Seedling growth responses to soil resources in the understory of a wet tropical forest

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Abstract. Plant growth responses to resources may be an important mechanism that influences species' distributions, coexistence, and community structure. Irradiance is considered the most important resource for seedling growth in the understory of wet tropical forests, but multiple soil nutrients and species have yet to be examined simultaneously with irradiance under field conditions. To identify potentially limiting resources, we modeled tree seedling growth as a function of irradiance and soil nutrients across five sites, spanning a soil fertility gradient in old-growth, wet tropical forests at La Selva Biological Station, Costa Rica. We measured an array of soil nutrients including total nitrogen (total N), inorganic N (nitrate [NO₃⁻] and ammonium [NH₄⁺]), phosphate (PO₄³⁻), and sum of base cations (SBC; potassium, magnesium, and calcium). Shade in the forest understory did not preclude seedling growth correlations with soil nutrients. Irradiance was a significant predictor of growth in 52% of the species, inorganic N in 54% (NO₃⁻ in 32%; NH₄⁺ in 34%); total N in 47%, SBC in 39%, and PO₄³⁻ in 29%. Overall, growth was correlated with both irradiance and soil nutrients in 45% of species and with soil nutrients only in an additional 48%; rarely was irradiance alone correlated with growth. Contrary to expectations, the magnitudes of growth effects, assessed as the maximum growth response to significant resources for each species, were similar for irradiance and most soil nutrients. Among species whose growth correlated with soil nutrients, the rank importance of nutrient effects was SBC, followed by N (total N, NO₃⁻, and/or NH₄⁺) and PO₄³⁻. Species' growth responsiveness (i.e., magnitudes of effect) to irradiance and soil nutrients was negatively correlated with species' shade tolerance (survival under 1% full sun). In this broad survey of species and resources, the nearly ubiquitous effects of soil nutrients on seedling growth challenge the idea that soil nutrients are less important than irradiance in the light-limited understory of wet tropical forests.

Key words: forest understory; irradiance; La Selva Biological Station, Costa Rica; neotropics; plant growth; seedlings; shade tolerance; soil nutrients; wet tropical forest.

INTRODUCTION

Tropical forest understories are spatially heterogeneous in irradiance (Nicotra et al. 1999) and soil resources (E. K. Holste et al., unpublished manuscript), and species-specific seedling growth and survivorship responses to resource levels could influence community structure. In both temperate and tropical forests, there is an interspecific trade-off between survivorship under low light (i.e., shade-tolerant species) vs. growth under high light (i.e., light-demanding species) that could promote species coexistence across light gradients (Kobe et al. 1995, Kobe 1999). Similarly, interspecific trade-offs between growth and survivorship exist along edaphic gradients, potentially contributing to species' distributions (Schreeg et al. 2005, Russo et al. 2008). These resource-based trade-offs could be a mechanism for resource partitioning (Grubb 1977), which could sustain tree species diversity in tropical forests. Therefore, understanding species-specific seedling growth responses to resources may be crucial for predicting forest dynamics.

In tropical forests, irradiance is considered to be “the single most limiting resource” (Pearcy 2007), with sometimes <1% of above canopy radiation transmitted to the forest floor (Chazdon and Fetcher 1984). Wet tropical forest seedlings exhibit both intra- and interspecific variation in growth to differing light levels (Augspurger 1984, Poorter 1999). Even in low-light environments, such as beneath closed canopy forests, tropical seedling growth varies interspecifically in response to light availability (Montgomery and Chazdon 2002).

Soil nutrients also can influence tree seedling growth (Burslem et al. 1995, Dent and Burslem 2009). In tropical forests, species differ in the direction and strength of growth responses to soil factors (Baraloto et al. 2006). Phosphorus (P) is widely thought to be
more limiting than nitrogen (N) in lowland tropical forests because most tropical soils are N rich relative to other nutrients (Hedin et al. 2009). Seedling growth responses to P additions support limitation by P (Lawrence 2001, Ceccron et al. 2003). Yet, N also could alleviate P limitations by providing a substrate to construct extracellular phosphatases to acquire P (Treseder and Vitousek 2001). Based on reviews of plant-soil relations in lowland wet tropical forests, Solis (1998) proposed the rank order of nutrients most strongly influencing species’ composition, and by extension seedling performance, are P, base cations (potassium, calcium, magnesium), and N.

