

Performance Trade-offs Driven by Morphological Plasticity Contribute to Habitat Specialization of Bornean Tree Species

Daisy H. Dent¹ and David F. R. P. Burslem

Department of Plant and Soil Science, School of Biological Sciences, University of Aberdeen, St Machar Drive, Aberdeen, AB24 3UU, UK

ABSTRACT

Growth-survival trade-offs play an important role in niche differentiation of tropical tree species in relation to light-gradient partitioning. However, the mechanisms that determine differential species performance in response to light and soil resource availability are poorly understood. To examine responses to light and soil nutrient availability, we grew seedlings of five tropical tree species for 12 mo at < 2 and 18 percent full sunlight and in two soil types representing natural contrasts in nutrient availability within a lowland dipterocarp forest in North Borneo. We chose two specialists of nutrient-rich and nutrient-poor soils, respectively, and one habitat generalist. Across all species, growth was higher in high than low light and on more nutrient rich soil. Although species differed in growth rates, the ranking of species, in terms of growth, was consistent across the four treatments. Nutrient-rich soils improved seedling survival and increased growth of three species even under low light. Slower-growing species increased root allocation and reduced specific leaf area (SLA) and leaf area ratio (LAR) in response to decreased nutrient supply. All species increased LAR in response to low light. Maximum growth rates were negatively correlated with survival in the most resource-limited environment. Nutrient-poor soil specialists had low maximum growth rates but high survival at low resource availability. Specialists of nutrient-rich soils, plus the habitat generalist, had the opposite suite of traits. Fitness component trade-offs may be driven by both light and belowground resource availability. These trade-offs contribute to differentiation of tropical tree species among habitats defined by edaphic variation.

Key words: Biomass allocation; Dipterocarpaceae; edaphic variation; niche partitioning; Southeast Asia.

ECOLOGICAL TRADE-OFFS may permit closely related tree species to coexist in highly diverse tropical tree communities (Kitajima 1994; Baraloto *et al.* 2005, 2006; Fine *et al.* 2006; Poorter & Kitajima 2007). Trade-offs occur when the traits that maximize the growth rate or fitness of plants in one context are inappropriate for another (Dalling & Burslem 2005). There are two main views on how trade-offs promote the coexistence of species with different maximum growth rates (Baraloto *et al.* 2006). On the one hand, traits that sustain high maximum growth rates may limit allocation to storage and defense, and reduce the likelihood of survival (Kitajima 1994, Kitajima & Bolker 2003, Baraloto *et al.* 2005, Poorter & Kitajima 2007). Alternatively, traits that confer rapid growth rate at high resource availability may be disadvantageous to growth at low resource availability, and vice versa (Sack & Grubb 2001, 2003). The first mechanism predicts a negative relationship between growth and survival across species, and the second predicts rank shifts in species growth rates from high to low resource availabilities (Baraloto *et al.* 2006).

Coexisting tropical tree species vary in their light requirements for regeneration at the seedling stage (Veneklaas & Poorter 1998, Montgomery & Chazdon 2002, Bloor & Grubb 2003). A trade-off between rapid growth in high light and survival in the shaded forest understory may be an important mechanism underlying these differential light requirements (Kitajima 1994, Sterck *et al.* 2006, Poorter & Kitajima 2007). In addition, there is substantial evidence of habitat partitioning of tropical tree species associated with fine-scale edaphic variation (Harms *et al.* 2001, Palmiotto *et al.* 2004, Paoli *et al.* 2006, John *et al.* 2007). A recent study in Amazonian Peru indicated that a trade-off between seedling growth rates

and survival, driven by a growth/defence allocation trade-off, determined tree species distributions between clay and white-sand soils, which differ markedly in nutrient availability (Fine *et al.* 2006). However, uncertainties remain as to the mechanisms of species-habitat partitioning in response to more fine-scale variation of soil resource availability (Dalling & Burslem 2005, John *et al.* 2007).

Tests of the hypothesis that tropical tree species respond differentially to nutrient supply and irradiance, resulting in niche-separation, have largely been addressed by addition of inorganic nutrients to seedlings growing in shade-houses that manipulate the light environment (Burslem *et al.* 1995, 1996; Raaimakers & Lambers 1996; Gunatilleke *et al.* 1997; Lawrence 2001). These experiments have provided valuable information on the extent and nature of nutrient limitation of tree seedling growth. However, the addition of inorganic nutrients may elevate nutrient availability beyond conditions that are likely to occur naturally. More recent studies have employed natural variation in soil fertility (Veenendaal *et al.* 1996; Palmiotto *et al.* 2004; Baraloto *et al.* 2005, 2006) and soil dilution techniques (Metcalf *et al.* 2002). Although these studies have addressed seedling responses to more realistic gradients in soil nutrient availability, they have not adequately explored responses to combinations of nutrient availability and light. Seedlings were either grown in field-scale reciprocal transplant experiments, where light could not be controlled independently of soil type (Palmiotto *et al.* 2004, Baltzer *et al.* 2005, Baraloto *et al.* 2005), in just one light environment (Baraloto *et al.* 2006), or in light treatments that do not represent fully the range of light environments that occur in natural forests (Veenendaal *et al.* 1996, Metcalf *et al.* 2002). Therefore, there remains a necessity for experimental studies that investigate growth rate trade-offs across environments that apply combinations of light and soil resource availability in realistic settings.

Received 3 March 2008; revision accepted 1 December 2008.

¹Corresponding author; current address: Smithsonian Tropical Research Institute, Unit 0948, APO AA 34002, U.S.A. e-mail: daisy.h.dent@gmail.com

Tropical and temperate tree species differ markedly in the minimum irradiance at which they respond to increased nutrient availability (Latham 1992, Burslem *et al.* 1996, Canham *et al.* 1996). Nutrient additions generally increase growth and survival rates at > 5 percent daylight (Coomes & Grubb 2000). However, in deep shade (< 2% daylight) increased nutrient supply has been reported either to increase growth rates (Burslem *et al.* 1996) or to reduce growth rates and survival (Coomes & Grubb 2000). A reduction in growth and survival might occur because respiration rates are upregulated by increased nutrient supply without any compensating increase in photosynthetic rates, thus inducing net carbon loss (Lambers & Poorter 1992, Reich *et al.* 1996). Frequently, species that are most responsive to nutrient addition, even at relatively low irradiance, have the highest relative growth rates at moderate nutrient supply (Latham 1992, Huante *et al.* 1995, Denslow *et al.* 1998; but see Veenendaal *et al.* 1996).

To understand the mechanisms that underlie growth rate trade-offs it is necessary to investigate the morphological and physiological determinants of growth rate, which are intercorrelated. In general, species that are capable of attaining high maximum growth rates have high values of specific leaf area (SLA), leaf area ratio (LAR), leaf mass ratio (LMR) and maximum rate of photosynthesis, and low root mass ratio (RMR) (Reich *et al.* 1997, Poorter 2005). Plasticity in these traits may provide seedlings with a competitive advantage in environments with substantial temporal and spatial variability of essential resources (Rice & Bazzaz 1989, Bloor & Grubb 2003). High plasticity in these traits in response to variation in light is characteristic of fast-growing woody tropical species (Poorter 1999, Valladares *et al.* 2000). However, a recent study in French Guiana found a negative relationship between species phenotypic plasticity and maximum growth rates in comparisons across a soil fertility gradient (Baraloto *et al.* 2006). Therefore, differences in phenotypic plasticity between species may be determined by the resource that is most limiting to growth.

In this study, we grew seedlings of five tropical tree seedlings under controlled conditions of light and soil resource availability to address the following questions: (1) In terms of growth, survival, and biomass allocation, do species respond in a similar way to variation in light availability as they do to nutrients? (2) Do species rankings, in terms of growth, change with altered resource availability? (3) Are high maximum growth rates associated with low survival? (4) Do fast-growing species exhibit greater plasticity in the morphological components of growth than slow-growing species?

METHODS

STUDY SITE.—The study site was Sepilok Forest Reserve (5°10' N, 117°56' E), hereafter SFR, which is on the east coast of Sabah, Malaysia. The reserve is a 4475 ha patch of lowland dipterocarp and heath forest at 0–170 m asl (Fox 1973, DeWalt *et al.* 2006). Mean annual rainfall during 1976–1995 was 2975 mm, with no month receiving < 100 mm on average (Malaysian Meteorological Department, unpublished data). However, through the year there is

distinct variation in rainfall distribution; April is generally the driest month and December and January the wettest with 45 percent of the annual precipitation falling from early November to mid-February (Fox 1973).

