ECOPHYSIOLOGY

R. A. Montgomery · R. L. Chazdon

Light gradient partitioning by tropical tree seedlings in the absence of canopy gaps

Abstract To explore the importance of light availability for seedling growth in low light environments, we examined light-dependent growth, biomass allocation and mortality of tree seedlings growing in sites with 0.2–6.5% full sun, the range of light commonly encountered in the understory of closed canopy, lowland tropical forests. We transplanted seedlings of the canopy tree species, *Dipteryx panamensis*, *Virola koschnyii*, and *Brosimum alicastrum* into second-growth forest and native tree plantations at La Selva Biological Station, Costa Rica. We assessed seedling survival, growth, and seedling light environments bimonthly for 14 months. Plants were harvested at the end of the study to assess leaf area, total biomass, biomass partitioning and root growth. Survivorship of all species exceeded 60% across all microsites, although both *D. panamensis* and *B. alicastrum* had lower probabilities of survival in the darkest microsites. All species showed a strong positive relationship between light availability and growth, increasing in total biomass as light increased. However, the strength of the growth response differed among species causing a change in the rank order of species growth rates as light availability increased. Although *D. panamensis* showed the lowest growth rates in the darkest microsites, a strong response to increasing light led to a cross-over in performance, such that *D. panamensis* had the highest growth rate at the highest light levels studied. These data suggest that resource gradient partitioning could occur even in low light environments (0.2–6.5%). Given the limited range of light regimes sampled (i.e., non-gap microsites), our data demonstrate that growth of tropical tree seedlings beneath closed canopies is highly sensitive to light availability and that shade-tolerant species vary in these responses. Our results show that understory light heterogeneity, in the absence of canopy gaps, can significantly affect recruitment processes for shade-tolerant tree species.

Keywords Biomass allocation · Allometry · Mortality · Light heterogeneity · Shade tolerance

Introduction

Studies of forested ecosystems demonstrate that light availability on the forest floor plays an important role in growth, survival, and life history of tree seedlings and saplings (Denslow 1980, 1987; Chazdon 1988; Caldwell and Pearcy 1994). Direct irradiance through canopy gaps cues seed germination in several pioneer species (Vazquez-Yanes and Smith 1982; Vazquez-Yanes and Orozco-Segovia 1985) and increases growth rates of many species (Fisher et al. 1991; Whitmore and Brown 1996; Denslow et al 1998; Van der Meer et al. 1998). Some species may require repeated gap formation in order to reach the canopy, and many species differ in patterns of microsite occupancy as juveniles (Canham 1988; Clark and Clark 1992). Most studies exploring the significance of light availability for seedling performance use discrete, highly contrasting light levels (representative of conditions under gaps and closed canopy) and compare species thought to differ in regeneration strategy (Strauss-Debenedetti and Bazzaz 1991; Kitajima 1994; Kobe 1999; reviewed in Veneklaas and Poorter 1998; but see Mulkey 1986; Mulkey et al. 1991). Such studies consider the understory of closed canopy forests as one end of a resource axis, focusing primarily on the importance of gaps or clearings and species regeneration strategies with regard to high light patches.

Studies of the frequency distribution of light availability in tropical forests suggest that the gap versus non-gap paradigm overlooks the continuum of light levels be-

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Table 1 Descriptive statistics of % diffuse transmittance and daily totals of photosynthetic photon flux density (mol m^{-2} day^{-1}) in two second-growth and two tree plantations at the La Selva Biological Station, Costa Rica. Sampling unit is the individual seedling (for %T) and individual sensor (for PFD)

Site	%T (yearly average of 6 censuses)				Daily totals of PFD (mol m^{-2} day)			
	Mean	Min–max	CV	n	Mean	Min–max	CV	n
Second-growth								
PEJ	0.7	0.22–1.5	35.71	120	0.3	0.06–1.0	73.59	32
LSUR	1.6	0.34–6.2	69.18	117	1.0	0.13–2.2	58.35	34
Plantation								
Plant1	4.3	2.8–6.5	15.05	117	2.0	1.3–2.8	17.16	28
Plant2	4.6	2.0–6.1	19.18	120	1.7	0.85–3.1	33.33	33

neath closed canopy (Lieberman et al. 1989; Clark et al. 1996; Brown and Jennings 1998; Nicotra et al. 1999; Montgomery and Chazdon 2001). Within such forests, the frequency distribution of light is highly skewed towards environments with less than 2% full sun (Smith et al. 1992; Clark et al. 1996; Connell et al. 1997; Nicotra et al. 1999). Although the drastic changes in the resource environment produced by gap formation play an undisputed role in tree life-history, more subtle changes in magnitude and spatial distribution of light beneath closed canopies are also likely to influence long-term survivorship and recruitment of seedlings composing advanced regeneration. Microsite variation in direct and diffuse light availability can also strongly influence daily carbon gain and plant growth in closed canopy understories (Chazdon 1986; Oberbauer et al. 1993; Chazdon et al. 1996). Tropical forest understory species can respond positively to relatively small changes in light availability, potentially leading to sizable differences in carbon gain and growth (Pearcy 1983; Chazdon 1986; Mulkey et al. 1991, 1993). In a Hawaiian rain forest, relative growth rates of *Euphorbia* and *Claoxylon* increased significantly with light availability within closed canopy sites (Pearcy 1983). Similarly, two tropical *Piper* species showed significant physiological and growth responses to changes in light availability across a gap transect including sensitive growth responses at the low light end of the gradient (Chazdon 1992; Chazdon et al. 1996).