Soil nutrients may interact with irradiance to influence tree seedling performance (e.g., Kobe 2006). A common assumption is that light-demanding species invest more in traits that maximize growth (Herms and Mattson 1992) since they tend to have small seeds, small initial seedling size, and photosynthetic cotyledons (Kitajima 2002). In contrast, shade-tolerant species have larger seeds, storage cotyledons, larger initial seedling height and mass, and invest in functions that improve survivorship such as defense against natural enemies (Coley and Barone 1996) and carbohydrate storage (Myers and Kitajima 2007). The growth of both light-demanding and shade-tolerant seedlings respond to soil nutrients under high-light availability (reviewed by Lawrence 2003), likely because faster growth increases demand for nutrients (Peace and Grubb 1982). Seedlings in the shaded understory also could benefit from increased soil nutrient availability via improved light capture (Fahey et al. 1998). Soil nutrients can influence light-demanding and shade-tolerant seedling growth in the forest understory (Yavitt and Wright 2008, Palow and Oberbauer 2009), yet shade-tolerant species presumably have a lower nutrient demand due to their cotyledon reserves and slower growth. Thus, we expect seedling growth of light-demanding species to be more dependent upon soil resources than more shade-tolerant species. Furthermore, seedling dependency on external sources generally develops earlier for light than mineral nutrients, suggesting greater importance of light than soil nutrients during early seedling establishment (Kitajima 2002). Thus, we expect growth–irradiance correlations to be more prevalent and irradiance to have a greater effect than soil nutrients on seedling growth in the shaded forest understory.

In this study, we examined the growth responses of 94 species of woody seedlings (represented by 12 800 individuals) to irradiance and soil nutrients under field conditions to better understand species-specific seedling performance and implications for forest dynamics. We hypothesized that: $H_1$, Irradiance limitations to seedling growth are more prevalent among species and are of a greater magnitude than soil resource limitations to seedling growth; $H_2$, Among the species whose seedling growth is sensitive to soil nutrients, the rank importance of soil nutrients is (in decreasing order) P, base cations, and N; and $H_3$, Across species, the effect of irradiance and soil nutrients on seedling growth is negatively correlated with shade tolerance.

**Methods**

**Site description**

The study took place in five sites in mainly old-growth wet tropical forest at La Selva Biological Station, Costa Rica. A portion of 1 site contained secondary forest, which was associated with higher wood productivity (T. W. Baribault, personal communication), but not higher seedling growth. La Selva is located in the Atlantic lowlands at the Sarapiqui and Puerto Viejo rivers’ convergence (10°26' N, 84°00' W) and receives mean annual rainfall of 4367 mm (mean monthly minimum of 124 mm). La Selva soils span a fertility gradient from relatively fertile entisols and ultisols developed on old lava flows (McDade and Hartshorn 1994); sites were established on three volcanic and two alluvial soils. Each site was centered on a transect of 200 contiguous 1-m$^2$ quadrats. In each transect, seedlings were identified and height measurements taken every six weeks from February 2000 to September 2009.

**Resource measurements**

We measured light and soil nutrient availability for each 1-m$^2$ quadrat, which is an appropriate spatial scale to assess seedling resource availability (E. K. Holste et al., unpublished manuscript). Light availability was measured with hemispherical canopy photos six times during the course of the study. We also measured a broad suite of soil characteristics for each quadrat (three composited subsamples per 1-m$^2$ quadrat), including inorganic nitrogen (nitrate [NO$_3^-$] and ammonium [NH$_4^+$]), total nitrogen (total N), phosphate (PO$_4^{3-}$), potassium (K$^+$), calcium (Ca$^+$), and magnesium (Mg$^+$. Extractable K$^+$, Ca$^+$, and Mg$^+$ were highly correlated and were combined into a composite metric of sum of base cations expressed in charge equivalents (SBC). However, total N, NO$_3^-$, and NH$_4^+$ were not strongly correlated, so all N forms were examined individually. Detailed methods for resource measurements are presented in Appendix A.