SFR supports two lowland dipterocarp forest communities (alluvial forest and sandstone hill forest) that differ significantly in their species composition and occur in association with changes in the underlying soil and geological substrate (Fox 1973, Nilus 2004). Alluvial forest occurs on ultisols overlying alluvial flats and gently sloping, low mudstone and sandstone hills (Fox 1973), while the sandstone hill forest occurs on well-drained ultisols and lithosols on steeply sloping sandstone ridges and valleys interbedded with mudstone (for further details see Fox 1973, Baltzer *et al.* 2005, Dent *et al.* 2006, DeWalt *et al.* 2006). Tree species diversity and basal area are lower in the sandstone hill forest than in the alluvial forest, and stem density is greater (Nilus 2004).

Alluvial forest soils have significantly greater concentrations of total P and N than the sandstone hill forest soils (Table 1; see also Dent 2004, Baltzer *et al.* 2005, Dent *et al.* 2006). Concentrations of nitrate and the base cations are also significantly greater in alluvial than sandstone soils, while pH and concentrations of phosphate, ammonium and Al do not differ. Monthly sampling of surface soil matric potential and gravimetric water content over one year revealed no consistent difference in matric potential between alluvial and sandstone soils (Dent 2004). However, gravimetric soil water content and soil water storage were significantly lower in the well-drained sandstone derived soils than in alluvial soils (Dent 2004). The alluvial forest understory has lower mean irradiance than the sandstone forest understory (2.81 ± 0.15 vs. 3.21 ± 0.19 mol/m²/day respectively), which suggests that canopy structure and light environments differ (Baltzer *et al.* 2005).

STUDY SPECIES.—Five species were selected for the study: two species native to alluvial forest (*Dryobalanops lanceolata* Burck and *Shorea leprosula* Miq.), two species found exclusively on sandstone soils (*Hopea beccariana* Burck and *Shorea multiflora* (Burck) Sym.), and one ubiquitous species (*Shorea smithiana* Sym.). *Dryobalanops lanceolata* is a shade-tolerant species that is widespread on fertile soils in north Borneo (Zipperlen & Press 1996, Bungard *et al.* 2002). *Shorea leprosula* is a common and widespread emergent dipterocarp species in Malaysian lowland forests. It is a relatively light-demanding nonpioneer species and exhibits rapid growth rates (Zipperlen & Press 1996, 1997). *Shorea multiflora* and *H. beccariana* are common in the sandstone hills and ridges of SFR (Nicholson 1965, Burgess 1966). *Shorea multiflora* is reported as having shade-tolerant seedlings (Turner 1990). *Shorea smithiana* is one of only two dipterocarp species that has approximately equal abundance in both the alluvial and sandstone hill forest areas of SFR. It can grow to a very large size, is one of the most common *Shorea* species in Borneo, and is frequent on undulating land (Meijer & Wood 1964). There is no published information on the shade-tolerance of *H. beccariana* and *S. smithiana*, but seedlings of both species persist in small numbers in the shaded understory at our study site (D. F. R. P. Burslem, pers. obs.).

TABLE 1. Environmental characteristics of experimental gap and understory sites in alluvial and sandstone hill forests at SFR, Malaysia, including total daily PPFD ($\text{mol m}^{-2}/\text{day}$; Baltzer et al. 2005), yearly mean soil gravimetric water content (g/g) at 12–17 cm below the litter layer, and pH and concentrations of major nutrients (mg/kg) at 0–5 cm below the litter layer. All values represent means (± 1 SE) based on $N = 5$ (PPFD measurements), $N = 12$ (soil water content), and $N = 10$ (soil chemical analyses). Means with the same superscript are not significantly different ($P > 0.05$) using Tukey's HSD range test. For details of sampling and analytical techniques see Dent (2004).

	Alluvial		Sandstone	
	Gap	Understory	Gap	Understory
Total daily PPFD ($\text{mol m}^{-2}/\text{day}$)	14.9 \pm 0.10	2.81 \pm 0.15	11.9 \pm 0.10	3.21 \pm 0.19
Gravimetric water content soil (g/g)	0.38 \pm 0.03 ^a	0.28 \pm 0.02 ^b	0.32 \pm 0.03 ^b	0.21 \pm 0.02 ^c
Total P	281.1 \pm 22.39 ^a	343.7 \pm 70.50 ^a	53.01 \pm 12.11 ^b	74.82 \pm 14.11 ^b
Total N	2882 \pm 247 ^a	3306 \pm 276 ^a	1046 \pm 218 ^b	1517 \pm 161 ^b
Exchangeable P	0.83 \pm 0.17 ^a	0.96 \pm 0.22 ^a	0.88 \pm 0.35 ^a	2.12 \pm 0.87 ^a
NO ₃	17.3 \pm 3.13 ^a	13.1 \pm 3.82 ^a	5.51 \pm 0.73 ^b	5.15 \pm 1.44 ^b
NH ₄	31.4 \pm 5.28 ^a	22.7 \pm 2.67 ^a	20.1 \pm 4.77 ^a	23.2 \pm 3.12 ^a
Exchangeable K	0.135 \pm 0.023 ^a	0.125 \pm 0.022 ^a	0.060 \pm 0.012 ^b	0.056 \pm 0.007 ^b
Exchangeable Ca.	0.446 \pm 0.059 ^a	0.354 \pm 0.040 ^a	0.137 \pm 0.021 ^b	0.111 \pm 0.012 ^b
Exchangeable Mg	0.148 \pm 0.050 ^a	0.134 \pm 0.045 ^a	0.038 \pm 0.011 ^b	0.039 \pm 0.006 ^b
pH	4.65 \pm 0.05 ^a	4.67 \pm 0.17 ^a	4.54 \pm 0.03 ^a	4.45 \pm 0.14 ^a

GROWTH CONDITIONS.—Seedlings of *D. lanceolata*, *S. leprosula*, and *S. smithiana* were grown from seed in the nursery of the Forest Research Centre, Sabah, adjacent to SFR. Seeds were collected during January 2002 from primary forest in SFR. Seedlings were grown initially in cylindrical polyethylene bags containing 100 ml of clay-rich forest soil. Seedlings of *H. beccariana* and *S. multiflora* were collected from the understory of sandstone hill forest in SFR, during 22–26 January 2002, and were transplanted immediately into 100 ml polyethylene bags containing sandstone hill soil. The seedlings were stored for 3–4 weeks in a shade house transmitting approximately 18 percent of full daylight prior to their use in the experiment. At the time of transplantation the mean height of seedlings was 20 cm, 11 cm, 14 cm, 11 cm, and 10 cm for *D. lanceolata*, *S. leprosula*, *S. smithiana*, *H. beccariana*, and *S. multiflora*, respectively. Mean leaf number was six for *D. lanceolata*, nine for *H. beccariana*, and three for *S. leprosula*, *S. smithiana*, and *S. multiflora*.

Seedlings of each species were transplanted into 1.2 l plastic pots containing either alluvial or sandstone hill forest soils in a balanced factorial design comprising all combinations of the five species and two soil types. Soil was collected from ca. 5–50 cm depth to exclude soils highly enriched in organic matter close to the soil surface. Soils were collected at three alluvial and three sandstone primary forest sites in SFR and passed through a 2 \times 2 mm sieve. On 26 March 2002, seedlings were distributed among seven tables shaded by two layers of shade cloth (high-light environment) and seven tables with four layers of cloth (low-light environment, see below). On each table, plants were randomly arranged within two blocks of 10 seedlings, with one replicate of each species by soil type treatment per block. Hence, five species were grown in two light environments each with seven shade tables that had two soil types randomly arranged in two blocks (five species \times two light levels \times seven tables \times two soil types \times two blocks = 280

plants, with 14 replicates of each species/ treatment combination). Seedlings were grown for 12 mo and watered daily with tap water until the soil in the pots was saturated to minimize differences in water availability. Although differences in moisture availability between the two soil types were not incorporated into this experimental design, it is recognized that traits related to this resource are potentially important for growth. Plants were re-randomized within the shade tables on 26 June and 28 September 2002, and 4 January 2003.