Few studies have examined environmentally induced variation in canopy tree seedling growth beneath closed canopies, despite evidence indicating that the majority of tropical tree species establish in closed canopy microsites where they persist for undetermined periods of time (Hubbell and Foster 1986; Welden et al. 1991; Clark et al. 1993, 1996). Long-term survivorship, essential for recruitment into the canopy, may largely be determined by differential performance of individuals and species with respect to variation in light availability among closed canopy microsites (Kobe et al. 1995; Kobe 1999).

This paper is part of a broad study examining physiology, growth and mortality of seedlings of three shade-tolerant, canopy trees common in lowland tropical forests of northeastern Costa Rica (Montgomery 1999). Here, we examine above- and below-ground growth, biomass allocation, and mortality in relation to microsite variation in light availability. In contrast to previous studies, we focus only on responses to microsite variation beneath closed canopy – the most commonly encountered conditions within the forest understory – and explore seedling responses to changes in the magnitude and spatial pattern of light availability. We examine the following questions: (1) Do relatively small changes in light availability (0.2–6.5% diffuse transmittance) within closed canopy sites affect tree seedling growth and mortality? (2) Do species differ in light-dependent growth and mortality? (3) How do species differences in biomass allocation influence growth as a function of light?

Materials and methods

Study sites

This study was conducted at La Selva Biological Station located in the Sarapiquí region of northeastern Costa Rica. This area is classified as tropical wet premontane forest and receives more than 4 m of rain each year (McDade et al. 1994). Study sites were located in two stands of second-growth forest and two tree plantations. These two stand-types differ in both average light availability and in the spatial heterogeneity of light availability (Table 1). All stands occurred on residual soils, derived from lava flows (Sollins et al. 1994). Although soil nutrients were not measured in this study, there was no apparent heterogeneity across the transplant areas.

The two second-growth forests differed in age and history. Lindero El Peje (LEP) was converted to pasture between 1972 and 1974, grazed for 5 years and then abandoned (Pierce 1992). At the time of the study, this forest had been regenerating for ca. 20 years. This site is adjacent to the Peje stand studied by Nicotra et al. (1999) and Guariguata et al. (1997). The younger Lindero Sur (LSUR) forest was converted to pasture ca. 1976, grazed for approximately 10 years and abandoned in 1986 (ca. 11 years of regeneration). These sites are part of a long-term monitoring project examining spatial and temporal patterns of forest regeneration at the community level. Mean tree heights were higher in the older LEP stand (n=284, mean=19.7 m SD=5.6) than the younger LSUR (n=203, mean=16.7 m SD=5.5).

The tree plantations sites (Plant1 and Plant2), established in 1989 (Butterfield 1994), consisted of two 0.25-ha monospecific blocks of *Vochysia ferruginea* Mart., a common canopy tree native to the La Selva area. At the time of our study, *Vochysia* trees had a mean (±SD) diameter at breast height (d.b.h.) of 23.8±1.99 cm and a mean height of 16.5±1.3 m (P. Arroyo, unpublished data). These plantations are comparable in mean height to the second-growth stands (16.5 m), but showed considerably lower variation. The light environment in the tree plantations (2–6% transmittance), was similar in absolute values to conditions in small canopy gaps (Chazdon and Fetcher 1984), but differed from gaps in that most of the incoming light was diffuse. Thus, though tree plantations

are not 'typical' of forest understory sites in this region, they expanded the range of closed canopy sites for this study.

Species and transplant design

The three species studied – *Dipteryx panamensis* (Pittier) Record & Mell*, Virola koschnyii* Warb.*,* and *Brosimum alicastrum* Sw. – are canopy or emergent trees occurring at La Selva and surrounding areas. Although none are classified as pioneer species, *D. panamensis* has been called gap-dependent due to low survivorship of 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. *B. alicastrum* and *D. panamensis* were less common than *V. koschnyii* in the second-growth forest study sites (R.L. Chazdon, unpublished data).

We collected seeds in January 1997 from 5–10 parent trees of *V. koschnyii* and *D. panamensis* growing at La Selva and in nearby forest fragments. Seeds of *B. alicastrum* were provided by the Escuela Agricola del Tropico Humedo (EARTH) an agricultural university near La Selva. Although they are of unknown genetic origin, they were collected in the vicinity of the field sites. Seeds were germinated in sand in nursery flats. When the first set of leaves had expanded, they were transferred to plastic seedling bags (*Dipteryx*) or root trainers (*Virola* and *Brosimum*) filled with a mixture of local soil and compost (Wightman 1997) and placed under shadecloth (~20% transmittance) in a partially shaded nursery.