**Data analyses**

Across the five sites, the data set encompassed 522 woody species (including lianas and canopy, subcanopy, and understory trees) and 14 000 individuals. With the aid of a database compiled by C. F. Vriesendorp (available online), we identified all seedlings to species (89% of individuals) or morphospecies. Any misidentified seedlings would be a small percentage of the total sample. Among the 522 potential species, only 95 species had sample sizes $\geq$ 20 individuals (represented by

4 http://fm1.fieldmuseum.org/seedlings/index.php)
expected growth rate (compounding of growth for longer lived seedlings. We indicates a diminishing, while different from zero (or unity for least two, (2) parameter estimates that were significantly different from zero (calculated as the square of the Pearson correlation coefficient between observed and predicted final heights). For each species, 10% of the seedlings were randomly selected as a holdout set (i.e., not used for model calibration) for model validation. For each species, the best fit model was used to predict final height for holdout set seedlings, and \( r^2 \) values were calculated.

In general, seedlings of a given species were broadly distributed across transects and quadrats. Seedlings were included if they were alive for at least two censuses so that height growth over an interval could be calculated (i.e., \( \Delta \text{Height} = \text{Height}_{\text{final}} - \text{Height}_{\text{initial}} \)).

Measurements of final height were truncated at September 2009, the last available seedling census. Because a decrease in seedling height can signal the start of the death process (and often was), we determined final height as the last census at which \( \Delta \text{Height} \) for the most recent interval was zero or positive. Seedling life span was calculated as the time (in months) between final height and initial height. The growth of a seedling for a particular species can be characterized as a compound interest formula:

\[
\text{Height}_{\text{final}} = \text{Height}_{\text{initial}} (1 + R)^{\text{life span}} + \epsilon \sim N(0, \sigma^2)
\]

where \( R \) is the growth rate and is specified as a linear function of resources (irradiance, NO\(_3\)\(^-\), NH\(_4\)\(^+\), total N, PO\(_4\)\(^-\), and/or SBC), \( \theta \) accounts for changes in the compounding of growth with seedling age, and \( \epsilon \) is normally distributed error with variance \( \sigma^2 \), estimated as a parameter from the data. The compounding of seedling growth may slow over time due to exhaustion of seed reserves, the accumulation of respiring non-photosynthetic tissue, or cumulative effects of natural enemies such as pathogens or herbivores. When \( \theta = 1 \), compounding of growth is constant over seedlings of different life spans within the same species; \( \theta < 1 \) indicates a diminishing, while \( \theta > 1 \) indicates increasing compounding of growth for longer lived seedlings. We expected growth rate \( (R) \) to increase with increasing irradiance and soil resources. Seedling growth often is asymptotically related to irradiance, especially across broad ranges of irradiance (e.g., Pacala et al. 1994; Kobe 2006). However, the range of canopy openness encountered in this study was limited (0% to 6.72%), so we used linear models to characterize the relationship between growth and irradiance.

Nonlinear models were fit using maximum likelihood in R project computing software (R package nlme; Pinheiro et al. 2011). The best species’ models were chosen based upon (1) lowest Akaike’s information criterion (AIC) with a minimum AIC difference of at least two, (2) parameter estimates that were significantly different from zero (or unity for \( \theta \)), and (3) model fit as assessed by \( r^2 \) values (calculated as the square of the Pearson correlation coefficient between observed and predicted final heights). For each species, 10% of the seedlings were randomly selected as a holdout set (i.e., not used for model calibration) for model validation. For each species, the best fit model was used to predict final height for holdout set seedlings, and \( r^2 \) values were calculated.

In this broad survey of species and resources, we found support for both soil nutrients and irradiance...
effects on seedling growth in a wet tropical forest understory (Appendix C). Across all species, a mean of 58% of the variation in growth (median $r^2 = 0.70$) was explained by simple size- and resource-based growth models (e.g., Fig. 1). On average, resources explained $\sim 25\%$ of the variation in growth within species (mean of differences in $r^2$ values between models containing initial height and resources vs. only initial height) and initial