On 12 March 2002 two photosynthetically active radiation (PAR) sensors (sensor model SKP 215 attached to two Datalog model 2, SDL 5000 Series, Skye Instruments Ltd., Llandrindod Wells, UK) were placed on the floor of each of two shade tables within each light treatment. Over the subsequent 15 d the light sensors were moved to randomly selected shade tables to record the light environment of five high-light and five low-light shade tables. The same procedure was repeated from 1 April 2003 to assess whether the shade cloth had degraded and to quantify the extent of this degradation. In March 2002, the sensors recorded a mean PAR of 8.71 ± 0.214 $\text{mol m}^{-2}/\text{day}$ (mean \pm SE) in the high-light and 0.659 ± 0.0241 $\text{mol m}^{-2}/\text{day}$ in the low-light treatment. These values correspond to 18.4 ± 1.1 percent and 1.4 ± 0.05 percent PAR in full sunlight in the high-light and low-light treatments, respectively, when compared with an adjacent unshaded sensor. In April 2003, the sensors recorded 23.5 ± 0.7 percent and 1.8 ± 0.04 percent of full daylight PAR in the same two treatments. Measurements of the R:FR ratio were taken in April 2003 using the same protocol (Skye Instruments Ltd. Llandrindod Wells, UK). Sensors recorded R:FR ratios of 0.79 ± 0.01 in the low-light treatment and 1.14 ± 0.01 in the high-light treatment. The two light treatments imposed in this experiment simulate the PAR of a small gap and the forest understory in SFR (D. H. Dent, unpublished data), but the

TABLE 2. Summary of ANOVA for seedling growth rates and morphological traits, and analysis of deviance for seedling survival. *df*, F-statistics, and degrees of significance are reported. Growth rate data are calculated over 1 yr and all other traits were measured at the final harvest of five dipterocarp species planted into pots of either alluvial or sandstone derived soil, in either high (18% PAR) or low-light (< 2% PAR) shade house environments. Prior to analysis, relative growth rates, total dry-mass, and SLA were log-transformed and mass ratios were arc-sine transformed. Degrees of significance: ****P* < 0.001; ***P* < 0.01; **P* < 0.05.

Factor	df	RGR _{height}	RGR _{diameter}	Dry-mass	LMR	SMR	RMR	SLA	Survival
Initial seedling size	1	34.9***	140***	3.82	3.79	5.21*	0.36	2.30	1.71
Soil	1	12.6***	11.0***	55.6***	15.3***	1.52	14.3***	1.78	4.42*
Light	1	8.11*	9.98**	26.0***	46.6***	1.49	36.6***	212***	1.45
Species	4	72.3***	71.6***	163***	4.33**	7.81***	6.82***	32.8***	0.96
Soil × light	1	0.07	2.05	3.22	1.02	0.01	0.70	0.09	0.01
Soil × species	4	1.21	0.69	6.89***	4.17**	2.76*	7.42***	0.86	0.43
Light × species	4	3.03*	4.07**	5.81***	1.52	1.39	2.38	1.74	0.32
Soil × light × species	4	0.80	0.98	1.51	1.15	0.72	1.07	1.34	0.87
Block (light)	12	1.23	2.12*	1.97*	1.15	1.65	1.48	0.60	–
Model <i>R</i> ²		0.66	0.65	0.88	0.38	0.43	0.60	0.77	–

R:FR in both treatments was higher than would be encountered in these forest environments.

SEEDLING MEASUREMENTS.—After 12 mo (27–28 March 2003) seedlings were harvested, divided into leaf, stem, and root fractions, dried to constant mass at 60°C for 48 h and weighed. Mass ratios (mass of a plant part divided by total plant mass) were calculated for leaves (LMR), stems and petioles (stem mass ratio, SMR), and roots (RMR), as described by Evans (1972). Prior to drying, all leaves (with petiole removed) were photocopied, and the area of each leaf was then calculated by weighing the photocopies and a known area of paper. Mean SLA (leaf area divided by total leaf dry-mass excluding petiole) and LAR (total plant leaf area divided by total plant dry-mass) were calculated per plant. Plasticity in relation to soil or light was defined as the magnitude of change in allocation to specific plant parts in response to these environmental variables and was thus computed as the difference in the mean value of biomass ratios between the two light environments or the two soil types. For all seedlings, diameter at 5 cm above soil surface, seedling height and leaf number were recorded on 25–26 March 2002, and 27–28 March 2003. Relative growth rates (RGR) of stem diameter, height, and leaf number were calculated as follows (Evans 1972):

$$\text{RGR} = \log_e W_2 - \log_e W_1 / t_2 - t_1,$$

where W_2 and W_1 are final and initial growth measurements and $t_2 - t_1$ was 12 mo.

STATISTICAL ANALYSIS.—To examine variation in survival we derived a linear mixed-effects model with binomial errors using the glmmPQL function, MASS library, R version 2.5.1. Light, species, and soil type were treated as fixed factors, and block nested within light as a random factor (Sokal & Rohlf 1995). It should be noted that the number of replicates per treatment combination (14) provides limited statistical power for the detection of treatment effects and interactions in the survival analysis. Prior to analysis propor-

tional values of leaf, stem and root dry-mass were arcsine transformed and total dry-mass and relative growth rates were log transformed if residuals were not normally distributed (Sokal & Rohlf 1995). Relative growth rate, final dry-mass, and dry-mass allocation ratios were analyzed using a linear mixed effects model, with light, species, and soil type as fixed factors and block nested within light as a random factor. Initial seedling height was included as a covariate for the analysis of RGR_{height} and initial diameter was used as a covariate for all other variables. These analyses indicated that RGR_{diameter} and RGR_{height} responded similarly to the effects of soil, light, and species (Table 2). Therefore RGR_{diameter} is presented as a surrogate for relative growth rates in this paper and RGR_{max} is defined as RGR_{diameter} on alluvial soil in high light. Multiple comparisons among means were made using Tukey's honest significant difference tests with the error rate corrected to 0.05. The significance of differences within species was tested using analogous mixed models to those described above. Pearson correlations were fitted to describe the trends of association between growth components and both RGR_{max} and survival, and to test the statistical significance of those relationships (Sokal & Rohlf 1995). All statistical analyses were conducted using R 2.5.1 (The R Foundation for Statistical Computing, 2006).

RESULTS

SEEDLING GROWTH AND SURVIVAL.—Species, soil type, and light environment all significantly affected measures of relative growth rate and final dry-mass (Table 2). Across all species, relative growth rates were higher in high than low light and on alluvial rather than sandstone soil (Table 2; Fig. 1). Growth rates varied significantly among species but the ranking of species, in terms of growth rate, did not change with soil type (*i.e.*, there was no significant species × soil type interaction; Table 2). In contrast, there was evidence of an interaction between species and light environment for both