In July 1997, we transplanted the seedlings when they were approximately 5 months old. Mean (±SE) seedling height was 19.7±1.6 cm for *D. panamensis*, 19.1±0.32 cm for *V. koschnyii* and 17.0±1.6 cm for *B. alicastrum*. Forty seedlings of each species were planted in each second-growth and tree plantation site. In total, the experiment included 480 seedlings (3 species×2 habitats×2 sites×40 individuals). Sites were chosen to represent a range of closed canopy light conditions. In each second growth forest site (LSUR and PEJ), we planted seedlings in 20×50 m plots within 1-ha monitoring plots. One seedling of each species was planted into three of the four quadrats created by subdividing a 5×5 m subplot into 2.5×2.5 m quadrats. In the *Vochysia* plantations, we planted seedlings within two 15×30 m plots. Due to limitations imposed by plantation size, seedlings were planted in rows spaced 2.5 m apart, but with seedlings spaced at 1-m intervals along each row. There was no physical interaction between crowns or apparent overlap of root systems in any of the experimental sites.

To assess transplant effects, we checked for leaf abscission and plant mortality during the first 3 months of the study and compared them to rates later in the study. There was no evidence for significant transplant effects on final patterns of growth for any species.

Field and harvest methods

At the time of transplant, we harvested a sample of seedlings (*n*=6–10 per species) to document initial patterns of biomass partitioning. We separated seedlings into leaves, stems and roots. Leaf area was measured using a leaf area meter (LI-3100, Li-Cor, Neb., USA) and all material was dried at 70°C. For each species, we regressed total biomass or root biomass 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.

We measured 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) at the start and the end of the experiment. In September 1998, 14 months after transplantation, we harvested all surviving seedlings. We separated each individual into root, shoot, and leaf components. *V. koschnyii* and *B. alicastrum* lack distinct petioles and all material from the point of insertion on the stem was considered leaf. *D. panamensis* had compound leaves and the rachis of each leaf was considered part

of the stem (or support) component. Leaf area was measured (LI-3100, Li-Cor), and seedlings were dried at 70°C for 48 h and weighed.

Light measurements

We measured light availability using two methods: (1) instantaneous censuses of diffuse transmittance to relate growth and biomass allocation and (2) daily courses of photosynthetic photon flux density (PFD) to quantify the forest understory conditions in general. Six bimonthly censuses of percent diffuse transmittance above the study seedlings were used to quickly measure overall light environment. Instantaneous measures of percent diffuse transmittance have been shown to be highly correlated with total daily photosynthetic flux density and are more sensitive to small differences in the light environment than the commonly used hemispherical photo technique (Parent and Messier 1996; Nicotra et al. 1999). Daily courses of PFD provided general data on sunfleck activity, average PFD levels and daily totals of PFD in the understory of our sites.

We calculated instantaneous percent diffuse transmittance as the ratio of PFD below the forest canopy to that above the canopy. Below-canopy PFD was measured using a ceptometer, a line sensor consisting of 80 photodiodes (Decagon Devices, Washington, USA). Each below-canopy sample was an average of five successive measurements (1 s between measurements) of 20 adjacent photodiodes. These 20 sensors covered approximately 20 cm, roughly the diameter of the seedling crown. We referenced each below-canopy measurement to an above-canopy measurement made in a nearby clearing. Open sites were fully exposed for 58° from the zenith. Above-canopy measurements used a quantum sensor (LI-190SA, Li-Cor) mounted on a 6-m pole and attached to a datalogger (CR21X, Campbell Scientific, Utah, USA) that stored 10-s averages of 0.5-s measurements. All measurements were made on overcast days to avoid influence of direct light, and to ensure that the above- and below-canopy measurements were made under the same sky conditions. All measurements within a site were made on the same day. On several occasions, we repeated measurements in the morning and afternoon of the same day and found no significant difference in %*T* due to time of measurement.

We made direct measurements of diurnal patterns of light using GaAsP photodiodes (Hammamatsu, New Jersey, USA) attached to a datalogger (CR21X, Campbell Scientific). We mounted photodiodes atop a levelled PVC tube at a height of 50 cm. We established a single linear array of 35 sensors in the center of each site (4 arrays in total) Individuals sensors were spaced 50 cm apart. PFD was logged during daylight hours (0600–1800 hours) using 10-min averages of instantaneous 5-s readings for 2 weeks at each site. Measurements were made from July to September 1998 during the wet season, including both sunny and overcast days. We compiled frequency distributions of PFD for morning and afternoon using instantaneous 5-s readings for each measurement day.

Statistical analysis

We examined probability of mortality during the 14 months of this experiment using two separate generalized linear models that examined the dependence of mortality on light or diameter increment. For each model, we used a binomial response variable (alive/dead), a logit link function and two independent variables (species = categorical, light or diameter growth = continuous). For each individual plant, we averaged percent diffuse transmittance and diameter growth measurements over the lifetime of the plant. The test of significance of the logistic regression model is the Wald statistic, based on the asymptotic normality property of maximum likelihood estimates and is tested against the chi-square distribution (StatSoft 1999). We assessed the goodness of fit of individual species models by calculating the proportion of variance explained by the model using $(L_0-L_p)/L_0$, where L_0 is the –2×log

