

Relative importance of photosynthetic physiology and biomass allocation for tree seedling growth across a broad light gradient

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Summary Studies of tree seedling physiology and growth under field conditions provide information on the mechanisms underlying inter- and intraspecific differences in growth and survival at a critical period during forest regeneration. I compared photosynthetic physiology, growth and biomass allocation in seedlings of three shade-tolerant tree species, *Virola koschynii* Warb., *Dipteryx panamensis* (Pittier) Record & Mell and *Brosimum alicastrum* Swartz., growing across a light gradient created by a forest–pasture edge (0.5 to 67% diffuse transmittance (%T)). Most growth and physiological traits showed nonlinear responses to light availability, with the greatest changes occurring between 0.5 and 20 %T. Specific leaf area (SLA) and nitrogen per unit leaf mass (N_{mass}) decreased, maximum assimilation per unit leaf area (A_{area}) and area-based leaf N concentration (N_{area}) increased, and maximum assimilation per unit leaf mass (A_{mass}) did not change with increasing irradiance. Plastic responses in SLA were important determinants of leaf N and A_{area} across the gradient. Species differed in magnitude and plasticity of growth; *B. alicastrum* had the lowest relative growth rates (RGR) and low plasticity. Its final biomass varied only 10-fold across the light gradient. In contrast, the final biomass of *D. panamensis* and *V. koschynii* varied by 100- and 50-fold, respectively, and both had higher RGR than *B. alicastrum*. As light availability increased, all species decreased biomass allocation to leaf tissue (mass and area) and showed a trade-off between allocation to leaf area at a given plant mass (LAR) and net gain in mass per unit leaf area (net assimilation rate, NAR). This trade-off largely reflected declines in SLA with increasing light. Finally, A_{area} was correlated with NAR and both were major determinants of intraspecific variation in RGR. These data indicate the importance of plasticity in photosynthetic physiology and allocation for variation in tree seedling growth among habitats that vary in light availability.

Keywords: *Brosimum alicastrum*, Costa Rica, *Dipteryx panamensis*, growth response coefficients, leaf nitrogen, natural light gradient, photosynthesis, relative growth rate, tropical rain forest, *Virola koschynii*.

Introduction

In tropical forests, light is an important limiting resource for

tree seedling establishment, growth and survival (Denslow 1987, Chazdon et al. 1996, Aygeman 1999). Much research has focused on the role of light availability in processes at the leaf, whole-plant, population and community levels (Welden et al. 1991, Oberbauer et al. 1993, Kobe 1999, Poorter 1999). The classification of species into functional groups (e.g., pioneer, non-pioneer, gap-dependent, shade-tolerant) is based on species' light requirements (Swaine and Whitmore 1988). Pioneer tree species have received considerable attention, whereas research on non-pioneers lags behind (Brokaw 1987, Ackerly and Bazzaz 1995, Dalling et al. 1998, Davies 1998). Broadly defined, non-pioneers are species that can germinate and establish in the shade (Swaine and Whitmore 1988). The most shade-tolerant trees can persist in shade, defend against or tolerate herbivores and pathogens, and survive repeated mechanical damage (Clark and Clark 1985, Coley 1985, Hubbell 1998). Because non-pioneer species often experience dramatic increases and decreases in their light environment during their lifetime (Clark et al. 1993), they can maintain high seedling and sapling fitness (at this life stage, equated to survival) in both dimly lit, closed-canopy conditions and high-irradiance canopy gaps. Few studies have explored variation among shade-tolerant species in physiology and growth across gradients in irradiance (Mulkey 1986, Strauss-DeBenedetti and Bazzaz 1991, Mulkey et al. 1991, 1993, Oberbauer et al. 1993, Montgomery and Chazdon 2002). Moreover, only a handful of studies have examined photosynthetic physiology under field conditions in any tropical tree species (Oberbauer et al. 1993), despite the numerical importance of shade-tolerant species, which may represent > 80% of all tree species in tropical wet forests and are an important component in gaps (Welden et al. 1991).

Functional responses to increasing light availability involve biochemical and anatomical changes at the leaf and whole-plant level. Plants possess a suite of photosynthetic traits that shift with growth irradiance and theoretically maximize survival, carbon gain or growth at a given irradiance (Boardman 1977, Bjorkman 1981, Walters and Field 1987, Givnish 1988, Sims and Pearcy 1991, Strauss-DeBenedetti and Bazzaz 1991, Kamaluddin and Grace 1992, Kitajima 1994). Plants grown in high-light environments have high photosynthetic capacity

and high respiration rates and require more light to saturate photosynthesis compared with plants grown in low light conditions (Walters and Field 1987, Givnish 1988, Sims and Pearcy 1991, Strauss-Debenedetti and Bazzaz 1991, Kama-luddin and Grace 1992). Within and among species, leaves decrease specific leaf area (SLA; $\text{cm}^2 \text{g}^{-1}$) as growth irradiance increases such that, in sunny microsites, a greater mass is displayed over a smaller area (Jurik 1986). As a result, species often show increases in maximum assimilation per unit leaf area (A_{area}) with increasing irradiance. From an economic perspective, as irradiance increases, carbon gained per unit of carbon invested (e.g., A_{mass}) should also increase (Givnish 1988); however, plants differ in their ability to implement this strategy (Chazdon and Field 1987, Chazdon 1992, Mulkey et al. 1993, Newell et al. 1993, Ducrey 1994, Davies 1998, Sims et al. 1998). Also, plants from high-light environments tend to allocate relatively more biomass to roots than leaves, reflecting the limitation of belowground resources relative to aboveground resources.

Most research has examined plant responses at the endpoints of the sun–shade continuum. Such studies provide no information about the shape of a trait's response across a range of light conditions. For example, it is unknown if photosynthetic capacity increases in a linear, asymptotic or threshold fashion. All three functional responses could generate the observed differences in physiology and growth at the endpoints; however, they imply different mechanisms of response. It is also unknown if species or functional groups differ in the shape of their response. Several studies suggest that shade-tolerant species exhibit an asymptotic response in both photosynthesis and growth across light gradients (Ducrey 1994, Poorter 1999). If this is the case, what limits the increase in photosynthetic capacity or growth as light increases? This question introduces a second aspect, that of shifting ratios of limiting resources across the sun–shade continuum (Bloom et al. 1985). In the shade, light limits fixation of CO_2 relative to nutrients and water, whereas the converse occurs in the sun, with water and nutrients becoming relatively more limiting (Bloom et al. 1985). At high irradiances, the costs of nutrient and water acquisition required to support a high photosynthetic capacity may not balance returns on investment (Givnish 1986). In other words, as light availability increases, investment in high photosynthetic capacity may come with diminishing returns. Such a prediction underlies the functional equilibrium theory of biomass allocation (Brouwer 1983). Roughly, this theory posits that when aboveground resources are limiting, plants allocate more resources to shoot function, and when belowground resources are limiting, plants allocate more resources to root function. The theory has been applied in the context of understanding biomass allocation but not to understanding leaf physiology and how it relates to growth.

This paper presents field data on growth, biomass allocation and photosynthesis in tree seedlings grown across a field light gradient. I used a transplant approach to control for seedling history and studied three shade-tolerant canopy tree species. There were no controls of pathogens or herbivores or mediation through fertilization or watering. My goal was to explore

functional responses (physiology, allocation and growth) to light availability pertinent to understanding patterns of plasticity in shade-tolerant species across a light gradient. I used continuous variation in light (forest–pasture boundary) to explore nonlinearity in the shape of a species' response, which goes undetected when only the endpoints of a resource gradient are assessed. I sought to answer the following questions. How do leaf physiology, growth and allocation shift across a gradient of light availability; do species differ in their plasticity to a natural range of light conditions? What are the functional relationships among these traits? What are the determinants of intraspecific variation in growth?

Materials and methods

The study was conducted at La Selva Biological Station, located in the Sarapiquí region of NE Costa Rica. This area is classified in the Holdridge life-zone system as tropical premontane wet forest and receives more than 4000 mm of rain annually (McDade et al. 1994). Currently, this region is a mosaic of agricultural lands, tree plantations, second-growth, selectively logged and old-growth forests (Butterfield 1994). The study site was located at the border between a 23-year-old second-growth forest and an abandoned pasture. The abandoned pasture was dominated by the fern, *Hypolepis repens* (L.) C. Presl., which decreased in abundance at the forest edge. Soils were derived from ancient lava flows and classified as typic trophumults. They are strongly acidic, rich in organic matter and highly leached, and exhibit a low degree of base saturation (Sollins et al. 1994).

The three species studied, *Dipteryx panamensis* (Pittier) Record & Mell (Fabaceae), *Virola koschnyii* Warb. (Myristicaceae) and *Brosimum alicastrum* Swartz. (Moraceae), are canopy or emergent trees occurring at La Selva and surrounding areas. Although none are classified as pioneer species, *D. panamensis* has been described as gap-dependent because of the low survivorship of young seedlings in mature forest (Clark and Clark 1985). All are considered to be shade-tolerant as seedlings, capable of germination, growth and survival in the shade. Of the three species, *V. koschnyii* was most common among naturally occurring seedlings in the second-growth forest study sites (R.L. Chazdon, University of Connecticut, unpublished data).

Seeds were collected in January 1997 from 5–10 parent trees of *V. koschnyii* and *D. panamensis* growing at La Selva and in nearby forest fragments. Escuela Agrícola del Tropico Humedo (EARTH), an agricultural university near La Selva, provided *B. alicastrum* seeds of unknown genetic origin, collected in the vicinity of the field sites. Seeds were germinated in sand in nursery flats. When the first set of leaves had expanded, the seedlings were transferred to plastic seedling bags (*D. panamensis*) or root trainers (*V. koschnyii* and *B. alicastrum*) filled with a mixture of local soil and compost (Wightman 1997) and placed under 80% shade cloth in a shaded nursery. The growing environment was ~7% of full sun.