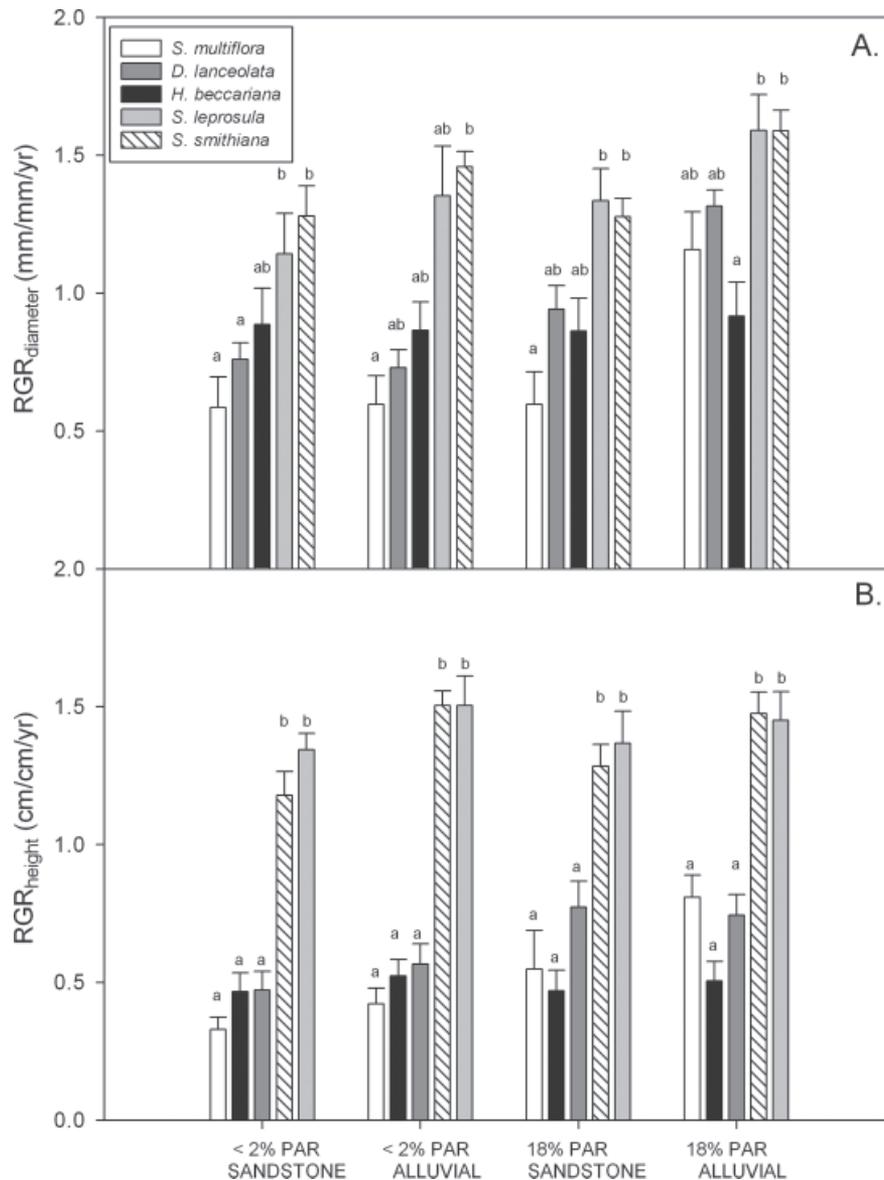


FIGURE 1. The effects of light environment and soil type on RGR_{height} and $RGR_{diameter}$ of seedlings of five dipterocarp species planted into pots of either alluvial or sandstone derived soil, in either high (18% PAR) or low light (< 2% PAR) shade house environments. All bars represent means (\pm SE; $N = 14$). Within each treatment group species sharing the same superscript letter are not significantly different, $P > 0.05$, Tukey's HSD test.

$RGR_{diameter}$ and RGR_{height} (Table 2). In all environments, *S. leprosula* and *S. smithiana* grew significantly faster than the three other species, but growth rates within these two groupings did not differ for RGR_{height} (Fig. 1). Seedling survival was high in all treatments but was significantly higher in alluvial (97%) than sandstone soil (87%), and did not vary significantly with irradiance or species (Table 2). Survival was 95 percent in the high light treatment and 89 percent in low light.

Species differed in their dry-mass growth in response to soil type and light environment (Table 2). Mean seedling dry-mass was significantly higher at high than at low light availability for all

species except *H. beccariana* and greater in alluvial than sandstone soil for all species except *S. smithiana*. The relative effect of soil type on final dry-mass was greater than the effect of light environment for the sandstone specialist species, *S. multiflora* and *H. beccariana* (Table 3). In contrast, dry-mass of seedlings of the alluvial specialist *D. lanceolata* was more strongly affected by light than soil type, and growth of soil generalist *S. smithiana* was affected only by light. The nature of the interaction between soil-type and light-environment on dry-mass varied among species: in *S. leprosula* and *S. multiflora* the increase in dry-mass in response to growth in alluvial soil was greater at high light than low light, while there was

TABLE 3. The effects of light environment and soil type on mean final dry-mass (g), leaf (LMR), stem (SMR) and root mass ratios (RMR), specific leaf area (SLA, cm²/g) and leaf area ratio (LAR, cm²/g) for seedlings of five dipterocarp species planted into pots of either alluvial (A) or sandstone (SS) derived soil, in either high or low light shade house environments (F and P values from ANOVA presented by variable). Species soil affinity is indicated after the species name. Degrees of significance: NS = not significant; ***P < 0.001; **P < 0.01; *P < 0.05. (N = 14).

Light treatment Soil type	High light		Low light		Soil F	Light F	Soil × light F
	A	SS	A	SS			
<i>Dryobalanops lanceolata</i> —Alluvial							
Final dry-mass	14.8 ^a	11.4 ^{ab}	8.33 ^b	7.57 ^b	5.35*	20.4***	NS
LMR	0.290 ^a	0.296 ^a	0.470 ^b	0.381 ^{ab}	NS	16.8***	5.22*
SMR	0.313 ^{ab}	0.346 ^a	0.257 ^b	0.302 ^{ab}	4.81*	4.61*	NS
RMR	0.397 ^a	0.359 ^a	0.273 ^b	0.317 ^{ab}	NS	12.5**	4.76*
SLA	128 ^a	109 ^a	155 ^b	161 ^b	NS	27.0***	4.15*
LAR	36.7 ^a	31.6 ^a	72.5 ^b	60.1 ^b	4.05*	17.9***	NS
<i>Shorea leprosula</i> —Alluvial							
Final dry-mass	10.9 ^a	5.19 ^b	5.79 ^b	3.07 ^b	37.1***	13.1***	5.26*
LMR	0.273 ^a	0.290 ^a	0.415 ^b	0.392 ^b	NS	14.7***	NS
SMR	0.293 ^a	0.342 ^b	0.303 ^a	0.320 ^a	5.28*	NS	NS
RMR	0.435 ^a	0.368 ^{ab}	0.282 ^b	0.288	NS	12.2**	NS
SLA	154 ^a	170 ^{ab}	196 ^b	205 ^b	NS	27.2***	NS
LAR	46.2 ^a	50.0 ^a	82.9 ^b	79.4 ^b	NS	17.2***	NS
<i>Shorea smithiana</i> —Generalist							
Final dry-mass	13.6 ^a	15.6 ^a	7.00 ^b	6.25 ^b	NS	44.1***	NS
LMR	0.286 ^a	0.291 ^a	0.359 ^{ab}	0.422 ^b	NS	9.4**	NS
SMR	0.292 ^a	0.301 ^a	0.328 ^a	0.285 ^a	NS	NS	NS
RMR	0.422 ^a	0.408 ^a	0.313 ^b	0.293 ^b	NS	16.3***	NS
SLA	131 ^a	115 ^a	192 ^b	182 ^b	NS	52.1***	NS
LAR	37.2 ^a	33.9 ^a	69.6 ^b	76.2 ^b	NS	11.8**	NS
<i>Hopea beccariana</i> —Sandstone							
Final dry-mass	0.753 ^a	0.469 ^b	0.971 ^a	0.430 ^b	15.8***	NS	NS
LMR	0.244 ^a	0.193 ^a	0.470 ^b	0.295 ^a	8.8**	30.6***	NS
SMR	0.282 ^a	0.289 ^a	0.249 ^a	0.256 ^a	NS	NS	NS
RMR	0.474 ^a	0.518 ^a	0.280 ^b	0.448 ^a	14.3*	23.1***	NS
SLA	160 ^a	148 ^a	222 ^b	192 ^a	NS	19.8***	NS
LAR	40.1 ^a	24.2 ^a	104 ^b	56.3 ^a	10.6***	44.4***	NS
<i>Shorea multiflora</i> —Sandstone							
Final dry-mass	3.50 ^a	0.950 ^b	1.44 ^b	0.775 ^b	33.4***	5.15*	7.04**
LMR	0.460 ^a	0.282 ^b	0.474 ^a	0.370 ^{ab}	13.3***	NS	NS
SMR	0.223 ^a	0.246 ^a	0.191 ^a	0.222 ^a	NS	NS	NS
RMR	0.317 ^a	0.471 ^b	0.335 ^a	0.409 ^{ab}	11.1***	NS	NS
SLA	105 ^a	104 ^a	131 ^b	128 ^b	NS	17.1***	NS
LAR	48.4 ^{ab}	32.5 ^a	61.9 ^b	47.4 ^{ab}	7.94**	8.15**	NS

Mean values sharing the same superscript letter within a row are not significantly different, $P > 0.05$, Tukey's HSD test.

no such interaction for the other three species. In sandstone soils only species native to alluvial forest responded to the higher light environment by increasing seedling dry-mass (Table 3).

MORPHOLOGICAL TRAIT VARIATION IN RESPONSE TO ENVIRONMENTAL VARIATION.—Species differed in their dry-mass allocation in response to soil type and light environment (Table 3). Seedlings

of all species except *S. multiflora* decreased dry-mass allocation to leaves, by 28–43 percent of the low light value, in high light compared to low light (Table 3). For all species, values of SLA and LAR increased significantly at lower light availability. Only seedlings of the two sandstone specialists exhibited plasticity in mass allocation in response to soil type by increasing RMR when grown in sandstone soil, relative to their values in alluvial soil, and this came at the

TABLE 4. Pearson correlation coefficients between RGR_{diameter} on alluvial soil in high light and indices of plasticity in five plant traits in response to soil type and light environment variation. The indices of plasticity are presented for leaf mass (LMR), root mass (RMR), stem mass (SMR), and leaf area ratios (LAR) and specific leaf area (SLA; $N = 5$).