Fig. 1 Fitted logistic regression models of survival as a function of diameter increment (**A**) and % diffuse transmittance (**B**) for seedlings of three tropical tree species (*Virola koschnyii*, *Dipteryx panamensis*, and *Brosimum alicastrum*) growing in second-growth forest and tree plantations at La Selva Biological Station, Costa Rica
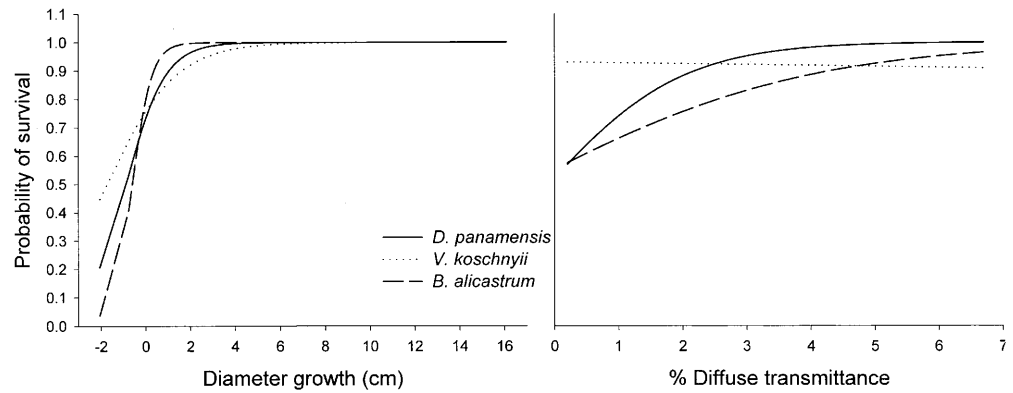
likelihood of a model including only intercept and L_p is the $-2 \times \log$ likelihood of the model in question (Hosmer and Lemeshow 2000).

We used dummy variable regression models to compare species differences in growth rates for each size variable (diameter, stem length, total biomass, and root biomass) in response to variation in light. This approach analysed 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: (1) equal slope, tests the null hypothesis of no difference among species in the slope of light-dependent growth and (2) equal intercepts, tests the null hypothesis of no difference among species in growth or allocation as light availability approached zero, i.e. no difference in growth rate or partitioning at very low light levels. Growth was calculated as a relative growth rate, ($\log_e$final size–$\log_e$initial size). We used the STATISTICA package (StatSoft, Oklahoma, USA) for all analyses.

Measures of biomass partitioning vary allometrically with plant size (Chazdon 1986; Coleman et al.1994; Farrar and Gunn 1998; McConnaughay and Coleman 1999). Plants growing in the same light environment that differ in size could have different patterns of allocation simply due to their size differences. In this study, where growth was strongly related to light, biomass partitioning reflects the combined effects of light availability and plant size. To explore partitioning, we used analysis of covariance (ANCOVA) and included light and species as main effects and final biomass as a covariate. We divided the light data into five categories (<1, 1–2, 2–4, 4–5, >5% diffuse transmittance). We collapsed the 2–3%T and 3–4%T categories because of low sample size in the 3–4%T.

Results

Light availability

Percent diffuse transmittance (%T) ranged from 1.9% to 6.4% in tree plantations with median levels of 4.2–4.8%, whereas second-growth stands ranged from 0.2% to 6.2%, with median levels of 0.7% and 1.3% for LEP and the younger LSUR, respectively (Table 1). Frequency distributions of PFD show that plantations had more sunflecks with high PFD than second-growth stands. Average PFD (0600–1800 hours) was lowest in LEP with 7.93 μmol m^{-2} s^{-1}, followed by LSUR with 20.27 μmol m^{-2} s^{-1} and was highest in the plantation sites, Plant1 and Plant2, averaging 38.05 and 43.33 μmol m^{-2} s^{-1}, respectively.

Survivorship

Survivorship of all species exceeded 60% across all microsites. Species differed significantly in survival as a function of diameter increment (Wald statistic for species×light interaction =7.28, P=0.026 for 2 df). For all species, individuals with low diameter increments had a higher probability of mortality (Fig. 1A). Species also differed significantly in their survival responses as a function of light availability (Wald statistic for species×light interaction =25.17, P<0.0001 for 2 df). Survival of *V. koschnyii* was high and remained constant at 92% across the light gradient, whereas survival of *B. alicastrum* and *D. panamensis* increased with increasing light availability (Fig. 1B). *B. alicastrum* and *D. panamensis* differed significantly in light-dependent survival (Wald statistic for species× light interaction in model including only *B. alicastrum* and *D. panamensis* =8.46, P=0.004 for 1 df). Across the light gradient, *B. alicastrum* had lower survival than *D. panamensis*. In general, these models rather poorly explained the variance in survival rates. For species-specific logistic regressions with light as the independent variable, coefficients of determination for *D. panamensis* and *B. alicastrum* were 0.19 and 0.02, respectively. For models of survival as a function of growth, coefficients of determination for *D. panamensis, V. koschnyii* and *B. alicastrum* were 0.24, 0.07 and 0.16, respectively. Stochastic events were probably an important factor weakening the relationship between survivorship, growth and light. We observed death in seedlings due to deer browsing, the establishment of a leaf cutter ant nest, human traffic and falling debris. Although individuals whose cause of death was clearly determined to be stochastic were excluded from the analysis, the 2- to 3-month census interval did not allow all stochastic events to be detected.