Fig. 1. Model fit of representative species at La Selva Biological Station, Costa Rica, as assessed by $r^2$ values for (A) *Hampea appendiculata*, $r^2 = 0.89$; (B) *Colubrina spinosa*, $r^2 = 0.49$; (C) *Heteropterys laurifolia*, $r^2 = 0.85$; (D) *Aegiphila* sp., $r^2 = 0.82$; (E) *Virola koschnyi*, $r^2 = 0.65$; and (F) *Psychotria* sp. 3, $r^2 = 0.58$. Dashed and solid lines represent 95% confidence intervals and prediction intervals, respectively.
height ~33% of growth variation. The holdout data set provided strong validation of the growth models (mean \( r^2 = 0.69 \) across species). Of the 94 species with \( \geq 20 \) individuals (and sufficient variation in growth and resources), three species had several single-resource models that contained significant parameters with similar AIC support and \( r^2 \) values. Growth of two species was influenced by outliers, and influential outlying points were eliminated in subsequent analyses. While con- and hetero-specific density influenced survivorship in related studies (e.g., McCarthy-Neumann and Kobe 2010, Kobe and Vriesendorp 2011), they were not correlated with growth in this study (residual growth vs. conspecific density, mean \( r^2 = 0.013 \), vs. heterospecific density, mean \( r^2 = 0.010 \)). Thus, con- and hetero-specific density may largely influence seedling survivorship, but not growth, and are not considered further.

**Soil resources and irradiance influenced seedling growth**

Contrary to expectation, irradiance was not the most prevalent or strongest correlate of seedling growth. With regard to prevalence, growth of 48% of the species was correlated with only soil nutrients, and growth of an additional 45% of species was related to both soil nutrients and irradiance (see Appendix C). In 7% of species, growth was correlated with only irradiance. Among soil nutrients, inorganic N (\( \text{NO}_3^- \) and/or \( \text{NH}_4^+ \)) was a significant predictor of growth in over half (54%) of the species (\( \text{NO}_3^- \) in 32%, and \( \text{NH}_4^+ \) in 34%), total N in 47% of the species, and SBC in 39% of species. Phosphate, typically assumed to be the most limiting nutrient in tropical systems, was least prevalent as a correlate of growth (29%). The range of resources for each species did not influence whether that factor was empirically supported, as resource ranges did not differ for significant and nonsignificant species responses (for irradiance, \( z = 1.47, P = 0.14 \); for \( \text{NO}_3^- \), \( z = 1.11, P = 0.27 \); for \( \text{NH}_4^+ \), \( z = 0.80, P = 0.42 \); for \( \text{PO}_4^{3-} \), \( z = 0.25, P = 0.81 \); for SBC, \( z = -0.40, P = 0.69 \)), with the exception of total N (\( z = -2.13, P = 0.03 \)). Positive growth–resource correlations occurred in 45% of species for irradiance, 38% for total N, 30% for SBC, 23% and 22% for \( \text{NO}_3^- \) and \( \text{NH}_4^+ \), respectively, and 18% for \( \text{PO}_4^{3-} \); approximately 6–12% of species’ resource–growth relationships were negative, but not necessarily negative within the same species (Fig. 2).

Contrary to expectation, most soil nutrients (with the exception of \( \text{NO}_3^- \), \( t = 3.07, df = 130.55, P = 0.003 \)) had similar magnitudes of effect on seedling growth as irradiance (Figs. 3 and 4). Across the range of measured resources among species, irradiance’s mean potential effect on growth was 4.30 mm/month. Mean potential magnitudes of effect for soil nutrients were 4.62 mm/month for total N, 2.66 mm/month for SBC, 2.33 mm/month for \( \text{PO}_4^{3-} \), 2.42 mm/month for \( \text{NH}_4^+ \), and 1.69 mm/month for \( \text{NO}_3^- \) (see Appendix D). Among species for which both irradiance and a soil nutrient were correlated with growth, irradiance had a greater effect on growth in about half of the species, whereas the effects of a soil nutrient were greater than or comparable to irradiance in the other half (Table 1, Fig. 4A–C). Among species for which growth was correlated with only soil nutrients and not irradiance, the rank importance of nutrients was first SBC, followed by N (Total N, \( \text{NO}_3^- \), and/or \( \text{NH}_4^+ \)) and \( \text{PO}_4^{3-} \). SBC effects on magnitude of growth response were greater than total N in 42% of species, greater than \( \text{PO}_4^{3-} \) and \( \text{NO}_3^- \) in 47%, and greater than \( \text{NH}_4^+ \) in 59%; other nutrients had the strongest magnitudes of effect in fewer cases (Table 2).

