defenses than pioneers (Walter et al. 1993; Shure and Wilson 1993). Several tropical and temperate studies suggest that higher LMA is correlated with leaf toughness, leaf chemical defenses and longer leaf life span (Koike 1988; Lei and Lechowicz 1990; Reich et al. 1991). In addition, seedling shade tolerance is correlated with sapling and adult wood density for the species studied here (Table 1; Augspurger 1984b). Higher wood density might improve defense against physical damages and biotic agents in addition to providing structural support (Lei and Lechowicz 1990). What is important for survival in shade is how durable a seedling body is constructed even in a low-energy environment, not the maximization of net carbon gain and growth in shade.

Sun-shade acclimation of photosynthetic capacity

There was only a weak trade-off between ability to achieve high photosynthetic capacity in sun and ability to survive in shade. A_{\max} per unit leaf mass of sun-grown plants was weakly correlated with seedling mortality rates in shade, but not A_{\max} per unit leaf area (Table 2). Also, A_{\max} per unit mass was a better predictor of RGR than A_{\max} per unit area in sun. Thus, A_{\max} per unit mass might be of more interest than A_{\max} per unit area for interspecific comparisons, although more species showed significant phenotypic plasticity per unit area than per unit mass. In all but one study species, A_{\max} per unit leaf area was significantly higher in sun than in shade. Only one very shade tolerant species lacked any photosynthetic acclimation ability (*Aspidosperma*), while other equally shade tolerant species in the current study, e.g.,

Tachigalia and *Bombacopsis*, showed a large plasticity in A_{\max} per unit area. Thus, the results did not support the initial prediction that photosynthetic plasticity would be more limited in shade tolerant species than in pioneer species. Similarly, no correlation was found between the rank of seedling shade tolerance and the magnitude of phenotypic responses in photosynthetic capacity (Table 2). In several species that had similar A_{\max} per unit mass in sun and shade (Fig. 1B), the differences in A_{\max} per unit area (Fig. 1A) between sun- and shade-grown plants were due to morphological responses, while in the remaining species they were due to both physiological and morphological responses. Species that did not change A_{\max} per unit mass were found among both light demanding and shade tolerant species. Thus, physiological and morphological plasticity of leaves differed among species independently from their degree of shade tolerance or successional status.

A_{\max} per unit area of the species studied here were in the same range found for other tropical tree seedlings (Lugo 1970; Koyama 1981; Langenheim et al. 1984; Fetcher et al. 1987; Strauss-Debenedetti and Bazzaz 1991). The sun treatment used in this study (23% or 6.3 mol m⁻² d⁻¹) was similar to that in a medium-to-large gap center. Seedlings in the sun treatment received PPFD well over light saturation level for a large portion of the day but this was much lower than direct sun in a very large clearing. This light intensity might not be enough for some species (especially pioneers) to express their full photosynthetic capacity. However, a further increase of light above 25 % of full sun yielded little or no increase in photosynthetic capacity in seedling leaf photosynthesis in other studies (Oberbauer and Strain 1986; Fetcher et al. 1987; Turnbull 1991). Although upper canopy and pioneer trees in the full sun develop leaves with a maximum photosynthetic capacity of more than 20 μmol CO₂ m⁻² s⁻¹ (Stephens and Waggoner 1970; Koyama 1981), seedling leaves of such light demanding species in this and other studies did not develop such high photosynthetic capacities even in the full sun (Lugo 1970; Fetcher et al. 1987; Ramos and Grace 1990; Straus-Debenedetti and Bazzaz 1991; but see Oberbauer and Strain 1984). This may suggest an ontogenic constraint on seedling morphology, preventing them from developing large and heavy leaves like adults (Bazzaz and Pickett 1980; Hoflacher and Bauer 1982; Koike 1988).

Effect of R:FR ratio in shade

In the current study, the only effect of the low R:FR ratio simulating the forest shade was an elongation of the hypocotyl in three species (*Ochroma*, *Ceiba*, and *Pseudobombax*). All three species belonged to the Bombacaceae, a family with a large number of early successional, shade intolerant species. Similarly, in other studies, some light-demanding species have been found to respond to light quality with a morphological response

(Morikawa et al. 1976; Smith 1982; Kwesiga and Grace 1986). However, stem elongation is probably disadvantageous for survival in the shade under a tall canopy which can not be escaped by this response. Indeed, the seedlings of *Ochroma* in low R:FR shade suffered much higher mortality than in neutral shade. Several studies (Chow et al. 1990; Kwesiga et al. 1986; Turnbull 1991) have found some effect of light quality on photosynthetic characteristics, especially when plants were raised under somewhat unnatural combinations of very low R:FR ratio (e.g. 0.2) with relatively high photon flux ($> 90 \mu\text{mol m}^{-2} \text{s}^{-1}$). However, none of the tropical tree species examined here showed any differences in their CO_2 exchange characteristics. Furthermore, none showed any difference in allocation patterns or relative growth rates. Likewise, Morikawa et al. (1976) and Kwesiga and Grace (1986) found little change in growth rate in response to R:FR ratio despite large morphological changes. Thus, as an aspect of the natural shade, low R:FR ratio may influence morphological traits of some pioneer and light-gap species, but appears much less important than light intensity as a cue for modification of photosynthetic traits.

Respiration and light compensation point

Low dark respiration rates and low light compensation points in shade-leaves compared to sun-leaves are considered to be adaptive since both contribute to a more positive carbon budget in the low light environment (Loach 1967; Boardman 1977). Most studied species here showed this acclimation response, although more than half of them did not show a statistically significant response due to large within-treatment variation. The range of dark respiration rates was similar to those in other studies of tropical tree species (Fetcher et al. 1987; Fredeen and Field 1991). Light compensation points, especially of sun-grown plants, were generally lower than those found in other studies of tropical tree seedlings (Langenheim et al. 1984; Fetcher et al. 1987; Ramos and Grace 1990), but similar to those measured by Turnbull (1991). Several studies have found smaller dark respiration rates and lower light compensation points in shade-tolerant species than light demanding species when both were grown in a comparable shade (Fetcher et al. 1983; Mulkey 1986; Sims and Percy 1989), but not in the current and other studies (Fredeen and Field 1991; Turnbull 1991; Walters et al. 1993). Thus, there was no interspecific correlation between these traits that increase the net carbon gain rate of leaves in shade and the degree of shade tolerance at the early seedling stage.

Conclusion

Traits that maximize the rate of net carbon gain do not lead to higher survival in shade. Acclimation responses of individual photosynthetic traits were not necessarily

different between shade tolerant and intolerant tropical tree species. Fast-growing species in sun were also fast growing species in shade, and their greater positive carbon balance *per se* did not lead to higher survival. Instead, inherent growth rates, determined mainly by morphological traits, appear to be negatively correlated with the survival potential of the species in shade. This is probably because faster growth rates are achieved at the expense of defense and storage allocation.

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