Growth

All measures of growth varied within and among species. Although species differed in initial biomass and leaf area, differences in growth rates led to large disparities in final size among species. Final biomass and leaf

Fig. 2 Regression models of biomass (**A**), diameter (**B**), stem length (**C**), and root biomass (**D**) growth as a function of % diffuse transmittance for seedlings of three tropical tree species (*Dipteryx panamensis* (*solid lines*), *Virola koschnyii* (*dotted lines*), and *Brosimum alicastrum* (*dashed lines*) growing in second-growth forest and tree plantations at La Selva Biological Station, Costa Rica. For clarity data are presented as mean (±SD) for five light levels (<1, 1–2, 2–4, 4–5 and >5%). Regression lines are based on analysis of the entire data set
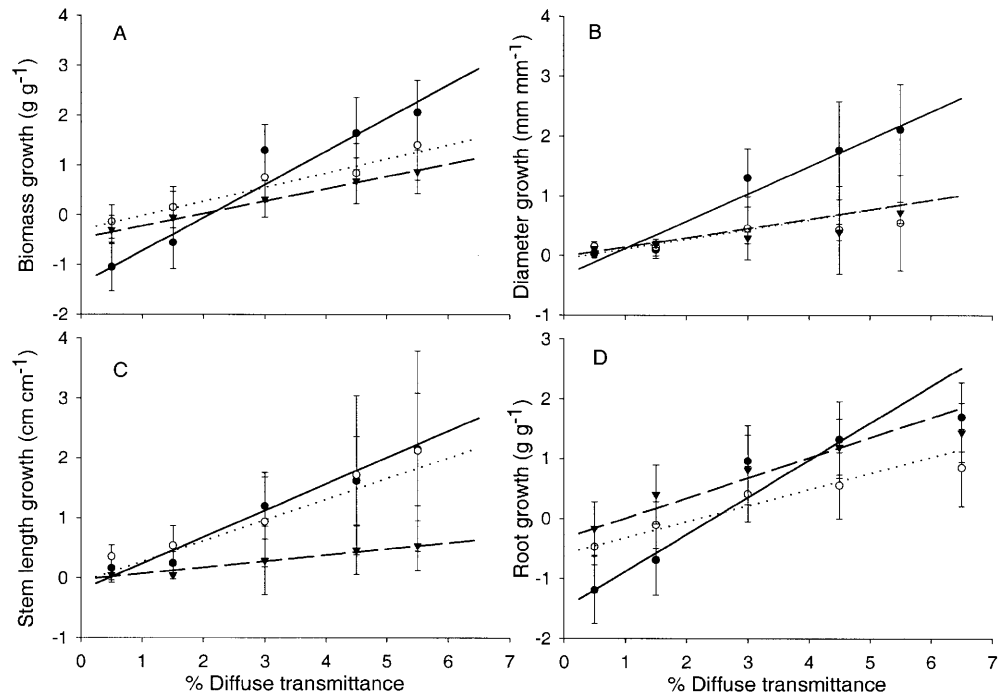

Table 2 Ranges of final diameter, stem length, root biomass, and total biomass for seedlings of three tropical tree species (*Virola koschnyii*, *Dipteryx panamensis*, and *Brosimum alicastrum*) growing in second-growth forest and tree plantations at La Selva Biological Station, Costa Rica

	D. panamensis (min–max)	*V. koschnyii* (min–max)	*B. alicastrum* (min–max)
Diameter (mm)	2.08–13.62	1.31–8.85	1.09–6.66
Stem length (cm)	15.5–151.5	12.5–130.5	12.5–54.4
Root biomass (g)	0.086–17.52	0.187–4.224	0.076–1.563
Total biomass (g)	0.452–107.27	0.925–25.3	0.387–4.72
Leaf area (cm^2)	17.4–9,673.1	23.8–2,095.9	6.9–331.4
Biomass growth rate (g g^{-1})	−1.37 to 3.30	−0.71 to 2.80	−0.47 to 1.06
Leaf area ratio (cm g^{-1})	5.03–131.38	10.46–145.5	5.20–86.6
Leaf weight ratio (g g^{-1})	0.05–0.36	0.07–0.53	0.05–0.39
Stem weight ratio (g g^{-1})	0.46–0.74	0.27–0.56	0.29–0.52
Root weight ratio (g g^{-1})	0.15–0.31	0.17–0.37	0.27–0.60

Table 3 Regression equations describing the relationship between stem length growth, diameter growth, root growth, total biomass growth, and light availability for seedlings of three tropical tree species (*Virola koschnyii*, *Dipteryx panamensis*, and *Brosimum alicastrum*) growing in second-growth forest and tree plantations at La Selva Biological Station, Costa Rica

	D. panamensis	R^2	*V. koschnyii*	R^2	*B. alicastrum*	R^2
Diameter growth (mm mm^{-1})	−0.343+0.458x	0.67	−0.060+0.164x	0.45	−0.020+0.158x	0.34
Stem length growth (cm cm^{-1})	−0.204+0.415x	0.60	−0.073+0.345x	0.33	−0.030+0.102x	0.18
Root growth (g g^{-1})	−1.50+0.618x	0.79	−0.588+0.268x	0.56	0.333+0.336x	0.62
Total biomass growth (g g^{-1})	−1.39+0.666x	0.80	0.297+0.284x	0.54	−0.471+0.249x	0.56

area of the largest *D. panamensis* was four times that of *V. koschnyii* and more than 20 times the final biomass and leaf area of the largest *B. alicastrum* (Table 2). All species exhibited significant positive relationships between PFD and biomass growth rates over the course of the experiment (Table 3, Fig. 2A). Regression lines differed significantly among species in both slope ($F_{2,324}$=208.42, $P<0.001$) and intercept ($F_{2,324}$=50.00, $P<0.001$). Among the three species, *D. panamensis* showed the lowest biomass growth rates in the darkest

microsites. However, a strong response to increasing light led to a cross-over in performance such that *D. panamensis* showed the highest growth rates at the highest light levels. Thus, species changed *rank order* of biomass growth rate as light availability increased (Fig. 2A).