Soil type plasticity	<i>R</i>	<i>P</i>	Light plasticity	<i>r</i>	<i>P</i>
LMR	0.89	0.044	LMR	-0.10	0.875
RMR	-0.90	0.036	RMR	-0.33	0.588
SMR	0.39	0.523	SMR	0.35	0.563
SLA	0.77	0.127	SLA	0.39	0.513
LAR	0.98	0.004	LAR	-0.18	0.766

expense of a lower LMR. Seedlings of *H. beccariana* decreased LMR and LAR by 29 and 40 percent, respectively and increased RMR by 27 percent on sandstone compared to alluvial soil, while seedlings of *S. multiflora* decreased both LMR and LAR by 32 percent and increased RMR by 26 percent (all percentages are relative to values on the alluvial soil). Although these changes were evident in both light environments, they were less pronounced at low light (< 2% PAR), where seedlings also increased allocation to leaves and thereby compromised proportional increases in root mass. The SMR was generally consistent across treatments, and so the increased values of LMR in the low light environment resulted in decreased RMR.

PLASTICITY OF MORPHOLOGICAL TRAITS AND ECOLOGICAL TRADE-OFFS.—Interspecific patterns of plasticity for dry-mass allocation to roots, leaves, and total leaf area in response to soil type were correlated with RGR_{max} (defined as RGR_{diameter} on alluvial soil in high light), but plasticity in morphological traits in response to light were not correlated with RGR_{max} (Table 4; Fig. 2A, B). Species with low maximum growth rates had a greater relative increase in mass allocation to roots and a greater relative decrease in allocation to leaf area in response to a reduction in nutrient availability than fast-growing species. There was no evidence to suggest that fast-growing species exhibited higher plasticity in morphological traits than slow-growing species. In cross species comparisons, RGR_{max} exhibited a negative relationship with seedling survival in sandstone soil in low light (Fig. 2D). Although this relationship was marginally nonsignificant ($r = -0.84$, $P = 0.073$), a negative relationship between maximum RGR_{height} and survival in sandstone soil in low light was also observed ($r = -0.88$, $P = 0.045$, data not shown). RGR_{max} did not show any relationship with seedling survival in any other environment. There was a nonsignificant negative relationship between plasticity in LAR in relation to soil type and seedling survival in sandstone soil in low light ($r = -0.71$, $P = 0.181$; Fig. 2C).

DISCUSSION

SEEDLING GROWTH AND SURVIVAL IN RELATION TO LIGHT AND SOIL RESOURCE AVAILABILITY.—Seedling growth and survival were enhanced in alluvial forest soil. The difference between soil type treatments must reflect the greater concentrations of most nutrients in alluvial forest soil (Table 1), because differences in soil water availability would have been eliminated by daily watering. The faster growth rates and improved survival of seedlings in the alluvial forest soil provides evidence that variation in soil nutrient availability at the habitat scale has the potential to influence dipterocarp seedling performance and may contribute to the species habitat partitioning observed at this site (Nilus 2004, DeWalt *et al.* 2006).

Responses to increases in the availability of light and nutrients support other recent studies. Seedling survival and growth rate both increased with light availability, except in the case of *H. beccariana*, which may have a whole-plant light compensation point for growth that is lower than the low light treatment in this experiment (*i.e.*, < 2 percent PAR). This study adds to recent work demonstrating that natural variability in soil nutrient availability may affect tropical tree seedling growth and survival (Palmiotto *et al.* 2004; Baraloto *et al.* 2005, 2006; Fine *et al.* 2006). In our study, responses in terms of relative growth rate were estimated from nondestructive measures of aboveground growth. However, these measures may not correlate directly to relative growth rate of biomass because allocation of dry-mass changes in response to environmental changes and through ontogeny, and species respond differentially (Table 2; Hunt 1982). Therefore, our conclusions require confirmation by further work to quantify relative growth rates of biomass from sequential harvests.

Higher nutrient availability increased final dry-mass of four species (*D. lanceolata*, *S. leprosula*, *H. beccariana*, and *S. multiflora*) and increased survival for all five species combined, even in low light environments. Nutrients stimulated aboveground growth by increasing LAR without otherwise impacting dry-mass allocation (in *D. lanceolata*), or by increasing proportional allocation of dry-mass to leaves at the expense of roots, as well as increasing SLA (in *H. beccariana* and *S. multiflora*). The positive response to nutrient supply in low light conditions shown here for dipterocarps is in marked contrast to the responses of seedlings of other nonpioneer tropical trees, which typically show a growth response to nutrient addition under conditions equivalent to our high-light treatment, but not at low irradiance (*e.g.*, Thompson *et al.* 1992, Huante *et al.* 1998). In a study conducted in forest soils from Singapore, Burslem *et al.* (1996) found that seedlings of two tree species were limited by one or more macro-nutrients when grown at < 1 percent daylight. These findings suggest that seedlings growing in the shaded understory of lowland dipterocarp forests in SE Asia may be limited by nutrients, as well as light. In our study, seedling survival was unaffected by reduced irradiance, whereas seedling mortality is typically higher in deep shade. However, increased mortality in forest understory sites may result from factors other than light limitation, such as herbivory and branchfalls (Myers & Kitajima 2007), and these biotic factors were not present in our study.

Residual effects of the light environment in which seedlings established or were stored prior to the experiment (18% of full