Seedlings were transplanted in July 1997 when they were

about 5 months old. At transplanting, the seedlings differed in initial sizes: mean height (cm \pm 1 SE) and biomass (g), respectively, were 30.6 (\pm 3.8) and 4.74 (\pm 1.8) for *D. panamensis*, 18.7 (\pm 1.8) and 2.68 (\pm 0.30) for *V. koschynii* and 26 (\pm 1.4) and 1.1 (\pm 0.10) for *B. alicastrum*. Seedlings were planted along two transects spanning the second-growth pasture edge. The two transects were not replicates but, rather, allowed a wider range of light conditions to be sampled than would any single transect. Fifteen individuals per species were planted on each transect. Seedlings were planted in three parallel rows, spaced 1 m apart within rows and 1.5 m between rows. There was no apparent interaction between roots or shoots of adjacent plants. To assess transplant effects, leaf abscission and plant mortality were checked during the first 3 months of the study and compared with rates later in the study. There was no evidence of significant transplant effects on final patterns of growth for any species.

At the time of transplanting, a sample of seedlings ($N = 6$ – 10 per species) was harvested to document initial patterns of biomass partitioning. Seedlings were separated into leaves, stems and roots. Leaf area was measured with a leaf area meter (LI-3100, Li-Cor, Lincoln, NE) and all material was dried at 70 °C. For each species, total biomass or root biomass was regressed on diameter to yield species-specific equations for estimation of initial seedling biomass and initial root biomass. These regressions all yielded r^2 values above 0.95. Initial leaf area for each seedling was estimated based on regressions of leaf width and leaf length.

Stem length (total length of main stem and any branches) and growth in diameter (taken at a marked section of stem to minimize measurement error) were measured at the start and the end of the experiment. In September 1998, 14 months after transplantation, all surviving seedlings were harvested and each was separated into root, shoot and leaf components. *Virola koschynii* and *B. alicastrum* lack distinct petioles and all material from the point of insertion on the stem was considered leaf. *Dipteryx panamensis* had compound leaves and the rachis of each leaf was considered part of the stem (or support) component. Leaf area was measured (Li-Cor LI-3100), and seedlings were dried at 70 °C for 48 h and weighed. Net assimilation rate (NAR) and relative growth rate (RGR) were calculated following Hunt (1982).

Photosynthetic light response curves were measured with a portable infrared gas analyzer (Li-Cor LI-6250) in closed mode and a red-blue LED light source (Quantum Devices, Barneveld, WI). Plants were induced at 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for 30 min; the irradiance was then gradually stepped down, allowing the leaf at least 5 min to adjust to each new irradiance. The chamber was opened between measurements to maintain ambient CO_2 , concentration, temperature and humidity within the chamber. The number of measurements between maximum photosynthetic rate and dark respiration varied depending on the individual plant; however, in all cases, a minimum of six measurements at irradiances below the light saturation point was included. Light saturation occurred between 200 and 600 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Measurements were made at ambient

CO_2 concentration (initiated between 350 and 360 ppm with a maximal drop of 20 ppm during measurement), 60–85% relative humidity and leaf temperatures less than 32 °C. Because of errors in the humidity sensors associated with humidities of > 70%, stomatal conductance readings were considered inaccurate and were discarded. Photosynthesis was measured on the newest fully expanded leaf of 10–12 individuals per species growing across the light gradient. Photosynthetic measurements were made on a subset of seedlings before transplanting and on transplanted seedlings in October 1997 and May 1998. The light response curve was modeled by a nonrectangular hyperbola (Prioul and Chartier 1977, Leverenz and Jarvis 1979).

Small leaf areas in all species at low light did not allow collection of leaf tissue at the time of photosynthetic measurements. Because removal would have significantly decreased total leaf area and affected measurements of growth and biomass partitioning, leaf punches were taken in August 1998 during the final biomass harvest. Samples were dried at 70 °C and weighed. Total leaf nitrogen (N) was analyzed by isotope ratio mass spectrometry (Europa Scientific Integra, PDZ Europa, Cheshire, U.K.) at the University of California-Davis Stable Isotope Facility. From these data, photosynthesis on a leaf mass and leaf N basis was calculated. Because leaf punches were taken at the end of the study, photosynthesis on a mass and N basis was calculated only for data collected in May 1998.

To assess leaf life span, a census of individuals was taken every 2 months. At each census, new leaves were counted and marked and the number of leaves remaining in previous cohorts was recorded. From these data, the life span of each leaf was determined as the number of days between birth (first census marked) and death (census at which leaf was recorded). Leaves that outlived the study period were treated as censored in a survival analysis (STATISTICA, StatSoft, Tulsa, OK).

Bimonthly censuses of percent diffuse transmittance (% T) above seedlings were used to estimate the overall light environment. Instantaneous measures of % T are correlated with total daily photosynthetic flux density (PFD) and are sensitive to small changes in the light environment (Parent and Messier 1996, Nicotra et al. 1999). I calculated % T as the ratio of PFD below the forest canopy to that above the canopy. Below-canopy PFD was measured with a sunfleck ceptometer, a line sensor consisting of 80 photodiodes (Decagon Devices, Pullman, WA). The user can program the number of sensors used for measurement. Each below-canopy sample was an average of five successive 1-s measurements by 20 adjacent photodiodes. These 20 sensors covered approximately 20 cm, roughly the diameter of the seedling crown. I referenced each below-canopy measurement to an above-canopy measurement made in the center of the pasture. This site was fully exposed for 58° from the zenith. Above-canopy measurements were made with a Li-Cor quantum sensor (LI-190SA) mounted on a 6-m pole and attached to a data logger (21X, Campbell Scientific, Logan, UT) that stored 10-s means of 0.5-s measurements. All measurements were made on overcast days in the early morn-

ing or late afternoon to avoid the influence of direct light, and to ensure that the above- and below-canopy measurements were made under similar sky conditions.

There were no statistical differences between the area-based light response curves measured in October and May; therefore, analyses of these data (A_{area} , dark respiration rate per unit leaf area (R_{area}), instantaneous compensation point and light saturation point) combine the two field measurement periods (ANOVA, $F_{1,48} = 1.95$, $P = 0.17$). Mass-based estimates of photosynthetic parameters were calculated only for the May data set. All analyses of mass-based parameters and leaf N were for the May data set. Dummy variable regression models were used to compare species differences in response to variation in %T (STATISTICA). This approach analyzed multiple partial F -statistics for full model versus reduced models. Reduced models were designed to test specific hypotheses about species' differences in light response. These specific hypotheses included: H_0 : equal slope, tests the null hypothesis of no difference among species in light-dependent physiology; H_0 : equal intercepts, tests the null hypothesis of no difference among species in physiology as light availability approached zero, i.e., no difference at low irradiances. In cases where the slopes are equal, this approach is equivalent to an analysis of covariance.

Measures of biomass partitioning, such as leaf weight ratio (LWR) and root weight ratio (RWR), are influenced by plant mass and can change through ontogeny independently of resource environment (Coleman et al. 1994, Farrar and Gunn 1998, McConnaughay and Coleman 1999). I used multiple regressions to analyze the responses of leaf area ratio (LAR; cm^2 leaf g^{-1} total biomass), RWR (g root g^{-1} total biomass), leaf weight ratio (g leaf g^{-1} total biomass), and stem weight ratio (SWR; g stem g^{-1} total biomass) as a function of light and plant mass.

To understand the functional basis of variation in RGR, I used a method that calculates growth response coefficients (GRC) for each of the components of RGR (e.g., LAR, NAR, LWR and SLA; Poorter and Van der Werf (1998)). I explored intraspecific variation in RGR among individual plants growing across a light gradient. The GRCs were calculated for each species based on regressions of $\ln\text{LAR}$, $\ln\text{LWR}$, $\ln\text{SLA}$ or $\ln\text{NAR}$ on $\ln\text{RGR}$.

Results

Light gradient

Mean light availability ranged from 0.5 %T at the shady end of the gradient to 67 %T at the sunny end. Measured %T varied significantly with month (repeated measures ANOVA $F_{5,290} = 112.2$, $P < 0.0001$); it was highest in September and April and lowest in August. This variation did not appear to be related to vegetation change at the site, because a similar pattern was observed at four closed-canopy sites that were measured concurrently (Montgomery 1999). For any sampling point, standard deviation in %T ranged from 0.25 to 0.5% at the shady end of the gradient to 5 to 10% at the sunny end. The mean coefficient

of variation (CV) at a single point across sampling times was 27%, whereas the mean CV across sampling points was almost 5 times larger at 116%. Rank order of positions shifted little over time. Occasionally, adjacent positions swapped order, but mean %T strongly reflected mean rank.

Light response of leaf traits

Maximum assimilation rate per unit leaf area (A_{area} ; $\mu\text{mol m}^{-2} \text{s}^{-1}$) varied from 1.24 in the forest understory to 8.38 in an abandoned pasture. In *D. panamensis* and *V. koschynii*, A_{area} increased with increasing irradiance; however, the response was nonlinear (Figure 1). Instead, A_{area} was an asymptotic function of light microsite. Below ~20 %T, species exhibited substantial increases in photosynthetic capacity with increasing light, whereas above ~20 %T, seedlings did not substantially increase their A_{area} (Figure 1). Comparing individuals of *D. panamensis* and *V. koschynii* growing at the same irradiances, *D. panamensis* seedlings had significantly higher A_{area} than *V. koschynii* seedlings ($F_{2,49} = 7.29$, $P = 0.002$, Table 1), but the rate of increase was not significantly different ($F_{1,49} = 0.051$, $P = 0.822$, Table 1). *Brosimum alicastrum* had the lowest A_{area} across all irradiances ($F_{2,49} = 19.38$, $P < 0.0001$).