Root, diameter and stem length growth revealed considerable differences among species and across light microsites. All seedlings increased diameter growth rates as a function of light availability (Table 3, Fig. 2B). Regression lines differed significantly among species in

slope ($F_{2,337}$=37.5, P<0.0001) but not intercept ($F_{2,337}$=2.6, P=0.052). All species had similar diameter increments at the lowest light levels but as light availability increased *D. panamensis* allocated more to diameter growth than the other two species. Similarly, stem length growth rates differed significantly among species in slope ($F_{2,335}$=108.5, P<0.0001) and intercept ($F_{2,335}$=8.0, P=0.01). Stem length growth rate of *B. alicastrum* increased little with increasing light, while *V. koschnyii* and *D. panamensis* showed some light dependent change in growth rates (Table 3, Fig. 2C).

Root growth rates showed a strong positive relationship to increasing light (Table 3, Fig. 2D). Again, species differed in light dependent growth ($F_{2,326}$=98.6, P<0.0001) and low light growth ($F_{2,326}$=163.4, P<0.0001). *D. panamensis* appeared to be the most sensitive to variation in light. This species had negative root growth rates at low light but converged on the root growth rates of *B. alicastrum* as light availability increased. *V. koschnyii* and *B. alicastrum* had similar light dependent root growth rates across light levels, however *B. alicastrum* always had higher root growth rate than *V. koschnyii*.

Biomass allocation

Across light levels, species differed in biomass allocation to stem, leaf and root tissue (Table 2).

Across light levels, species differed significantly in allocation to leaf tissue (species effect: $F_{1,318}$=11.99, P<0.0001, Fig. 3A). *D. panamensis* allocated more to leaf tissue than *V. koschnyii*, which allocated more than *B. alicastrum* (Tukey's HSD, P<0.05 for all pairwise comparisons). Across species, as light availability increased, allocation to leaf increased (light effect: $F_{4,318}$=5.81, P<0.001). There were significant differences between species in their response to light (species × light interaction: $F_{8,318}$=3.19, P<0.01). *B. alicastrum* decreased allocation to leaf tissue; *V. koschnyii* did not shift leaf allocation and *D. panamensis* increased allocation to leaf tissue as light availability increased (Fig. 3A). In addition to differences in relative mass of leaf tissue, leaf area ratio (LAR; ratio of total leaf area to plant dry mass) differed among species (species effect: $F_{2,304}$=84.41, P<0.0001) but was not related to light availability or final biomass. Across light levels, *D. panamensis* had significantly higher LAR (87.7±2.1 cm² leaf g⁻¹ plant) than *V. koschnyii* (76.3±2.0), which was significantly higher than *B. alicastrum* (43.1±2.0). There was a significant species×light interaction ($F_{8,304}$=4.44, P<0.0001). This interaction was driven by *D. panamensis,* which had a significantly higher LAR than *V. koschnyii* or *B. alicastrum* in all microsites above 1%T (Scheffe post hoc comparison P<0.05). Specific leaf area (SLA) differed among species (species effect: $F_{2,304}$=231.86 P<0.0001) and was related to light ($F_{4,304}$=13.7, P<0.0001) and final biomass ($F_{1,314}$=14.3 P<0.001, R^2=0.04). Across light levels, *D. panamensis* (327.8±5.7 cm² leaf g⁻¹ leaf) had significantly higher SLA than *V. koschnyii*

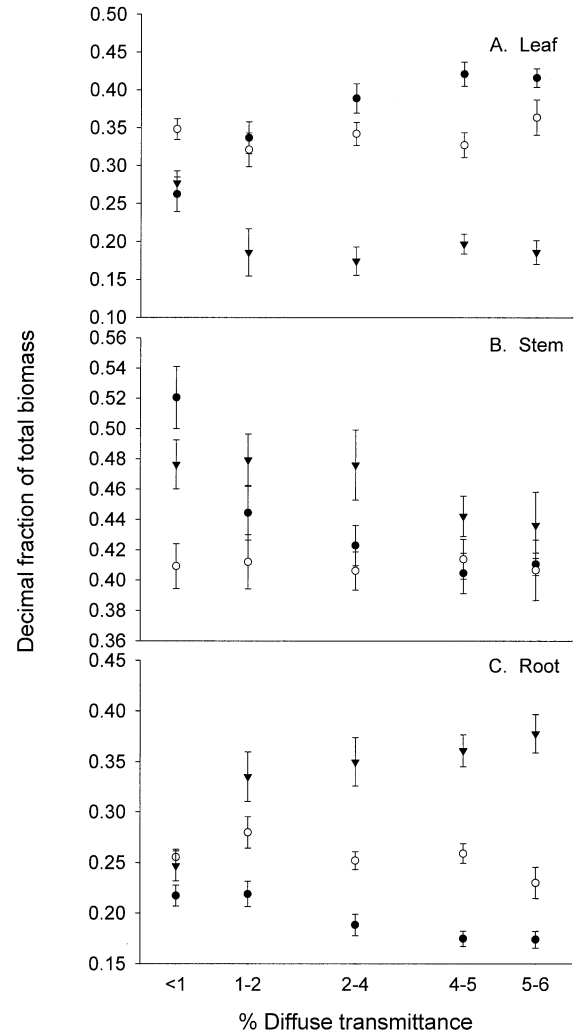
Fig. 3 Decimal fraction of biomass allocated to (**A**), leaf stem (**B**) or root (**C**) across a range of light environments for seedlings of *Dipteryx panamensis* (solid circles), *Virola koschnyii* (open circles), and *Brosimum alicastrum* (solid triangles) growing in second-growth forest and tree plantations at La Selva Biological Station, Costa Rica. Points represent mean percentage (±SE)