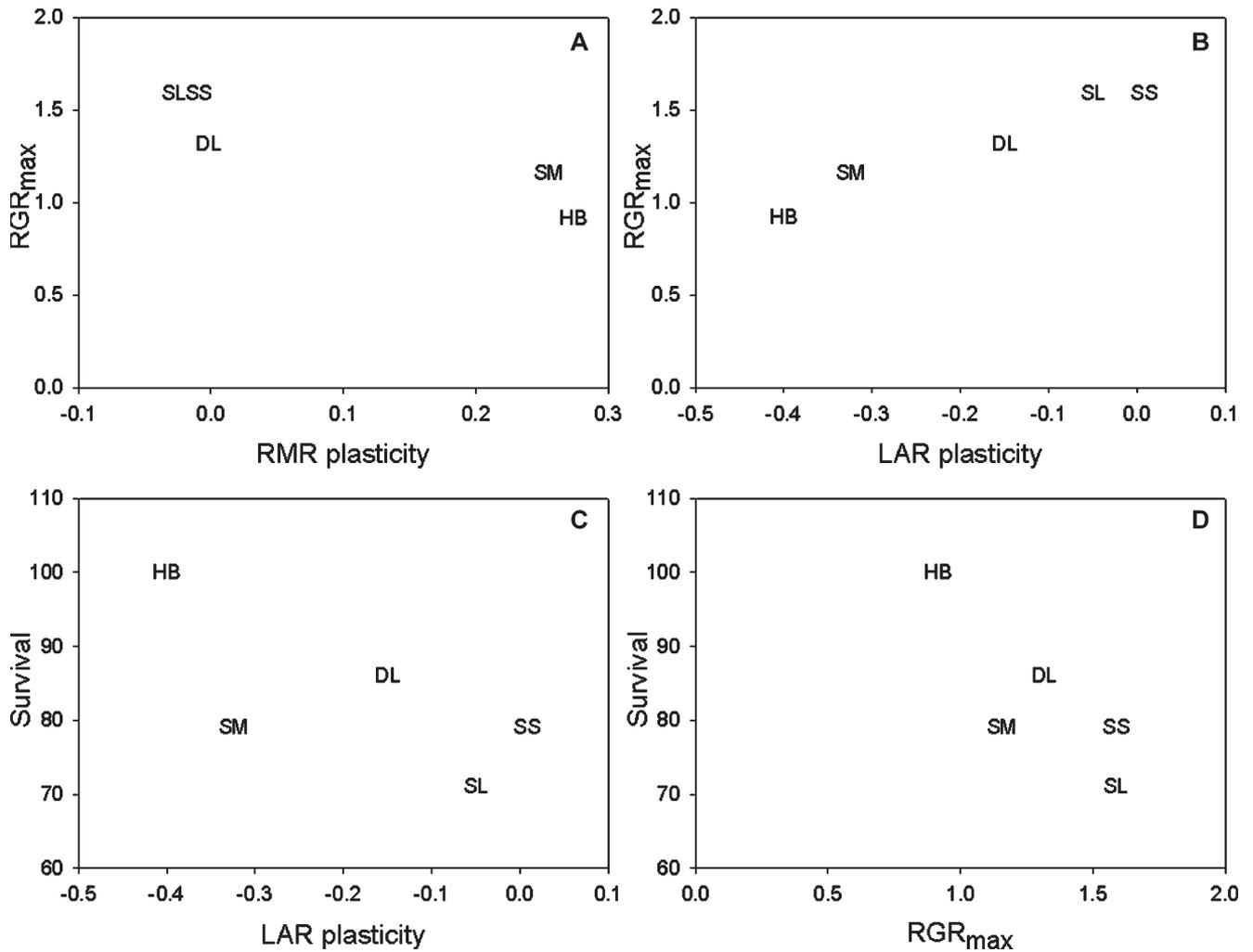


FIGURE 2. The relationships between (A) RMR plasticity in relation to soil type and RGR_{max} (defined as $RGR_{diameter}$ on alluvial soil in high light; $r = -0.90$, $P = 0.036$); (B) LAR plasticity in relation to soil type and RGR_{max} ($r = 0.98$, $P = 0.004$); (C) LAR plasticity in relation to soil type and percentage seedling survival in sandstone soil in low light ($r = -0.71$, $P = 0.181$); (D) RGR_{max} and percentage seedling survival in sandstone soil in low light ($r = -0.84$, $P = 0.073$) for five dipterocarp species comprising two sandstone specialists (SM = *Shorea multiflora*; HB = *Hopea beccariana*), two alluvial specialists (DL = *Dryobalanops lanceolata*; SL = *S. leprosula*), and one generalist (SS = *S. smithiana*).

daylight PAR) could have impacted seedling traits. Morphological traits of tropical rain forest tree species take from a few weeks (SLA) to many months (LAR) to acclimate to changes in light availability (Popma & Bongers 1991). However, given the small size of seedlings, the short period of storage, and the long growth period it is likely that complete acclimation to experimental growth conditions had taken place by the final harvest.

PERFORMANCE TRADE-OFFS.—Although seedling growth varied significantly with changes in soil type and light availability, the species' growth rate hierarchy was consistent across the four environmental treatments. These data do not support the hypothesis that traits conferring rapid growth at high resource availability trade-off against traits that maintain relatively fast growth even when resources are

low, resulting in shifts in species growth rankings from high to low resource availabilities (Sack & Grubb 2001, 2003). Similar patterns of highly consistent species growth rate rankings were observed across eight different soil treatments (Baraloto *et al.* 2006) and across gradients of both light and soil resources (Baraloto *et al.* 2005) in two recent studies of nine tropical tree seedlings in French Guiana. However, for the Bornean dipterocarps in our study we did find tentative evidence for a growth/survival trade-off, even over the relatively short duration of one year. Maximum growth rate was inversely correlated with survival in the most light and nutrient-limited environment. This finding parallels the observation that the traits that maximize growth in high-light trade-off against traits that confer increased survival in the shade in studies of differential shade tolerance (Kitajima 1994, 2002; Davies 2001; Poorter &

Kitajima 2007). However, this negative relationship was not evident in all gap versus understory comparisons, and was found only when growth in the least resource-limited treatment was correlated with survival in the most resource-limited treatment. This finding suggests that fitness component trade-offs may not be driven solely by differential light availability (Kitajima 1994) but by responses to the availability of both light and belowground resources (Baraloto *et al.* 2005). It is possible that the growth-survival trade-off was not manifested in all high-low light comparisons because the factors that reinforce increased seedling mortality in the forest understory, such as pathogens, falling debris, and herbivores (Myers & Kitajima 2007), were absent from this study.

In our controlled environment experiment the growth versus survival trade-off was manifested even though the seedlings were not exposed to herbivory and fungal pathogens, which are often purported to underlie this trade-off and its link to patterns of adult distribution (Baraloto *et al.* 2005, Fine *et al.* 2006, Poorter & Kitajima 2007). This discrepancy suggests that, in the current study, the mechanism underpinning the trade-off is unlikely to be connected to defense allocation. Instead, the growth versus survival trade-off must be determined by differential physiological tolerance to nutrient limitation at low light. A reciprocal transplant experiment of five dipterocarp species grown in alluvial and sandstone forest habitats at Sepilok suggested that invertebrate herbivory has a relatively minor impact on seedling growth and survival (Eichhorn *et al.* 2006), and that habitat specialist species had contrasting gas exchange characteristics (Baltzer *et al.* 2005). These studies lend support to our interpretation that the growth/survival trade-off observed under controlled environment conditions has significance for the mechanism of habitat specialization in the context of physiological constraints and not differential growth and defense allocation.

PLASTICITY OF MORPHOLOGICAL TRAITS.—Tropical tree seedlings have been reported to increase SLA and allocate a greater proportion of dry-mass to leaves to maximize carbon gain and reduce carbon losses in response to low irradiance (Veneklaas & Poorter 1998, Poorter 1999, Bloor & Grubb 2003). Consistent with these trends, in low light, the seedlings in our study altered their morphology to increase leaf area for light capture and photosynthesis. All species increased SLA and LAR in low light and seedlings of all species, except *S. multiflora*, allocated a greater proportion of dry-mass to leaves in low light. Increased allocation to leaf area in low light may increase seedling survival, thus allowing seedling populations to persist in the forest understory until canopy gaps, and increased irradiance, support onward growth (Veneklaas & Poorter 1998, Poorter 1999).

Differential plasticity of morphological traits among species did not vary according to expectation. High plasticity of morphological traits in response to variation in light is characteristic of fast-growing woody tropical species (Poorter 1999, Valladares *et al.* 2000), but we found that the proportional increase in allocation to leaf area in the shade was approximately equal across all species. Therefore, although morphological plasticity is important for survival in the forest understory, a lack of differentiation among the dipterocarp species in this study suggests that plasticity in these

traits is not significant for light partitioning at the seedling stage in this system. In contrast, seedlings with low growth rates, which did not allocate an intrinsically greater proportion of dry-mass to roots than faster-growing species (Aerts & Chapin 2000, but see Reich 2002), possessed a greater capacity to increase dry-mass allocation to roots, and to reduce SLA and LAR, in response to decreased nutrient supply. Therefore, our data do not support the hypothesis that fast-growing species exhibit greater plasticity in morphological traits (Poorter 1999, Valladares *et al.* 2000). Conversely, we found a negative relationship between phenotypic plasticity and maximum growth rate in response to natural variation in soil nutrient availability. A similar interpretation was reported by Baraloto *et al.* (2006) working with seedlings of nine tropical tree species across a soil fertility gradient in French Guiana.

Plasticity in morphological traits in response to edaphic variation may be driven by adaptations to cope with shortage of nutrients and/or water. At our study site, the surface soil of sandstone forest has lower concentrations of total P and N, nitrate and available base cations (K, Ca, and Mg) than that of alluvial forest, and the fluxes of nutrients via litterfall and litter decomposition are also lower in the sandstone forest (Dent 2004, Dent *et al.* 2006). There is also evidence of limitation by low water availability during occasional dry spells on the summits of the well-drained sandstone ridges, and no such evidence for the low-lying alluvial forest (Dent 2004, Dent *et al.* 2006). Increased dry-mass allocation to roots is observed frequently as a response to nutrient limitation, and implies that increased nutrient uptake may improve long-term survival on nutrient-poor soils (Evans 1972). Similarly, reduced values of SLA and LAR may be driven by water or nutrient limitation (Aerts & Chapin 2000; Wright *et al.* 2001, 2002; Wright & Westoby 2002; Reich *et al.* 2003). Lowered SLA and LAR both contribute to a reduction in relative growth rates, which reduces turnover of carbon and nutrients in low-nutrient environments (Aerts & Chapin 2000). However, low SLA and LAR may also reduce the total leaf area available for water loss and so are consistent with a strategy of water conservation, which may be an important adaptation to survive periods of seasonal drought. A field study of seedling physiological traits at the SFR suggested that divergent water-use strategies may contribute to the mechanisms underlying differences in edaphic associations, as sandstone specialist dipterocarp species consistently exhibited higher water-use efficiencies than alluvial specialist or generalist species (Baltzer *et al.* 2005). These studies support the perspective that both nutrient and water availability contribute to differentiation of dipterocarp habitat associations at our study site and elsewhere in Borneo (Palmiotto *et al.* 2004, Baltzer *et al.* 2005, Dent *et al.* 2006, Paoli *et al.* 2006).