Maximum assimilation per unit leaf mass (A_{mass} ; $\text{nmol CO}_2 \text{g}^{-1} \text{s}^{-1}$) was not related to growth irradiance in any species. *Brosimum alicastrum* showed the strongest trend, with A_{mass} decreasing with increasing irradiance (Pearson's $r = -0.57$, $P = 0.18$). Species differed significantly in mean A_{mass} (Table 2). Across light environments, *D. panamensis* had higher A_{mass} than *B. alicastrum* (Tukey's HSD post-hoc test, $P = 0.001$). *Virola koschynii* was intermediate and did not differ significantly from the other species. Species did not differ significantly in dark respiration rates (R_d) on a leaf mass or leaf area basis (Table 2). Non-reciprocal changes in A_{area} and R_d influenced patterns of change in the light compensation points.

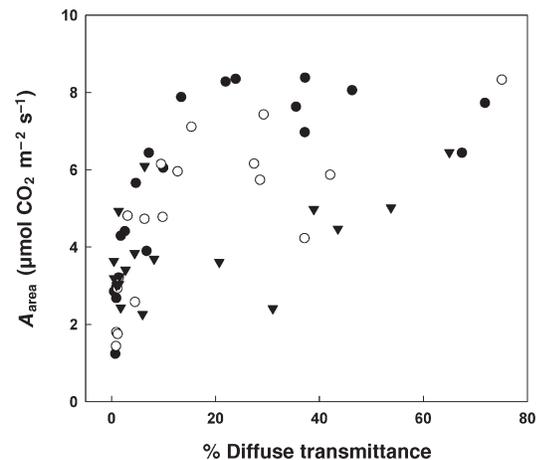


Figure 1. Relationship of maximum assimilation per unit leaf area (A_{area}) to percent diffuse transmittance for seedlings of *Dipteryx panamensis* (●), *Virola koschynii* (○) and *Brosimum alicastrum* (▼) growing across a forest–pasture edge at La Selva Biological Station, Costa Rica.

Table 1. Regression equations ($y = a + bx$) describing relationships among assimilation, leaf morphology, nitrogen (N) and light availability for seedlings of *Dipteryx panamensis*, *Virola koschnyii* and *Brosimum alicastrum* growing across a forest–pasture edge at La Selva Biological Station, Costa Rica. Data are shown for regressions with $P < 0.10$. Abbreviations: A_{area} = maximum assimilation per unit leaf area; % T = percent diffuse transmittance; LCP = light compensation point; LSP = light saturation point; SLA = specific leaf area; N_{area} = leaf nitrogen per unit leaf area; N_{mass} = leaf nitrogen per unit leaf mass; and A_{mass} = maximum assimilation per unit leaf mass.

Species	Regression parameters and coefficients					
	y	a	b	x	P	r^2
Maximum assimilation per unit leaf area versus light availability						
<i>D. panamensis</i>	A_{area}	3.182	1.237	ln% T	0.0010	0.78
<i>V. koschnyii</i>	A_{area}	2.264	1.200	ln% T	0.0100	0.66
Light compensation point versus light availability						
<i>D. panamensis</i>	LCP	6.12	2.781	ln% T	0.0800	0.17
<i>B. alicastrum</i>	LCP	8.47	5.998	ln% T	0.0290	0.27
Light saturation point versus light availability						
<i>D. panamensis</i>	LSP	97.6	68.62	ln% T	0.0001	0.78
<i>V. koschnyii</i>	LSP	150.5	32.11	ln% T	0.0600	0.21
<i>B. alicastrum</i>	LSP	125.5	43.04	ln% T	0.0110	0.34
Specific leaf area versus light availability						
<i>D. panamensis</i>	SLA	447	60.5	ln% T	0.0001	0.54
<i>V. koschnyii</i>	SLA	349	50.4	ln% T	0.0001	0.87
<i>B. alicastrum</i>	SLA	267	34.5	ln% T	0.0001	0.63
Leaf nitrogen per unit leaf area versus light availability						
<i>D. panamensis</i>	N_{area}	0.636	0.151	ln% T	0.0001	0.60
<i>V. koschnyii</i>	N_{area}	0.528	0.209	ln% T	0.0001	0.84
<i>B. alicastrum</i>	N_{area}	1.110	0.070	ln% T	0.0806	0.20
Leaf nitrogen per unit leaf mass versus light availability						
<i>D. panamensis</i>	N_{mass}	29.5	-1.218	ln% T	0.0001	0.60
<i>B. alicastrum</i>	N_{mass}	29.9	-3.33	ln% T	0.0001	0.64
Leaf nitrogen per unit leaf area versus specific leaf area						
<i>D. panamensis</i>	N_{area}	1.7	-23.3	SLA	0.0001	0.89
<i>V. koschnyii</i>	N_{area}	1.9	-39.4	SLA	0.0001	0.87
<i>B. alicastrum</i>	N_{area}	1.7	-24.3	SLA	0.0030	0.48
Leaf nitrogen per unit leaf mass versus specific leaf area						
<i>D. panamensis</i>	N_{mass}	22.6	146	SLA	0.0030	0.39
<i>V. koschnyii</i>	N_{mass}	24.1	113	SLA	0.0680	0.16
<i>B. alicastrum</i>	N_{mass}	10.4	666	SLA	0.0010	0.58
Maximum assimilation per unit leaf area versus specific leaf area						
<i>D. panamensis</i>	A_{area}	11.2	-195.9	SLA	0.0010	0.87
<i>V. koschnyii</i>	A_{area}	9.2	-194.0	SLA	0.0160	0.54
Maximum assimilation per unit leaf mass versus specific leaf area						
<i>D. panamensis</i>	A_{mass}	6.5	2703	SLA	0.0160	0.72
Maximum assimilation per unit leaf area versus N per unit leaf area						
<i>D. panamensis</i>	A_{area}	-1.78	7.37	N_{area}	0.0080	0.71
<i>V. koschnyii</i>	A_{area}	1.67	3.03	N_{area}	0.1130	0.28
<i>B. alicastrum</i>	A_{area}	0.884	1.80	N_{area}	0.1460	0.37
Maximum assimilation per unit leaf mass versus N per unit leaf mass						
<i>B. alicastrum</i>	A_{mass}	-24	3.66	N_{mass}	0.0370	0.62

Brosimum alicastrum, with the lowest A_{area} but similar R_d to the other species, had significantly higher instantaneous light compensation points compared with the other species (Table 1, $F_{3,49} = 7.44$, $P < 0.001$). Both light compensation point and light required to saturate photosynthesis increased asymptotically with light in all species. *Dipteryx panamensis* and *V. koschnyii* did not differ in the relationship between the light compensation point and seedling light microsite ($F_{3,49} = 0.581$, $P = 0.63$). *Dipteryx panamensis* required increasingly more light to saturate photosynthesis as light availability increased (e.g., steeper slope than *V. koschnyii*, $F_{4,51} = 4.04$, $P = 0.01$, Table 1).

Specific leaf area decreased in a nonlinear fashion with increasing light availability in all species (Table 1 and Figure 2). Species differed slightly in the slope of the relationship between % T and SLA ($F_{2,55} = 4.07$, $P = 0.01$, Table 1) and, for a given % T , *D. panamensis* had higher SLA than *V. koschnyii*, which was higher than SLA of *B. alicastrum* ($F_{2,55} = 32.5$, $P < 0.0001$). Leaf life span differed significantly between species (ANOVA; $F_{2,388} = 6.29$, $P = 0.002$). *Brosimum alicastrum* had significantly longer-lived leaves (287 ± 9.2 days, 1 SE) than *D. panamensis* (250 ± 7.1) or *V. koschnyii* (244 ± 10.9 ; Tukey's HSD, $P < 0.01$).

Instantaneous photosynthetic nitrogen-use efficiency (PNUE; $\mu\text{mol CO}_2 \text{ mol}^{-1} \text{ N}$) was not related to seedling micro-environment, but species differed in mean PNUE (Table 2). *Dipteryx panamensis* and *V. koschnyii* had significantly higher PNUE than *B. alicastrum* (Table 2). Lifetime nutrient-use efficiency depends on leaf life span. When life span was incorporated in the analysis, the longer-lived leaves of *B. alicastrum* still had lower PNUE, but species differences were no longer significant (Table 2).

Variation in leaf N concentration and the determinants of photosynthetic capacity

Nitrogen is an important component of two of the central biochemical determinants of photosynthetic capacity: chlorophyll, the primary receptor of solar energy, and Rubisco, the primary carboxylation enzyme. Leaf N concentration was expected to respond strongly to the light gradient and to be positively related to photosynthetic capacity. Leaf N_{area} (g N m^{-2} leaf) increased with irradiance in *D. panamensis* and *V. koschnyii* (not significant in *B. alicastrum*), whereas N_{mass} (mg N g^{-1} leaf) decreased with irradiance in *D. panamensis* and *B. alicastrum* (ns in *V. koschnyii*, Figure 3). These patterns resulted from changes in leaf area allocated for a given leaf mass (SLA). Within species, as light availability decreased, SLA increased, N_{area} decreased (Figure 4A, Table 1) and N_{mass} increased (Figure 4B, Table 1). Similarly, A_{area} decreased with SLA in *D. panamensis* and *V. koschnyii*, whereas A_{mass} increased with SLA in *B. alicastrum* (Table 1).