(228.4±3.5), which was signicantly higher than *B. alicastrum* (204.8±3.1).

D. panamensis and *B. alicastrum* had significantly higher allocation to stem that *V. koschynii* (species effect: $F_{1,318}$=20.8, P<0.0001; Tukey's HSD P<0.05 for pairwise comparisons between *D. panamensis* and *V. koschnyii*, *B. alicastrum* and *V. koschnyii*). Across species, as light availability increased, allocation to stem tissue decreased ($F_{4,318}$=2.5, P<0.05). This pattern was driven by *D. panamensis* and *B. alicastrum*, while in *V. koschnyii*, stem allocation decreased little with light (Fig. 3B).

Finally, species differed significantly in allocation to roots (species effect: $F_{1,318}$=24.77, P<0.0001). *B. alicastrum* allocated more to roots than *V. koschnyii* followed by *D. panamensis* (Tukey's HSD, P<0.05 for all pairwise comparisons). There was a significant light effect across

species with significantly lower root allocation in the lowest light environment compared to the others (light effect: $F_{4,318}=4.12$, $P<0.01$, Tukey $P<0.05$ for pairwise comparison of <1 vs other light environments). Species differed significantly in response to light (species × light interaction: $F_{8,318}=5.75$, $P<0.0001$). *B. alicastrum* showed an increase in allocation to root tissue as diffuse transmittance increased, whereas *D. panamensis* showed a decrease in the allocation to root tissue. *V. koschnyi*, in contrast, showed little variation in response to light availability (Fig. 3C). Allocation to root tissue was negatively related to plant size in all species, but this relationship was weak ($F_{1,315}=4.42$, $P<0.05$, $R^2=0.01$).

Patterns of allocation were unrelated to growth rates in *V. koschnyii* or *B. alicastrum*. In contrast, growth rates of *D. panamensis* were positively related to allocation to leaf biomass ($R^2=0.37$, $P<0.0001$, biomass growth= –2.15+10.65×LWR) and negatively related to allocation to stem biomass ($R^2=0.31$, $P<0.0001$, biomass growth= 4.9–9.30×SWR).

Discussion

Intraspecific patterns of light-dependent growth

The linear response of photosynthesis at low light suggests that changes in the magnitude of light, albeit small, could lead to significant differences in growth response in the absence of canopy gaps (Chazdon and Pearcy 1991; Chazdon 1986). How strong is the signal of light on seedling growth? Nutrients, water, herbivores and stochastic events all conspire to slow a plants progress towards the canopy. Our data show strong growth responses to increases in light availability within low light environments suggesting a measurable coupling between the light response of photosynthesis and growth (Fig. 2). Across stands, over half of the variation in growth rates could be explained by the variation in light (Table 3). In our study, the average PFD across sites ranged from ca. 7 to 40 μmol m^{-2} s^{-1}, well below photosynthetic saturation in these species (Montgomery 1999), and growth responses to light were linear for all characters measured. These data corroborate work by Pearcy (1983) that showed similar increases in the growth of two Hawaiian understory species in response to small changes in the light environment.

Light-dependent mortality

Attaining a position in the forest canopy depends not only on growth but also on long-term survival under dimly lit conditions. Seedlings may spend 20 years or more growing slowly beneath closed forest canopies before they even reach 1 cm in stem diameter. Hubbell (1998) estimated that the median age of a 1-cm d.b.h. sapling in a Panamanian forest is 16.6 years. Estimated ages of saplings of slow-growing species can exceed 80 years

(Hubbell 1998). Furthermore, Hartshorn (1978) estimated that the average number of years between successive treefalls at La Selva ranges from 79 to 137 years. This interval is considerably longer in secondary forests (Brokaw 1982). Therefore, long-term survival may be more important over this time scale than appreciable growth. Survivorship was high (60–92% over 14 months) in all species and across light environments (Fig. 1). While *B. alicastrum* and *D. panamensis* showed decreased survivorship in very low light, even in these sites, survival was greater than fifty percent. *V. koschnyii* mortality was insensitive to differences in light availability examined here, surviving equally across the light gradient. The ability to survive and grow in low light may explain the high abundance of *V. koschnyii* seedlings and saplings in these forests (R.L. Chazdon, unpublished data).