IMPLICATIONS FOR SPECIES PARTITIONING.—Performance trade-offs may play an important role in the partitioning of tree species in response to resource heterogeneity in tropical forests. Our results indicate that a trade-off exists between traits that confer high maximum growth rates and traits that confer high survival when resources are limiting. This finding provides support for the hypothesis that trade-offs similar to those seen across light gradients (Kitajima 1994) may contribute to species differentiation

across soils of different nutrient status (Baraloto *et al.* 2005, 2006). Recent studies have identified ecophysiological traits that underlie the trade-off between growth in high light versus survival in the forest understory, such as the ability to store nonstructural carbohydrates (Myers & Kitajima 2007, Poorter & Kitajima 2007). Results from existing studies on the mechanisms that underpin growth versus survival trade-offs in relation to soil resource availability are not consistent, possibly due to differences in experimental designs. In this study, slower-growing species were able to withstand limited soil resource availability by increasing allocation to roots and reducing leaf area to reduce growth and transpiration rates. However, for tree seedlings growing in French Guiana the increased survival of slower-growing species in response to limited soil resource availability was related to greater plasticity in assimilation rates and not plasticity in allocation to roots (Baraloto *et al.* 2006). Our study of Bornean dipterocarps was not designed to address the role of plasticity in assimilation rates in coping with limitations in soil resource availability, and further research is required to address this issue.

ACKNOWLEDGMENTS

We thank the Natural Environment Research Council (studentship to DHD) and the British Ecological Society's Overseas Research Programme for financial support. The Economic Planning Unit of the Federal Government of Malaysia kindly granted permission to conduct research in Malaysia. We also thank R. Nilus and C. Maycock for advice and O. Johnny, R. Yudot, and B. Seligi for their contribution to the field and laboratory work in Sepilok.

LITERATURE CITED

- AERTS, R., AND F. S. III CHAPIN. 2000. The mineral nutrition of wild plants revisited: A re-evaluation of processes and patterns. *Adv. Ecol. Res.* 30: 1–67.
- BALTZER, J. L., S. C. THOMAS, R. NILUS, AND D. F. R. P. BURSLEM. 2005. Edaphic specialization in tropical forest trees: Physiological correlates and responses to reciprocal transplantation. *Ecology* 86: 3048–3062.
- BARALOTO, C., D. E. GOLDBERG, AND D. BONAL. 2005. Performance trade-offs among tropical tree seedlings in contrasting microhabitats. *Ecology* 86: 2461–2472.
- BARALOTO, C., D. BONAL, AND D. E. GOLDBERG. 2006. Differential seedling growth response to soil resource availability among nine Neotropical tree species. *J. Trop. Ecol.* 22: 487–497.
- BLOOR, J. M. G., AND P. J. GRUBB. 2003. Growth and mortality in high and low light: Trends among 15 shade-tolerant tropical rain forest tree species. *J. Ecol.* 91: 77–85.
- BUNGARD, R. A., S. A. ZIPPERLEN, M. C. PRESS, AND J. D. SCHOLES. 2002. The influence of nutrients on growth and photosynthesis of seedlings of two rainforest dipterocarp species. *Funct. Plant Bio.* 29: 505–515.
- BURGESS, P. F. 1966. *Timbers of Sabah*. Sabah Forestry Record: 6, Malaysia.
- BURSLEM, D. F. R. P., P. J. GRUBB, AND I. M. TURNER. 1995. Responses to nutrient addition among shade-tolerant tree seedlings of lowland tropical rain forest in Singapore. *J. Ecol.* 83: 113–122.
- BURSLEM, D. F. R. P., P. J. GRUBB, AND I. M. TURNER. 1996. Responses to simulated drought and elevated nutrient supply among shade-tolerant tree seedlings of lowland tropical forest in Singapore. *Biotropica* 28: 636–648.
- CANHAM, C. D., A. R. BERKOWITZ, V. R. KELLY, G. M. LOVETT, S. V. OLLINGER, AND J. SCHNURR. 1996. Biomass allocation and multiple resource limitation in tree seedlings. *Can. J. For. Res.* 26: 1521–1530.
- COOMES, D. A., AND P. J. GRUBB. 2000. Impacts of root competition in forests and woodlands: A theoretical framework and review of experiments. *Ecol. Monogr.* 70: 171–207.
- DALLING, J. W., AND D. F. R. P. BURSLEM. 2005. Role of life-history trade-offs in the equalization and differentiation of tropical tree species. *In* D. F. R. P. Burslem, M. A. Pinard, and S. E. Hartley (Eds.). *Biotic interactions in the tropics: Their role in the maintenance of species diversity*, pp. 65–88. Cambridge University Press, Cambridge, UK.
- DAVIES, S. J. 2001. Tree mortality and growth in 11 sympatric *Macaranga* Species in Borneo. *Ecology* 82: 920–932.
- DENSLOW, J. S., A. M. ELLISON, AND R. E. SANFORD. 1998. Treefall gap size effects on above- and below-ground processes in a tropical wet forest. *J. Ecol.* 86: 597–609.
- DENT, D. H. 2004. The mechanistic basis of habitat specialization of dipterocarps: Are species differentiated by specialisation to environmental variation? PhD Dissertation, University of Aberdeen, UK.
- DENT, D. H., R. BAGCHI, N. MAJALAP, D. ROBINSON, AND D. F. R. P. BURSLEM. 2006. Nutrient fluxes via litterfall and leaf litter decomposition across a gradient of soil nutrient supply in a lowland tropical rain forest. *Plant Soil* 288: 197–215.
- DEWALT, S. J., K. ICKES, R. NILUS, K. E. HARMS, AND D. F. R. P. BURSLEM. 2006. Liana habitat associations and community structure in a Bornean lowland tropical forest. *Plant Ecol.* 186: 203–216.
- EICHHORN, M. P., S. G. COMPTON, AND S. E. HARTLEY. 2006. Seedling species determines rates of leaf herbivory in a Malaysian rain forest. *J. Trop. Ecol.* 22: 513–519.
- EVANS, G. C. 1972. *The quantitative analysis of plant growth*. Blackwell Scientific Publications, Oxford, UK.
- FINE, P. V. A., Z. J. MILLER, I. MESONES, S. IRAZUZTA, H. M. APPEL, M. H. H. STEVENS, I. SAAKSJARVI, J. C. SCHULTZ, AND P. D. COLEY. 2006. The growth-defense trade-off and habitat specialization by plants in Amazonian forests. *Ecology* 87: S150–S162.
- FOX, J. E. D. 1973. Kabili-Sepilok forest reserve. Sabah Forest Record: 9. Borneo Literature Bureau, Malaysia.
- GUNATILLEKE, C. V. S., I. A. U. N. GUNATILLEKE, G. A. D. PERERA, D. F. R. P. BURSLEM, P. M. S. ASHTON, AND P. S. ASHTON. 1997. Responses to nutrient addition among seedlings of eight closely-related species of *Shorea* in Sri Lanka. *J. Ecol.* 85: 301–311.
- HARMS, K. E., R. CONDIT, S. P. HUBBELL, AND R. B. FOSTER. 2001. Habitat associations of trees and shrubs in a 50-ha Neotropical forest plot. *J. Ecol.* 89: 947–959.
- HUANTE, P., E. RINCON, AND I. ACOSTA. 1995. Nutrient availability and growth rate of 34 woody species from a tropical deciduous forest in Mexico. *Funct. Ecol.* 9: 849–858.
- HUANTE, P., E. RINCON, AND F. S. CHAPIN. 1998. Foraging for nutrients, responses to changes in light, and competition in tropical deciduous tree seedlings. *Oecologia* 117: 209–216.
- HUNT, R. 1982. *Plant growth curves: The functional approach to plant growth analysis*. Edward Arnold, London, UK.
- JOHN, R., J. W. DALLING, K. E. HARMS, J. B. YAVITT, R. F. STALLARD, M. MIRABELLO, S. P. HUBBELL, R. VALENCIA, H. NAVARRETE, M. VALLEJO, AND R. B. FOSTER. 2007. Soil nutrients influence spatial distributions of tropical tree species. *Proc. Natl. Acad. Sci. USA* 104: 864–869.
- KITAJIMA, K. 1994. Relative importance of photosynthetic and allocation traits as correlates of seedling shade tolerance of 15 tropical tree species. *Oecologia* 98: 419–428.
- KITAJIMA, K. 2002. Do shade-tolerant tropical tree seedlings depend longer on seed reserves? Functional growth analysis of three Bignoniaceae species. *Funct. Ecol.* 16: 433–444.
- KITAJIMA, K., AND B. M. BOLKER. 2003. Testing performance rank reversals among coexisting species: Crossover point irradiance analysis by Sack & Grubb 2001 and alternatives. *Funct. Ecol.* 17: 276–281.