Multiple regression analysis was used to determine if variation in A_{area} within species could be predicted based on a combination of plant light environment (% T), leaf N concentration and SLA. There were strong differences among species. For *D. panamensis*, light environment alone predicted A_{area} with an r^2 of 0.78 (Table 1), and adding leaf N concentration and SLA

Table 2. Means (\pm SE) of physiological characteristics that did not vary with light availability in seedlings of *Dipteryx panamensis*, *Virola koschnyii* and *Brosimum alicastrum* growing across a gradient of light created by a forest–pasture edge at La Selva Biological Station, Costa Rica. The F -statistics for ANOVA models comparing species differences in each characteristic are presented. Letters denote significant pairwise comparisons ($P < 0.05$). Abbreviations: A_{mass} = maximum assimilation per unit leaf area; R_{mass} = dark respiration rate per unit leaf mass; R_{area} = dark respiration rate per unit leaf area; and PNUE = photosynthetic nitrogen-use efficiency.

Characteristic	Species			ANOVA	
	<i>Dipteryx panamensis</i>	<i>Virola koschnyii</i>	<i>Brosimum alicastrum</i>	F	P
A_{mass} (nmol $\text{g}^{-1} \text{s}^{-1}$)	134.8 (12.69) a	94.33 (9.89) ab	64.87 (9.94) b	9.11	0.001
R_{mass} (nmol $\text{g}^{-1} \text{s}^{-1}$)	8.76 (1.06)	8.62 (1.37)	7.22 (1.58)	0.36	0.700
R_{area} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	0.491 (0.065)	0.465 (0.064)	0.498 (0.066)	0.07	0.932
PNUE ($\mu\text{mol CO}_2 \text{ mol}^{-1} \text{ N s}^{-1}$)	0.379 (0.043) a	0.386 (0.036) a	0.186 (0.021) b	7.40	0.003
Lifetime PNUE (mol $\text{CO}_2 \text{ g}^{-1} \text{ N}$)	4.09 (0.54) a	3.89 (0.19) a	2.66 (0.93) a	2.16	0.139

did not improve the model. For *V. koschnyii*, the best model ($r^2 = 0.82$) included both seedling light environment and leaf N concentration; unexpectedly, leaf N concentration was negatively related to A_{area} .

$$A_{\text{area}} = 2.74 \log_e [\%T] - 6.24 \log_e [\text{N}] - 1.76$$

The best model for *B. alicastrum* ($r^2 = 0.96$) included all variables:

$$A_{\text{area}} = 0.89 \log_e [\%T] + 4.55 \log_e [\text{N}] + 5.01 \log_e \text{SLA} - 25.7$$

For *B. alicastrum*, a model that included only light yielded an r^2 of only 0.13. Differences among species reflected differences in the light response of leaf N concentration, SLA and A_{area} (cf. Table 1).

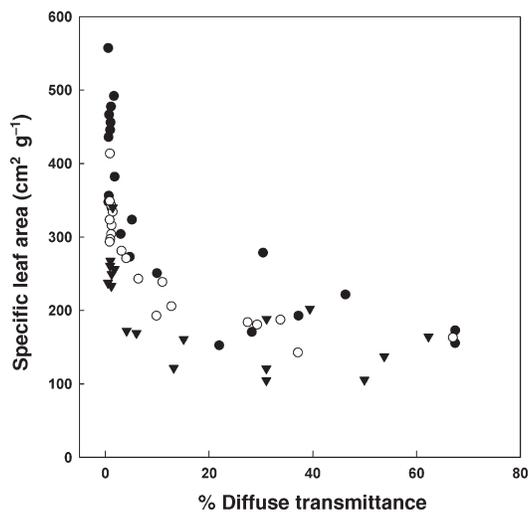


Figure 2. Relationship of specific leaf area to percent diffuse transmittance for seedlings of *Dipteryx panamensis* (●), *Virola koschnyii* (○) and *Brosimum alicastrum* (▼) growing across a forest–pasture edge at La Selva Biological Station, Costa Rica.

Light response of growth and biomass allocation

All species exhibited significant but nonlinear relationships between $\%T$ and biomass growth rates (Figure 5). Differences in biomass growth rates were reflected in final size of seedlings. Final biomass of the largest *D. panamensis* was four times that of the largest *V. koschnyii* and more than 60 times

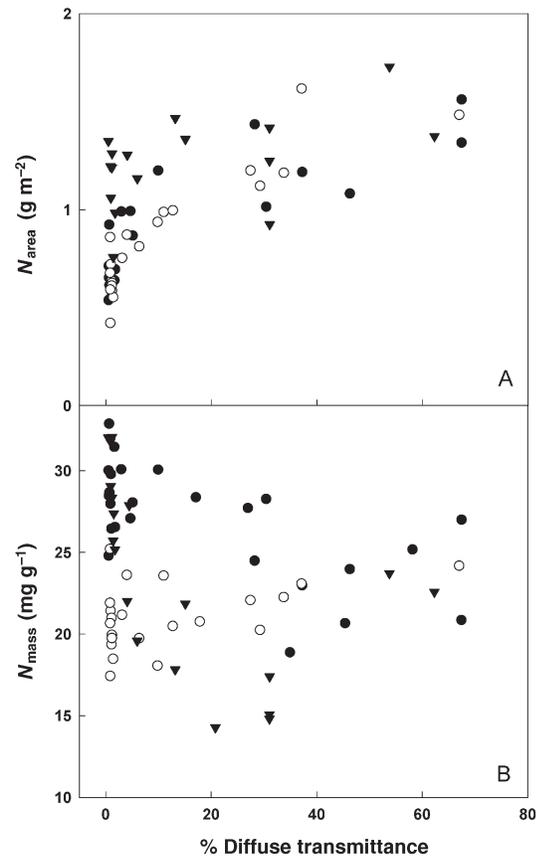


Figure 3. Relationship of leaf nitrogen per unit leaf area (N_{area}) and per unit leaf mass (N_{mass}) to percent diffuse transmittance for seedlings of *Dipteryx panamensis* (●), *Virola koschnyii* (○) and *Brosimum alicastrum* (▼) growing across a forest–pasture edge at La Selva Biological Station, Costa Rica.

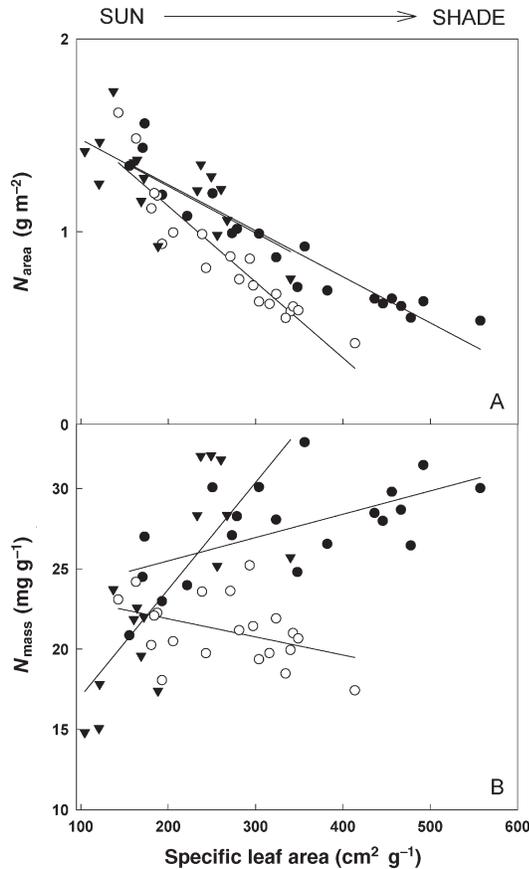


Figure 4. Relationships of leaf nitrogen per unit leaf area (N_{area}) and per unit leaf mass (N_{mass}) to specific leaf area for seedlings of *Dipteryx panamensis* (●), *Virola koschnyii* (○) and *Brosimum alicastrum* (▼) growing across a forest–pasture edge at La Selva Biological Station, Costa Rica.

the final biomass of the largest *B. alicastrum*, whereas final leaf area of the largest *D. panamensis* was twice that of the largest *V. koschnyii* and more than 30 times the final leaf area of the largest *B. alicastrum* (Table 3). Across the gradient, final biomass varied 100-fold for *D. panamensis*, whereas it varied 50- and 10-fold for *V. koschnyii* and *B. alicastrum*, respectively. These differences were similar for final leaf area. *Dipteryx panamensis* leaf area varied more than 70-fold compared with 40- and 22-fold variations for *V. koschnyii* and *B. alicastrum*, respectively (Table 3). Species growth rates showed some crossover, with *V. koschnyii* realizing the highest growth rates at intermediate irradiance and *D. panamensis* realizing highest growth rates at high irradiance. Differences in light-dependent growth curves of *D. panamensis* and *V. koschnyii* are largely a function of mortality of *V. koschnyii* caused by deer browsing at the highest irradiances (results not shown).