**Life span effects on compounding of growth**

Of the 94 species, 24 species (27%) experienced diminishing compounding of growth (\( \theta < 1 \)), and 7 species (8%) experienced accelerating growth (\( \theta > 1 \)) with increasing life span. Species estimates of \( \theta \) were

![Fig. 2](image-url)
weakly correlated with initial seedling size ($F_{1,92} = 4.36$, $P = 0.04$, $r = 0.21$), but not shade tolerance ($F_{1,89} = 0.47$, $P = 0.49$, $r = -0.07$).

Species growth responses to resources covaried with shade tolerance

Across species, seed size was strongly correlated with mean initial seedling height ($F_{1,31} = 50.17$, $P < 0.001$, $r = 0.79$). Since we had seed size for only one-third of species, we used species mean initial height as a surrogate for seed size. As expected, initial seedling height and shade tolerance (i.e., low-light survival) were positively correlated across species ($F_{1,89} = 21.66$, $P < 0.001$, $r = 0.44$).

Across species, magnitude of growth responses to resources were negatively correlated with low-light survival, but not with initial seedling size, with the exception that the growth effects of NO$_3^-$ decreased with seedling size (Appendix E). Low-light survival was negatively correlated with growth responses to irradiance, SBC, NO$_3^-$, NH$_4^+$, and PO$_4^{3-}$ (Fig. 5A–E). Growth responses to total N were similar for light-demanding and shade-tolerant species (Fig. 5F).

**DISCUSSION**

In wet tropical forest understories, both irradiance and seedling growth rates are generally very low (Clark and Clark 1992). Despite low light levels, this study highlights the potential importance of both irradiance and soil nutrients to tropical seedling growth (as proposed by Coomes and Grubb 2000) and suggests that growth by light-demanding species created a higher demand for resources.

Contrary to $H_1$, the growth of 93% of species correlated with at least one soil nutrient, and many soil nutrients had similar potential magnitudes of effect as irradiance. Seedlings growing in very low light levels might benefit from increased nutrient availability through increasing light capture (Fahey et al. 1998).

Nitrogen is a key component of chlorophyll for light capture and Rubisco for initial CO$_2$ fixation (Evans 1989); thus higher N acquisition by seedlings could lead to increased carbon gain even under light-limited conditions (Walters and Reich 1997). Base cations also were correlated with seedling growth; Mg$^{2+}$ is the central atom in the chlorophyll molecule (Shabala and Hariadi 2005), and even under low-light conditions (<1% PAR), seedling growth increased in response to Mg$^{2+}$ additions (Burslem et al. 1995). Therefore, irradiance and soil nutrients may be simultaneously limiting to seedling growth in the forest understory, and increased Mg$^{2+}$ and N may assist growth through improved light capture.

It was surprising that growth correlations with light were not stronger and more prevalent as numerous studies have shown the importance of increased light availability to seedling growth (Augspurger 1984, Poorter 1999). The unexpectedly weak growth–irradiance correlations could have arisen from the limited range of existing light conditions, but which nevertheless were representative of variation across 1 km of forest understory over nine years. In contrast to other studies (e.g., Kobe 1999), we did not intentionally stratify variation in irradiance, but wanted to represent typical conditions experienced by seedlings. We offer the caveat that infrequent light measurements early in the study could have partly obscured growth–light relationships and thus underestimated irradiance effects. However, strong correlations of irradiance through time suggest that low frequency of light measurements early in study was not a strong influence.

Contrary to $H_2$, base cations (SBC) had greater prevalence and magnitudes of effect than P, which is consistent with accumulating empirical evidence (see Lawrence 2003). Since base cations are more mobile than P, they can be depleted more rapidly, especially in tropical ecosystems where high precipitation levels increase nutrient leaching (Chadwick et al. 1999). Base cation leaching can result in low pH levels, high aluminum concentrations, and toxicity effects that could potentially affect plant growth. Because they co-varied,
we combined $\text{Ca}^{\text{+}}$, $\text{Mg}^{\text{+}}$, and $\text{K}^{\text{+}}$ into SBC, which precluded testing for effects of individual elements, yet each nutrient could influence seedling growth differently. For example, $\text{K}^{\text{+}}$ is the most mobile, and thus, most leachable base cation, and could be most limiting to growth. John et al. (2007) found that $\text{K}^{\text{+}}$ had the strongest effects on species’ distributions in two out of three studied forests, while $\text{Ca}^{\text{+}}$ and $\text{Mg}^{\text{+}}$ were most