- LAMBERS, H., AND H. POORTER. 1992. Inherent variation in growth-rate between higher-plants—a search for physiological causes and ecological consequences. *Adv. Ecol. Res.* 23: 187–261.
- LATHAM, R. E. 1992. Co-occurring tree species change rank in seedling performance with resources varied experimentally. *Ecology* 73: 2129–2144.
- LAWRENCE, D. 2001. Nitrogen and phosphorus enhance growth and luxury consumption of four secondary forest tree species in Borneo. *J. Trop. Ecol.* 17: 859–869.
- MEIJER, W., AND G. H. S. WOOD. 1964. Dipterocarps of Sabah (North Borneo). *Sabah Forestry Record*: 5, Malaysia.
- METCALFE, D. J., P. J. GRUBB, AND S. S. METCALFE. 2002. Soil dilution as a surrogate for root competition: Effects on growth of seedlings of Australian tropical rainforest trees. *Funct. Ecol.* 16: 223–231.
- 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.
- MYERS, J. A., AND K. KITAJIMA. 2007. Carbohydrate storage enhances seedling shade and stress tolerance in a Neotropical forest. *J. Ecol.* 95: 383–395.
- NICHOLSON, D. I. 1965. Proceedings of the symposium for ecological research in humid tropics vegetation, Kuching. pp. 67–87. UNESCO, Paris, France.
- NILUS, R. 2004. Effect of edaphic variation on forest structure, dynamics, diversity and regeneration in a lowland tropical rain forest in Borneo. PhD dissertation, University of Aberdeen, UK.
- PAOLI, G. D., L. M. CURRAN, AND D. R. ZAK. 2006. Soil nutrients and beta diversity in the Bornean Dipterocarpaceae: Evidence for niche partitioning by tropical rain forest trees. *J. Ecol.* 94: 157–170.
- PALMIOTTO, P. A., S. J. DAVIES, K. A. VOGT, M. S. ASHTON, D. J. VOGT, AND P. S. ASHTON. 2004. Soil-related habitat specialization in dipterocarp rain forest tree species in Borneo. *J. Ecol.* 92: 609–623.
- POORTER, L. 1999. Growth responses of 15 rain-forest tree species to a light gradient: The relative importance of morphological and physiological traits. *Funct. Ecol.* 13: 396–410.
- POORTER, L. 2005. Resource capture and use by tropical forest tree seedlings and their consequences for competition. *In* D. F. R. P. Burslem, M. A. Pinard and S. E. Hartley (Eds.). *Biotic interactions in the tropics: Their role in the maintenance of species diversity*, pp. 35–64. Cambridge University Press, Cambridge, UK.
- POORTER, L., AND K. KITAJIMA. 2007. Carbohydrate storage and light requirements of tropical moist and dry forest tree species. *Ecology* 88: 1000–1011.
- POPMA, J., AND F. BONGERS. 1991. Acclimation of seedlings of 3 Mexican tropical rain-forest tree species to a change in light availability. *J. Trop. Ecol.* 7: 85–97.
- RAAIMAKERS, D., AND H. LAMBERS. 1996. Response to phosphorus supply of tropical tree seedlings: A comparison between a pioneer species *Tapirira obtusa* and a climax species *Lecythis corrugata*. *New Phytol.* 132: 97–102.
- REICH, P. B. 2002. Root-shoot relations: Optimality in acclimation and adaptation or the “Emperor’s New Clothes”? *In* Y. Waisel, A. Eshel and U. Kafkafi, (Eds.). *Plant roots: The hidden half*, 3rd Edition, pp. 205–220. Marcel Dekker Inc., New York, New York.
- REICH, P. B., J. OLEKSYN, AND M. G. TJOELKER. 1996. Needle respiration and nitrogen concentration in Scots Pine populations from a broad latitudinal range: A common garden test with field-grown trees. *Funct. Ecol.* 6: 768–776.
- REICH, P. B., I. J. WRIGHT, J. CAVENDER-BARES, J. M. CRAINE, J. OLEKSYN, M. WESTOBY, AND M. B. WALTERS. 2003. The evolution of plant functional variation: Traits, spectra, and strategies. *Int. J. Plant Sci.* 164: S143–S164.
- REICH, P. B., M. B. WALTERS, AND D. S. ELLSWORTH. 1997. From tropics to tundra: Global convergence in plant functioning. *Proc. Natl. Acad. Sci. USA* 94: 13730–13734.
- RICE, S. A., AND F. A. BAZZAZ. 1989. Growth consequences of plasticity of plant traits in response to light conditions. *Oecologia* 78: 508–512.
- SACK, L., AND P. J. GRUBB. 2001. Why do species of woody seedlings change rank in relative growth rate between low and high irradiance? *Funct. Ecol.* 15: 145–154.
- SACK, L., AND P. J. GRUBB. 2003. Crossovers in seedling relative growth rates between low and high irradiance: Analyses and ecological potential (reply to Kitajima & Bolker 2003). *Funct. Ecol.* 17: 281–287.
- SOKAL, R. R., AND F. J. ROHLF. 1995. *Biometry*. W.H. Freeman and company, New York, New York.
- STERCK, F. J., L. POORTER, AND F. SCHIEVING. 2006. Leaf traits determine the growth–survival trade-off across rain forest tree species. *Am. Nat.* 167: 758–765.
- THOMPSON, W. A., P. E. KRIEDEMANN, AND I. E. CRAIG. 1992. Photosynthetic response to light and nutrients in sun-tolerant and shade-tolerant rain-forest trees. 1. Growth, leaf anatomy and nutrient content. *Aust. J. Plant. Physiol.* 19: 1–18.
- TURNER, I. M. 1990. Tree seedling growth and survival in a Malaysian rain forest. *Biotropica* 22: 146–154.
- VALLADARES, F., S. J. WRIGHT, E. LASSO, K. KITAJIMA, AND R. W. PEARCY. 2000. Plastic phenotypic response to light of 16 congeneric shrubs from a Panamanian rainforest. *Ecology* 81: 1925–1936.
- VEENENDAAL, E. M., M. D. SWAINE, R. T. LECHA, M. F. WALSH, I. K. ABEBRESE, AND K. OWUSU-AFRIYIE. 1996. Responses of West African forest tree seedlings to irradiance and soil fertility. *Funct. Ecol.* 10: 501–511.
- VENEKLAAS, E. J., AND L. POORTER. 1998. Growth and carbon partitioning of tropical tree seedlings in contrasting light environments. *In* H. Lambers, H. Poorter and M. M. I. Van Vuuren (Eds.). *Inherent variation in plant growth, physiological mechanisms and ecological consequences*. Backhuys, Leiden, The Netherlands.
- WRIGHT, I. J., AND M. WESTOBY. 2002. Leaves at low versus high rainfall: Coordination of structure, lifespan and physiology. *New Phytol.* 155: 403–416.
- WRIGHT, I. J., P. B. REICH, AND M. WESTOBY. 2001. Strategy shifts in leaf physiology, structure and nutrient content between species of high- and low-rainfall and high- and low nutrient habitats. *Funct. Ecol.* 15: 423–434.
- WRIGHT, I. J., M. WESTOBY, AND P. B. REICH. 2002. Convergence towards higher leaf mass per area in dry and nutrient poor habitats has different consequences for leaf lifespan. *J. Ecol.* 90: 534–543.
- ZIPPERLEN, S. A., AND M. C. PRESS. 1996. Photosynthesis in relation to growth and seedling ecology of two dipterocarp rain forest tree species. *J. Ecol.* 84: 863–876.
- ZIPPERLEN, S. A., AND M. C. PRESS. 1997. Photosynthetic induction and stomatal oscillations in relation to the light environment of two dipterocarp rain forest tree species. *J. Ecol.* 85: 491–503.