Because biomass is thought to change with ontogeny, my analyses of variation in biomass allocation across the light gradient examined the importance of changing plant size with light. Biomass partitioning ratios did not change with plant

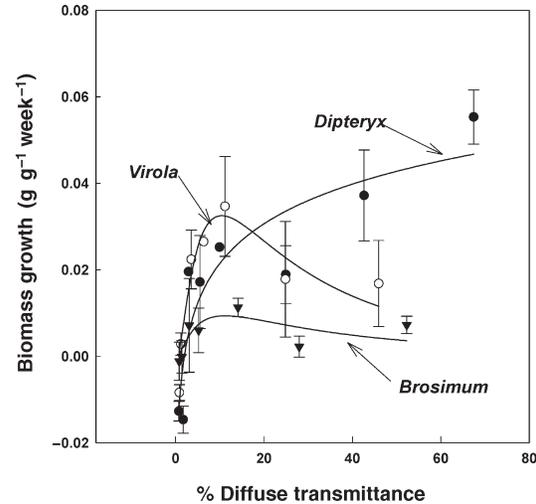


Figure 5. Relationship of seedling relative growth rate to percent diffuse transmittance for seedlings of *Dipteryx panamensis* (●), *Virola koschnyii* (○), and *Brosimum alicastrum* (▼) growing across a forest–pasture edge at La Selva Biological Station, Costa Rica. Means (± 1 SE) in light classes are presented for clarity. Regression equation for a two-parameter logarithmic function: *Dipteryx* RGR = $-0.009 + 0.0132 \log_e \%T$, $r^2 = 0.82$, $P = 0.002$. Regression equations for a three-parameter log-normal function: *Virola* RGR = $0.033 e^{(-0.5(\ln(\%T/10.45)/1.03)^2)}$, $r^2 = 0.83$, $P < 0.03$; *Brosimum* RGR = $0.009 e^{(-0.5(\ln(\%T/11.22)/1.11)^2)}$, $r^2 = 0.53$, $P < 0.04$.

mass in *D. panamensis* or *V. koschnyii*, but SWR was related to plant mass in *B. alicastrum*. In all species, as growth irradiance increased, biomass allocation to leaf tissue (LAR and LWR) decreased (Figure 6, Table 4). Root weight ratio was unrelated to irradiance in *D. panamensis*, whereas RWR increased slightly in *V. koschnyii* and increased strongly in *B. alicastrum*. In addition, each species had a unique pattern of biomass allo-

Table 3. Ranges of final mass and leaf area (min–max) during 14 months of growth measured for seedlings of *Dipteryx panamensis*, *Virola koschnyii* and *Brosimum alicastrum* growing across a gradient of light created by a forest–pasture edge at La Selva Biological Station, Costa Rica. Mean initial mass and leaf areas are presented in parentheses.

Characteristics	<i>Dipteryx panamensis</i>	<i>Virola koschnyii</i>	<i>Brosimum alicastrum</i>
Total biomass (g)	1.2–240.6 (5.33)	1.2–56.3 (2.67)	0.5–3.7 (1.10)
Final leaf area (cm^2)	31.5–2261 (545)	69.3–2549 (141)	6.2–134 (117)
Root biomass (g)	0.27–54.2 (1.23)	0.25–16.3 (0.95)	0.15–1.77 (0.25)
Stem biomass (g)	0.82–155 (2.09)	0.47–21.2 (1.00)	0.22–1.13 (0.38)
Leaf biomass (g)	0.016–31.8 (1.7)	0.13–18.8 (0.717)	0.058–0.88 (0.465)

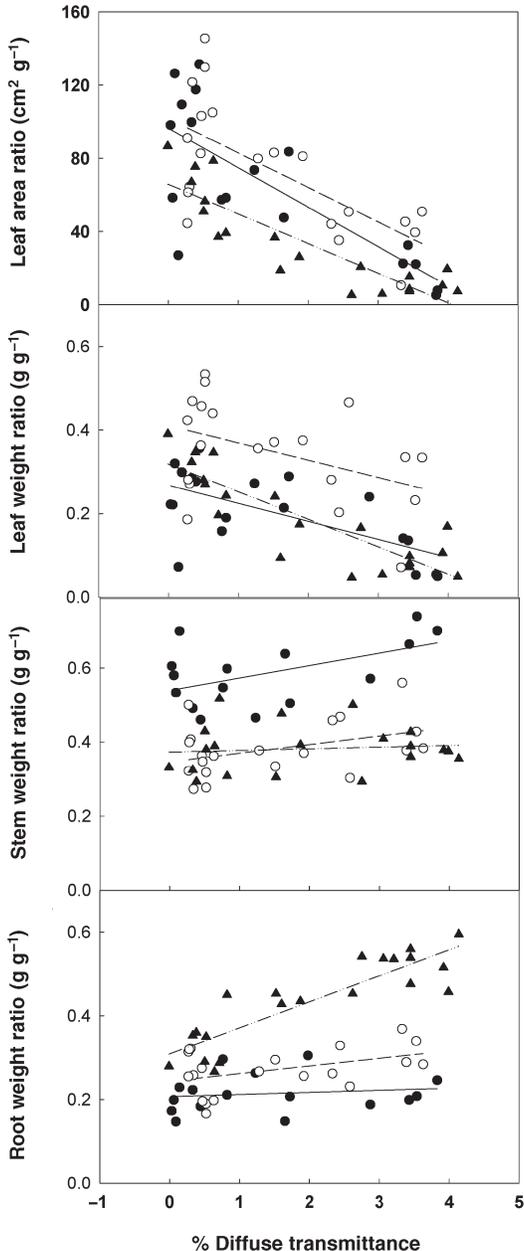


Figure 6. Leaf area ratio ($\text{cm}^2 \text{ leaf g}^{-1} \text{ plant}$) and decimal fraction of biomass allocated to stem, leaf or root for seedlings of *Dipteryx panamensis* (●), *Virola koschnyii* (○) and *Brosimum alicastrum* (▲) growing across a forest–pasture edge at La Selva Biological Station, Costa Rica. Partial correlations and statistical parameters are presented in Table 4.

cation across light environments (Figure 6). *Virola* had high biomass allocation to leaf and stem tissue compared with root tissue and had the highest leaf allocation when compared with *D. panamensis* and *B. alicastrum*. *Dipteryx panamensis* had the highest stem allocation of the three species, splitting the remaining tissue roughly equally between leaf and stem components. *Brosimum alicastrum* had high allocation to root and stem tissues compared with leaf tissue and the highest root allocation when compared with the other two species.

Table 4. Regression statistics for multiple regression models of the effects of light and plant mass on biomass partitioning ratios in seedlings of *Dipteryx panamensis*, *Virola koschnyii* and *Brosimum alicastrum* growing across a gradient of light created by a forest–pasture edge at La Selva Biological Station, Costa Rica. Abbreviations: LAR = leaf area ratio ($\text{cm}^2 \text{ leaf g}^{-1} \text{ plant}$); LWR = leaf weight ratio ($\text{g leaf tissue g}^{-1} \text{ plant}$); SWR = stem weight ratio ($\text{g stem tissue g}^{-1} \text{ plant}$); RWR = root weight ratio ($\text{g root g}^{-1} \text{ plant}$); ns = not significant; and df = degrees of freedom.

Characteristics	df	R^2	P	Predictor	Partial correlation
LAR					
<i>D. panamensis</i>	2, 11	0.37	0.03	$\ln\%T$	−0.75
<i>V. koschnyii</i>	2, 17	0.42	0.004	$\ln\%T$	−0.79
<i>B. alicastrum</i>	2, 17	0.73	<0.0001	$\ln\%T$	−0.89
LWR					
<i>D. panamensis</i>	2, 11	0.32	0.05	$\ln\%T$	−0.78
<i>V. koschnyii</i>	2, 17	0.24	0.04	$\ln\%T$	−0.80
<i>B. alicastrum</i>	2, 17	0.72	<0.0001	$\ln\%T$	−0.91
SWR					
<i>D. panamensis</i>	2, 11	0.27	0.07	$\ln\%T$	0.74
<i>V. koschnyii</i>	2, 17	0.17	0.08	$\ln\%T$	0.72
<i>B. alicastrum</i>	2, 17	0.25	0.04	Seedling mass	−0.60
RWR					
<i>D. panamensis</i>	ns				
<i>V. koschnyii</i>	2, 17	0.22	0.05	$\ln\%T$	0.78
<i>B. alicastrum</i>	2, 17	0.77	<0.0001	$\ln\%T$	0.79

Predictors of growth

Simultaneous measurements of photosynthetic physiology, biomass allocation and growth allow exploration of how physiological versus morphological changes affect plant growth across the sun–shade continuum. I was particularly interested in predicting variation in RGR within species based on traits related to leaf photosynthesis and whole-plant allocation. The strongest predictors of variation in growth rates were A_{area} and NAR (Figure 7), which were highly correlated themselves. In all species, A_{area} increased with increasing NAR and both increased with increasing RGR (Figure 7). The NAR is a measure of the increase in biomass for a given increase in leaf area and is generally considered the equivalent of A_{area} in growth analysis (Poorter and Van der Werf 1998). These data confirm its usefulness as an estimate of photosynthetic function. Although A_{area} and NAR increased, LAR declined as light availability increased (Figure 6), reflecting declines in SLA (Figure 2). The use of GRCs to analyze intraspecific variation in RGR across the light gradient indicated that, in all species, intraspecific variation in RGR was largely a function of NAR and not LAR or its components SLA and LWR (Table 5).