Interspecific differences in light-dependent growth and biomass allocation

Differences in growth rates led to strong differences in final biomass of our study species (Table 2). *D. panamensis* grew from a beginning advantage of 2 times the size of *V. koschnyii* to end 4 times larger in the brightest microsites. More drastically, *D. panamensis* went from an initial 5-fold advantage over *B. alicastrum* to become 20 times larger in high light sites. This large size differential resulted from the lack of appreciable stem length, leaf area or diameter growth in *B. alicastrum*. The majority of growth in this species occurred belowground. *B. alicastrum* had significantly higher root growth rates than the other species, especially in low light (Fig. 2). Ramos and Grace (1990) also found low stem length growth rates and low LARs in *B. alicastrum* growing in low light, but they did not investigate root growth. These data highlight the importance of quantifying belowground biomass. Without data on roots, growth of *B. alicastrum* would appear to be insensitive to variation in light availability beneath closed canopies. There exist contrasting data on the importance of root allocation for seedling survival. In a seasonal tropical forest, relatively large investment in roots has been positively related to survival in low light environments (Kitajima 1994). In contrast, 1-year seedling survival of four temperate tree species was strongly linked to non-structural carbohydrate levels in roots, but not to structural root biomass (Canham et al. 1999).

Difference in final size and growth of above- versus below-ground tissues reflects differences in biomass partitioning and the relationship of partitioning to growth. In *B. alicastrum* and *V. koschnyii*, distinctive allocation patterns of dry weight result in similar total biomass growth rates. *B. alicastrum* allocates very little to aboveground biomass and increases in total biomass are due almost entirely to growth in root biomass. In contrast, as light availability increases, *D. panamensis* and *V. koschnyii* minimize respiratory carbon loss by increasing

photosynthetic tissue and decreasing allocation to root and stem tissue. These allocation strategies affected biomass growth rates, at least for *D. panamensis*. In this species, allocation patterns were significantly related to biomass growth rates. Increases in leaf allocation led to higher growth rates, contributing to the increasing size advantage of *D. panamensis* as microsite light availability increased. An important factor influencing the size advantage of *D. panamensis* was the lower cost of light capture due to its high SLA across all light environments.

Resource gradient partitioning

Unlike previous studies, growth differences between species were not consistent across light environments (Kitajima 1994; Farnsworth and Ellison 1996; Poorter 1999). In particular, whereas *D. panamensis* had the lowest growth rate in the darkest microsites, it had the highest growth rate in higher light microsites (Fig. 3A). Thus, species changed the *rank order* of their growth rates as light availability increased. Differential performance along a resources gradient is one of the central requirements of the gap partitioning theory and its extension to light gradient partitioning in general (Brokaw and Busing 2000). Kobe (1999) summarized long held ideas regarding species "cross-over" along resource gradients (Horn 1971; Björkman et al. 1972; Givnish 1988) in what he termed a performance-based dominance test. In this test, partitioning occurs through changes in species performance rank such that a particular species has the highest relative rank across a specific portion of the resource gradient. In this study, interspecific differences in growth and mortality between 0.2–6.5% suggest that resource gradient partitioning could occur even in the absence of gaps. Given patterns of growth across this range of light, *V. koschnyii* and *D. panamensis* have different ranges of light in which they have the 'best' performance. Second-growth forests in the Atlantic lowlands of Costa Rica are characterized by low light availability, averaging about 1.5% transmittance and average PFD levels of ca. 7 μmol m^{-2} s^{-1} (R.L. Chazdon, unpublished data). At these light levels, *V. koschnyii* and *B. alicastrum* would outperform *D. panamensis* in biomass growth rate, but *V. koschnyii* would have higher survivorship (88%) than either *B. alicastrum* (71%) and *D. panamensis* (73%). Conversely, at higher light levels (ca. 4.5% diffuse transmittance), all species have similar survivorship but *D. panamensis* has faster growth (1.75 g g^{-1} versus 0.90 g g^{-1} for *V. koschnyii* and 0.70 g g^{-1} for *B. alicastrum)*. Further study of more species in the shade-tolerant guild is needed to address the existence of resource gradient partitioning within closed canopy, understory sites.

Fine-scale versus coarse-scale growth responses

Our data highlight the role of light for seedling growth in forested ecosystems (Chazdon 1988) and demonstrate that plants respond not only to the drastic variation in light availability caused by gaps, but also to smaller-scale heterogeneity within closed canopy, non-gap sites. The sensitive growth responses reported here draw our attention to a finer scale of light variation in forested ecosystems. To date, much of the literature has focused on coarse-scale response to large disturbances (gaps, hurricanes, landslides) and their role in forest regeneration (Whitmore and Burslem 1998). Our data show the first possibility of light gradient partitioning in low light environments through our demonstration of changes in the rank order of species performance across a relatively small range of light. We know that plant size plays an important role in recruitment from advanced regeneration after gap formation, as larger individuals have significantly lower probability of mortality during gap closure (Boot 1996; Kennedy and Swaine 1992). It follows that the patterns reported here, namely slow growth and high survival in closed canopy understory, could affect recruitment into the canopy through their impact on seedling size and seedling persistence at the time of gap formation. Our data, which take us into the dimly lit understory, are critical to understanding how the advanced regenerant community is structured. Future research needs to directly explore the consequences of these patterns for recruitment of individuals into the subcanopy and, ultimately, the canopy.

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