Discussion

Across lowland forests in Central America, *D. panamensis*, *V. koschnyii* and *B. alicastrum* all occupy the forest understory

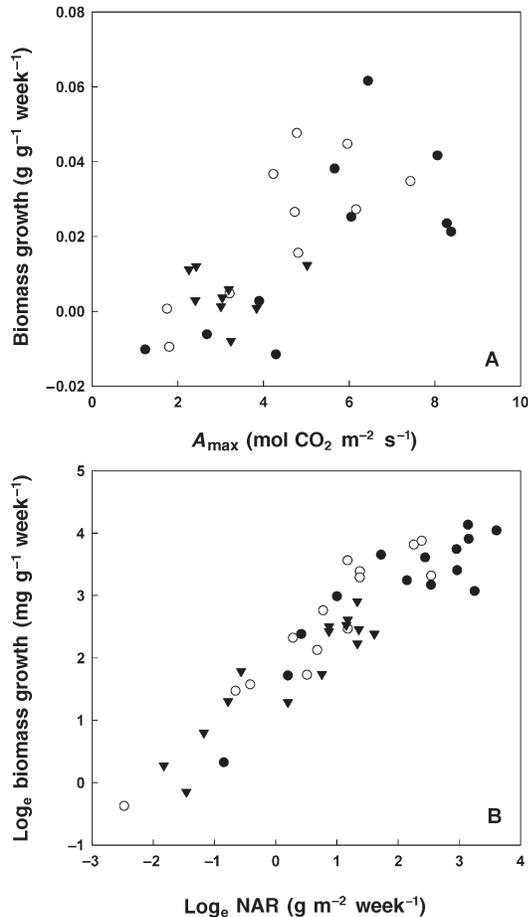


Figure 7. Relationships of relative growth rates (RGR) to net assimilation rate (NAR) and maximum assimilation (A_{max}) on a per leaf area basis for seedlings of *Dipteryx panamensis* (●), *Virola koschnyii* (○) and *Brosimum alicastrum* (▼) growing across a forest–pasture edge at La Selva Biological Station, Costa Rica. Regression equations: A. *Dipteryx* RGR = $0.0084A_{area} - 0.035$; *Virola* RGR = $0.012A_{area} - 0.059$; *Brosimum* RGR = ns; B. *Dipteryx* log_eRGR = $0.687\log_e NAR + 1.71$; *Virola* log_eRGR = $0.837\log_e NAR + 1.88$; *Brosimum* log_eRGR = $0.728\log_e NAR + 1.57$.

as seedlings and saplings. They represent a small sample of a large number of non-pioneer species (Welden et al. 1991) for which few data exist on autecology and demography across resource gradients in their native habitats (Oberbauer et al. 1993, Kobe 1999). My data showed strong light-dependent shifts in growth and physiology under field conditions, even in the company of multiple biotic and abiotic stressors. Moreover, variation in growth was strongly dependent on plasticity of photosynthetic capacity (A_{area}) and carbon gain per unit leaf area (NAR). Major results that merit further discussion include: (1) nonlinear responses of photosynthetic physiology and growth; (2) lack of variation in photosynthetic capacity on a leaf mass basis; (3) species differences in biomass allocation; and (4) NAR as a determinant of intraspecific variation in growth.

Table 5. Growth response coefficients (GRC) assessing the relative contributions of leaf area ratio (LAR; m² leaf kg⁻¹ plant), specific leaf area (SLA; m² leaf kg⁻¹ plant), leaf weight ratio (LWR; mg leaf g⁻¹ plant) and net assimilation rate (NAR; g plant m⁻² leaf) for intraspecific variation in relative growth rates (mg plant g⁻¹ plant) in seedlings of *Dipteryx panamensis*, *Virola koschnyii* and *Brosimum alicastrum* growing across a gradient of light created by a forest–pasture edge at La Selva Biological Station, Costa Rica.

Species	GRC _{LAR}	GRC _{NAR}	GRC _{SLA}	GRC _{LWR}
<i>D. panamensis</i>	0.41	1.174	-0.187	-0.206
<i>V. koschnyii</i>	0.245	1.08	-0.137	-0.108
<i>B. alicastrum</i>	0.261	1.165	-0.189	-0.072

Nonlinear responses of physiology and growth

For the leaf traits that responded to the light gradient (A_{area} , SLA, light compensation and saturation points), the relationships were strongly nonlinear; the initially steep response to light leveled off at microsities with more than 20–30% full sun (e.g., Figures 1 and 2). This asymptotic relationship between light availability and seedling physiological characteristics followed patterns reported for other shade-tolerant species (Chazdon 1992, Ducrey 1994, Sims et al. 1994, Agyeman et al. 1999, Poorter 1999). All seven tropical tree species from Guadeloupe studied by Ducrey (1994) showed strong increases in area-based photosynthetic capacity with irradiances up to 20% of full sun, after which photosynthetic capacity did not significantly increase. Similarly, in a study of relative growth rates in 15 West African species, species from a variety of functional groups exhibited this plateau (Agyeman et al. 1999). The inability to adjust to extremely high light may reflect the infrequency with which a tree seedling encounters these irradiances, the physiological trade-offs associated with maintaining a high photosynthetic capacity, and the constraints placed by a shift to water and nutrient limitation relative to light limitation (Givnish 1986, Sims and Pearcy 1994, Clark et al. 1996). Given the rapidity of gap closure and the low frequency of sites with irradiances greater than 35% full sun (Clark et al. 1996), the return on investment in high photosynthetic capacity may not offset the cost of leaf production or the respiratory cost if that sun leaf remains on the plant after gap closure. The maximum potential of a response may optimize the increased carbon gain in the short term (early gap light conditions) while minimizing carbon as a result of high respiration rates when light decreases during gap closure. Following this logic, one might expect species that establish in abandoned pastures, landslides and other larger scale disturbances to respond to a wider range of light conditions (Sims and Pearcy 1989, Turnbull 1991). Furthermore, one might also expect plants with short leaf life spans to respond to a greater range of irradiances. In a comparative study of *Alocasia macrorrhiza* Schott, a tropical understory species, and *Colocasia esculenta* (L.) Schott, a related crop species, Sims and Pearcy (1989) showed that *A. macrorrhiza* does not increase photosynthetic capacity in treatments with irradiances above

35% of full sun, whereas *C. esculenta* continues to increase A_{\max} at greater than 60% of full sun. In two tropical understory shrubs that differ in leaf life span, short leaf life span is associated with a greater increase in photosynthetic capacity, more leaf production and greater increases in growth following transfer to gaps (Kursar and Coley 1999).

Some authors suggest that shade-tolerant species show limited plasticity compared with pioneers (Bazzaz and Pickett 1980, Bazzaz 1996). Despite limited plasticity above 20–30 %T, plasticity below 20 %T in *V. koschynii* and *D. panamensis* (A_{area}) rivaled some pioneer and shrub species that grow in these and other tropical forests (Chazdon and Field 1987, Oberbauer et al. 1993, Davies 1998, Dalling et al. 1999). For example, in a group of pioneer *Macaranga* Thouars., A_{area} varies from 7 to 10 $\mu\text{mol m}^{-2} \text{s}^{-1}$ across a range of light environments (Davies 1998). Similarly, A_{area} in *Alseis blackiana* Hemsl., an apparent shade-tolerant pioneer, ranges from ~6 to 11 $\mu\text{mol m}^{-2} \text{s}^{-1}$ across a range of simulated gaps (Dalling et al. 2001) and A_{area} of *Luehea seemanii* Triana & Planch., a tropical pioneer, ranges from 6 to 11 $\mu\text{mol m}^{-2} \text{s}^{-1}$.

Light-dependent changes in A_{area} versus A_{mass}

In all species, individuals growing at increasing irradiance showed a classic sun–shade trait syndrome: thicker leaves (lower SLA) with higher A_{area} , N_{area} , light compensation points and light saturation points. However, no species increased A_{mass} as irradiance increased. Thus, from the perspective of light or resource harvesting (i.e., leaf area basis), I observed the expected response to increasing irradiance, but from the perspective of the economics of carbon allocation (i.e., leaf mass basis), I did not observe the expected response (Field and Mooney 1986, Givnish 1986). Evans (1998) argued that plants generally maintain a constant amount of Rubisco per leaf mass (V_m) and by extension a relatively constant A_{mass} while varying SLA and A_{area} . He stated that V_m can be factorized into (1) Rubisco content per unit leaf area, (2) surface area of chloroplast exposed to intercellular airspace and (3) leaf mass per area (LMA, the inverse of SLA). He further argued that the key trait for leaf photosynthetic capacity and growth is the surface area of chloroplasts exposed to intercellular space per unit of leaf mass (Evans 1998). For a species to increase A_{mass} , it must either invest dry mass in tissues that provide mesophyll cell surface area (more or larger mesophyll cells) or invest in resources to increase the mesophyll surface area covered by chloroplasts (more or larger chloroplasts). When considering the ability of a species to implement these changes, one must remember two important trade-offs created by the economics of gas exchange (Givnish 1986). First, plants lose water during CO_2 uptake (Trade-off 1) and second, high energetic costs are associated with acquiring resources to build and then maintain tissues with a high photosynthetic rate (Trade-off 2; Givnish 1986). In high-light environments, the relative importance of water conservation (Trade-off 1) or nutrient uptake (Trade-off 2) may affect the ability to shift A_{mass} . For example, to reduce water loss in high light, a leaf may develop a thicker epidermis. This causes a change in leaf mass but does not provide more mesophyll surface area for CO_2 fixation, and therefore

does not result in higher A_{mass} . Nutrient limitation may also limit the ability to invest in a greater number of chloroplasts per surface area of the mesophyll, because chloroplasts are rich in N-containing compounds.

Examining the tropical literature, Chazdon (1992) reported decreases in SLA but little change in A_{mass} for shade-tolerant *Piper arieianum* C. DC. growing across a gap–forest transect, whereas *P. sanctifelicis* Trel., a species more common in open sites, decreased SLA and increased A_{mass} as irradiance increased. In contrast, three other shade-tolerant *Piper* species decreased SLA, increased A_{area} and increased A_{mass} in high-irradiance treatments (Mulkey et al. 1993). Moreover, a study of the pioneer *Macaranga* showed no change in A_{mass} with growth irradiances in eight of nine species; increases in A_{area} resulted from the plasticity of SLA (Davies 1998). It appears that tropical species differ in their ability to change A_{mass} , and this ability does not fall clearly into ecological groups (e.g., shade-tolerant species with low plasticity of A_{mass}). More research on mechanisms that underlie the difference between the response of A_{mass} and A_{area} to light gradients is needed to fully understand the consequences of variation in A_{mass} for tree seedling growth.

Despite no change in A_{mass} , growth increased in all species across the light gradient, suggesting that either variation in A_{mass} was not a major determinant of variation in tree seedling growth or that A_{mass} must be considered in the context of the entire plant. The A_{mass} interacts with actual leaf light environments, which may depend on whole-plant traits such as leaf display and self-shading. Furthermore, leaf-level assimilation scaled by whole-plant leaf area is more tightly correlated with whole-plant carbon gain than leaf photosynthesis alone (Montgomery 1999). Finally, water and nutrient availability may have been limiting across part or all of the gradient, limiting the responses of A_{mass} and other traits to variation in light availability. Low leaf N concentrations and relatively low plasticity of N_{mass} suggest that nutrient limitation may have affected plant response throughout the site.

Causes and consequences of differences in biomass allocation

As resource limitation shifts from light to water or nutrients one expects changes not only in leaf physiology but also in biomass allocated to acquisition of the most limiting resource (Brouwer 1983). Thus, in a low-light environment, plants should allocate biomass to light-capturing tissue and minimize C losses; in high-light environments, allocation should shift to the acquisition of water and nutrients. As light availability increased, all three species allocated less to leaf area and leaf mass and more to biomass of roots and stems (Figure 6).

Differences in allocation among species may also reflect different life history strategies. Among the study species, *D. panamensis* had high height and diameter growth (Montgomery 1999) and the greatest stem allocation. In gaps, height growth is favored because competing vegetation rapidly fills the open space and shades shorter plants. Strong height growth coupled with relatively high photosynthetic rates could give *D. panamensis* the potential to respond strongly to canopy

opening. In contrast, *B. alicastrum* showed high root allocation associated with slow growth and high survival. Thus, whereas species had similarly shaped responses to light, they differed in the rank order of physiological performance, growth rates and final size. *Brosimum alicastrum* possessed a physiology with low plasticity and a suite of traits that limits its growth performance but enhances persistence across a range of light environments (Figure 5, Table 2). High allocation below ground (Figure 6) may facilitate recovery from mechanical damage, a stress that becomes a proportionally more important determinant of mortality and growth as seedlings and saplings age (Clark and Clark 1985). Moreover, high toughness, closely correlated with low SLA, may deter herbivores. *Brosimum alicastrum* had lower rates of deer browsing and tissue loss to herbivory than the other two species (results not shown). Low growth rates, tough leaves and high root allocation are consistent with the hypothesis that, in low-light conditions, characteristics that enhance survivorship are more important than characteristics that enhance growth rate (Augsburger 1984, Kitajima 1994, Kobe et al. 1995). However, *B. alicastrum* also maintained these characteristics in high light, suggesting it will be at a competitive disadvantage in sunny microsites compared with other species.

Dipteryx panamensis and *V. koschynii* had a more plastic physiology, higher growth rates, larger leaf areas and broader ranges of response than *B. alicastrum* (Tables 1 and 2, Figures 1 and 7). Despite similarities in leaf-level physiology, *D. panamensis* and *V. koschynii* differed in growth responses to light; *D. panamensis* outgrew *V. koschynii* in high light. These differences may have been caused by several factors. Higher SLA in *D. panamensis* than in *V. koschynii* may have allowed greater returns in whole-plant growth per unit invested in leaves. This hypothesis is supported by a literature review of the determinants of variation in interspecific growth (Poorter and Van der Werf 1998). In addition, whole-plant traits such as leaf display may also have affected the translation of leaf to whole-plant photosynthesis. Two plants with identical leaf area and leaf photosynthesis may differ in whole-plant photosynthesis because of differences in self-shading, which reduces actual leaf light exposure for lower crown leaves. Finally, I observed that *V. koschynii* appeared less able to recover from damage by herbivory than *D. panamensis* (results not shown).

Determinants of variation in intraspecific growth

Intraspecific variation in growth across irradiances was largely related to leaf function, not allocation. Both A_{area} and NAR were strongly and positively related to growth (Figure 7). These results contrast with hypotheses based largely on temperate zone data suggesting that LAR, not physiological function, is the most important determinant of variation in growth as light availability increases (Poorter and Van der Werf 1998). However, my data are consistent with those for tropical trees showing a strong effect of irradiance on NAR (Veneklaas and Poorter 1998). It is possible that these differences reflect the life-form examined. The review by Poorter and Van der Werf

(1998) was drawn from literature on herbaceous species. A fundamental difference between woody and herbaceous species may be in the allocation to structural mass in woody plants. This requirement reduces LAR and may make LAR less sensitive to changing resources.

In summary, all species showed physiological, growth and survival responses at low light consistent with shade tolerance. Both *V. koschynii* and *D. panamensis* were able to respond to increases in light availability, whereas the more conservative *B. alicastrum* was unable to significantly enhance growth in response to increasing irradiance. At longer time scales, these differences could play an important role in population processes across the landscape. Not only can *V. koschynii* and *D. panamensis* establish and survive in dark conditions, they also appear capable of utilizing the increased light that accompanies gap formation. The subsequent growth spurt would speed attainment of canopy status compared with *B. alicastrum* seedlings, which may simply grow slowly from germination to adult. This study provides further evidence of the importance of physiological traits such as photosynthesis and NAR for variation in growth across light gradients. However, the data raise questions about the relative importance of area-versus mass-based measures for predicting seedling growth. Although only three species were examined, I found diverse responses within the shade-tolerant guild that lead to the following questions. How does a species' autecology interact with gap frequency, gap size distribution, and spatial pattern of light across the landscape to affect relative success, diversity and abundance of shade-tolerant species? How are large numbers of non-pioneer tree species maintained? The importance of patterns that structure the advanced regeneration and the consequences of differences among non-pioneer species in their response to canopy opening remain poorly understood components of forests function and regeneration.

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References

- Ackerly, D.D. and F.A. Bazzaz. 1995. Leaf dynamics, self-shading and carbon gain in seedlings of a tropical pioneer tree. *Oecologia* 101:289–298.
- Agyeman, V.K., M.D. Swaine and J. Thompson. 1999. Responses of tropical forest seedlings to irradiance and the derivation of a light response index. *J. Ecol.* 87:815–827.
- Augsburger, C.K. 1984. Seedling survival of tropical tree species: interactions of dispersal distance, light-gaps, and pathogens. *Ecology* 65:1705–1712.

- Bazzaz, F.A. 1996. Plants in changing environments: linking physiological, population and community ecology. Cambridge University Press, Cambridge, U.K., 330 p.
- Bazzaz, F.A. and S.T.A. Pickett. 1980. Physiological ecology of tropical succession: a comparative review. *Annu. Rev. Ecol. Syst.* 11: 287–310.
- Björkman, O. 1981. Responses to different quantum flux densities. *In* Encyclopedia of Plant Physiology. Eds. O.L. Lange, P.S. Nobel, C.B. Osmond and H. Ziegler. Springer-Verlag, New York, pp 57–107.
- Bloom, A.J., F.S. Chapin, III and H.A. Mooney. 1985. Resource limitation in plants—an economic analogy. *Annu. Rev. Ecol. Syst.* 16: 363–392.
- Boardman, N.K. 1977. Comparative photosynthesis of sun and shade plants. *Annu. Rev. Plant Physiol.* 28:355–377.
- Brokaw, N.V.L. 1987. Gap-phase regeneration of three pioneer species in a tropical forest. *J. Ecol.* 75:9–19.
- Brouwer, R. 1983. Functional equilibrium: sense or nonsense? *Neth. J. Agric. Sci.* 31:335–348.
- Butterfield, R.P. 1994. Forestry in Costa Rica: status, research priorities, and role of La Selva Biological Station. *In* La Selva: Ecology and Natural History of a Neotropical Rain Forest. Eds. L.A. McDade, K.S. Bawa, H.A. Hespenheide and G.S. Hartshorn. University of Chicago Press, Chicago, IL, pp 317–328.
- Chazdon, R.L. 1992. Photosynthetic plasticity of two rain forest shrubs across natural gap transects. *Oecologia* 92:586–595.
- Chazdon, R.L. and C.B. Field. 1987. Determinants of photosynthetic capacity in six rainforest *Piper* species. *Oecologia* 73:222–230.
- Chazdon, R.L., R.W. Pearcy, D.W. Lee and N. Fetcher. 1996. Photosynthetic response of tropical forest plants to contrasting light environments. *In* Tropical Forest Plant Ecophysiology. Eds. S.S. Mulkey, R.L. Chazdon and A.P. Smith. Chapman and Hall, New York, pp 5–55.
- Clark, D.B. and D.A. Clark. 1985. Seedling dynamics of a tropical tree: impacts of herbivory and meristem damage. *Ecology* 66: 1884–1892.
- Clark, D.B., D.A. Clark and P.M. Rich. 1993. Comparative analysis of microhabitat utilization by saplings of nine tree species in neotropical rain forest. *Biotropica* 25:397–407.
- Clark, D.B., D.A. Clark, P.M. Rich, S. Weiss and S.F. Oberbauer. 1996. Landscape-scale evaluation of understory light and canopy structure: methods and application in a neotropical lowland rain forest. *Can. J. For. Res.* 26:747–757.
- Coleman, J.S., K.D.M. McConnaughay and D.D. Ackerly. 1994. Interpreting phenotypic variation in plants. *Trends Ecol. Evol.* 9: 187–191.
- Coley, P.D., J.P. Bryant and F.S. Chapin, III. 1985. Resource availability and antiherbivore defense. *Science* 230:895–899.
- Dalling, J.W., S.P. Hubbell and K. Silveira. 1998. Seed dispersal, seedling establishment and gap partitioning among tropical pioneer trees. *J. Ecol.* 86:674–689.
- Dalling, J.W., C.E. Lovelock and S.P. Hubbell. 1999. Growth responses of seedlings of two neotropical pioneer species to simulated forest gap environments. *J. Trop. Ecol.* 15:827–839.
- Dalling, J.W., K. Winter, J.D. Nason, S.P. Hubbell, D.A. Murawski and J.L. Hamrick. 2001. The unusual life history of *Alseis blackiana*: a shade-persistent pioneer tree? *Ecology* 82:933–945.
- Davies, S.J. 1998. Photosynthesis of nine pioneer *Macaranga* species from Borneo in relation to life history. *Ecology* 79:2292–2308.
- Denslow, J.S. 1987. Tropical rainforest gaps and tree species diversity. *Annu. Rev. Ecol. Syst.* 18:431–451.
- Ducrey, M. 1994. Influence of shade on photosynthetic gas exchange of 7 tropical rainforest species from Guadeloupe (French-West-Indies). *Ann. Sci. For.* 51:77–94.
- Evans, J.R. 1998. Photosynthetic characteristics of fast- and slow-growing species. *In* Inherent Variation in Plant Growth. Physiological Mechanisms and Ecological Consequences. Eds. H. Lambers, H. Poorter and M.M.I. Van Vuuren. Backhuys Publishers, Leiden, The Netherlands, pp 183–198.
- Farrar, J. and S. Gunn. 1998. Allocation: allometry, acclimation and alchemy? *In* Inherent Variation in Plant Growth. Physiological Mechanisms and Ecological Consequences. Eds. H. Lambers, H. Poorter and M.M.I. Van Vuuren. Backhuys Publishers, Leiden, The Netherlands, pp 183–198.
- Field, C.B. and H.A. Mooney. 1986. The photosynthesis–nitrogen relationship in wild plants. *In* On the Economy of Plant Form and Function. Ed. T.J. Givnish. Cambridge University Press, Cambridge, U.K., pp 25–56.
- Givnish, T.J. 1986. On the economy of plant form and function. Cambridge University Press, Cambridge, 717 p.
- Givnish, T.J. 1988. Adaptation to sun and shade: a whole-plant perspective. *Aust. J. Plant Physiol.* 15:63–92.
- Hubbell, S.P. 1998. The maintenance of diversity in a neotropical tree community: conceptual issues, current evidence, and challenges ahead. *In* Forest Biodiversity Research, Monitoring and Modeling: Conceptual Background and Old World Case Studies. Eds. F. Dallmeier and J.A. Comiskey. Parthenon Publishing, Paris, pp 17–44.
- Hunt, R. 1982. Plant growth curves. Edward Arnold Limited, London, 248 p.
- Jurik, T.W. 1986. Temporal and spatial patterns of specific leaf weight in successional northern hardwood tree species. *Am. J. Bot.* 73: 1083–1092.
- Kamaluddin, M. and J. Grace. 1992. Acclimation in seedlings of a tropical tree, *Bischofia javanica*, following a stepwise reduction in light. *Ann. Bot.* 69:557–562.
- Kitajima, K. 1994. Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia* 98:419–428.
- Kobe, R.K. 1999. Light gradient partitioning among tropical tree species through differential seedling mortality and growth. *Ecology* 80:187–201.
- Kobe, R.K., S.W. Pacala, J.A. Silander and C.D. Canham. 1995. Juvenile tree survivorship as a component of shade tolerance. *Ecol. Appl.* 5:517–532.
- Kursar, T.A. and P.D. Coley. 1999. Contrasting modes of light acclimation in two species of the rainforest understory. *Oecologia* 121: 489–498.
- Leverenz, J.W. and P.G. Jarvis. 1979. Photosynthesis in Sitka spruce. VIII. The effects of light flux density and direction on the rate of net photosynthesis and the stomatal conductance of needles. *J. Appl. Ecol.* 16:919–932.
- McConnaughay, K.D.M. and J.S. Coleman. 1999. Biomass allocation in plants: ontogeny or optimality? A test along three resource gradients. *Ecology* 80:2581–2593.
- McDade, L.A., K.S. Bawa, H.A. Hespenheide and G.S. Hartshorn. 1994. La Selva: ecology and natural history of a neotropical rain forest. University of Chicago Press, Chicago, IL, 486 p.
- Montgomery, R.A. 1999. Seedling performance in heterogeneous environments: a multi-scale approach. Ph.D. Diss., Univ. Connecticut, Storrs, CT, 183 p.
- Montgomery, R.A. and R.L. Chazdon. 2002. Light gradient partitioning by tropical tree seedlings in the absence of canopy gaps. *Oecologia* 131:165–174.

- Mulkey, S.S. 1986. Photosynthetic acclimation and water-use efficiency of three species of understory herbaceous bamboo (Gramineae) in Panama. *Oecologia* 70:514–519.
- Mulkey, S.S., A.P. Smith and S.J. Wright. 1991. Comparative life history and physiology of two understory neotropical herbs. *Oecologia* 88:263–273.
- Mulkey, S.S., S.J. Wright and A.P. Smith. 1993. Comparative physiology and demography of three neotropical forest shrubs: alternative shade adaptive character syndromes. *Oecologia* 96:526–536.
- Newell, E.A., E.P. McDonald, B.R. Strain and J.S. Denslow. 1993. Photosynthetic responses of *Miconia* species to canopy openings in a lowland tropical rainforest. *Oecologia* 94:49–56.
- Nicotra, A.B., R.L. Chazdon and S.V.B. Iriarte. 1999. Spatial heterogeneity of light and woody seedling regeneration in tropical wet forests. *Ecology* 80:1908–1926.
- Oberbauer, S.F., D.B. Clark, D.A. Clark, P.M. Rich and G. Vega. 1993. Light environment, gas exchange, and annual growth of saplings of three species of rain forest trees in Costa Rica. *J. Trop. Ecol.* 9:511–523.
- Parent, S. and C. Messier. 1996. A simple and efficient method to estimate microsite light availability under a forest canopy. *Can. J. For. Res.* 26:151–154.
- Pearcy, R.W. and D.A. Sims. 1994. Photosynthetic acclimation to changing light environments: scaling from the leaf to the whole plant. *In* *Exploitation of Environmental Heterogeneity by Plants*. Eds. M.M. Caldwell and R.W. Pearcy. Academic Press, San Diego, pp 145–174.
- Poorter, L. 1999. Growth responses of 15 rainforest tree species to a light gradient: the relative importance of morphological and physiological traits. *Funct. Ecol.* 13:396–410.
- Poorter, H. and A. Van der Werf. 1998. Is inherent variation in RGR determined by LAR at low irradiance and by NAR at high irradiance? A review of herbaceous species. *In* *Inherent Variation in Plant Growth. Physiological Mechanisms and Ecological Consequences*. Eds. H. Lambers, H. Poorter and M.M.I. Van Vuuren. Backhuys Publishers, Leiden, The Netherlands, pp 309–336.
- Prioul, J.L. and P. Chartier. 1977. Partitioning of transfer and carboxylation components of intracellular resistance to photosynthetic CO₂ fixation: a critical analysis of the methods used. *Ann. Bot.* 41:789–800.
- Sims, D.A. and R.W. Pearcy. 1989. Photosynthetic characteristics of a tropical forest understory herb, *Alocasia macrorrhiza*, and a related crop species, *Colocasia esculenta*, grown in contrasting light environments. *Oecologia* 79:53–59.
- Sims, D.A. and R.W. Pearcy. 1991. Photosynthesis and respiration in *Alocasia macrorrhiza* following transfers to high and low light. *Oecologia* 86:447–453.
- Sims, D.A., R.L.E. Gebauer and R.W. Pearcy. 1994. Scaling sun and shade photosynthetic acclimation of *Alocasia macrorrhiza* to whole-plant performance. II. Simulation of carbon balance and growth at different photon flux densities. *Plant Cell Environ.* 17: 889–900.
- Sims, D.A., J.R. Seemann and Y. Luo. 1998. The significance of differences in the mechanisms of photosynthetic acclimation to light, nitrogen and CO₂ for return on investment in leaves. *Funct. Ecol.* 12:185–194.
- Sollins, P., F. Sancho, R. Mata and R.L. Sanford, Jr. 1994. Soils and soil process research. *In* *La Selva: Ecology and Natural History of a Neotropical Rain Forest*. Eds. L.A. McDade, K.S. Bawa, H.A. Hespeneide and G.S. Hartshorn. University of Chicago Press, Chicago, IL, pp 317–328.
- Strauss-Debenedetti, S. and F.A. Bazzaz. 1991. Plasticity and acclimation to light in tropical Moraceae of different successional positions. *Oecologia* 87:377–387.
- Swaine, M.D. and T.C. Whitmore. 1988. On the definition of ecological species groups in tropical rain forest. *Vegetatio* 75:81–86.
- Turnbull, M.H. 1991. The effect of light quantity and quality during development on the photosynthetic characteristics of six Australian rainforest tree species. *Oecologia* 87:110–117.
- Veneklaas, E.J. and L. Poorter. 1998. Growth and carbon partitioning of tropical tree seedlings in contrasting light environments. *In* *Inherent Variation in Plant Growth. Physiological Mechanisms and Ecological Consequences*. Eds. H. Lambers, H. Poorter and M.M.I. Van Vuuren. Backhuys Publishers, Leiden, The Netherlands, pp 337–361.
- Walters, M.B. and C.B. Field. 1987. Photosynthetic light acclimation in two rainforest *Piper* species with different ecological amplitudes. *Oecologia* 72:449–456.
- Welden, C.W., S.W. Hewett, S.P. Hubbell and R.B. Foster. 1991. Sapling survival, growth and seedling establishment: relationship to canopy height in a neotropical forest. *Ecology* 72:35–50.
- Wightman, K.E. 1997. Nursery production and seedling establishment techniques for five native tree species in the Atlantic lowlands of Costa Rica. Ph.D. Diss., North Carolina State Univ., Raleigh, NC, 125 p.