Fig. 4. Representative models of height growth with respect to irradiance and soil nutrients.
important in the third. Base cation availability and growth are correlated in seedlings of species colonized by mycorrhizae (Denslow et al. 1987, Burslem et al. 1995), and in particular, Ca\(^{2+}\) amendments increase arbuscular mycorrhizal (AM) colonization (St. Clair and Lynch 2005, Juice et al. 2006), the common mycorrhizae associated with tropical forest plants. Calcium effects mediated through AM fungi could influence seedling growth through P uptake and defense against pathogens and herbivores. However, mutualisms in particular, Ca\(^{2+}\) and Lynch 2005, Juice et al. 2006), the common mycorrhizae associated with tropical forest plants. Calcium effects mediated through AM fungi could influence seedling growth through P uptake and defense against pathogens and herbivores. However, mutualisms in particular, Ca\(^{2+}\) and Lynch 2005, Juice et al. 2006), the common mycorrhizae associated with tropical forest plants. Calcium effects mediated through AM fungi could influence seedling growth through P uptake and defense against pathogens and herbivores. However, mutualisms in

Table 1. Resource effect comparisons between irradiance and soil nutrients across 94 woody species at La Selva Biological Station, Costa Rica.

<table>
<thead>
<tr>
<th>Comparison</th>
<th>Resource effects (%)</th>
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<tr>
<td></td>
<td>SBC PO(_4^{-}) Total N NO(_3^{-}) NH(_4^{+})</td>
</tr>
<tr>
<td>Greater irradiance effect</td>
<td>35 39 45 54 55</td>
</tr>
<tr>
<td>Greater soil nutrient effect</td>
<td>35 28 5 8 5</td>
</tr>
<tr>
<td>Effects indistinguishable</td>
<td>30 33 50 38 40</td>
</tr>
</tbody>
</table>

Notes: The table reports resource effect comparisons between irradiance and soil nutrients among species for which irradiance and at least one soil resource significantly influenced growth. Resource effects are considered significantly different when \(P \leq 0.05\) and there is \(\leq29\%\) overlap in 95% confidence intervals. SBC is the sum of base cations (potassium, magnesium, and calcium).

Table 2. Comparisons of the magnitude of resource effects between resources among species that responded to more than one soil resource.

<table>
<thead>
<tr>
<th>Comparison</th>
<th>Resource effects (%)</th>
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<tbody>
<tr>
<td></td>
<td>SBC PO(_4^{-}) Total N NO(_3^{-}) NH(_4^{+})</td>
</tr>
<tr>
<td>Greater SBC effect</td>
<td>47 42 47 59</td>
</tr>
<tr>
<td>Lesser SBC effect</td>
<td>0 25 18 12</td>
</tr>
<tr>
<td>Greater PO(_4^{-}) effect</td>
<td>18 21 39</td>
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<tr>
<td>Lesser PO(_4^{-}) effect</td>
<td>27 43 11</td>
</tr>
<tr>
<td>Greater total N effect</td>
<td>33 8</td>
</tr>
<tr>
<td>Lesser total N effect</td>
<td>27 33</td>
</tr>
<tr>
<td>Greater NO(_3^{-}) effect</td>
<td>33</td>
</tr>
<tr>
<td>Lesser NO(_3^{-}) effect</td>
<td>7</td>
</tr>
</tbody>
</table>

Notes: Resource effects denote the percentage of species in which a given soil resource in the first column had a greater or lesser effect on growth than other soil resources (columns 2–6). Resource effects are considered significantly different (\(P \leq 0.05\)) when there is \(\leq29\%\) overlap in 95% confidence intervals.
growth because of the generally low irradiance levels encountered in the study; nevertheless, our results are consistent with a broader trade-off between low-resource survival and high-resource growth (Kobe et al. 1995, Kobe 1999, Russo et al. 2008).

Conclusions

Predicting seedling growth under field conditions is important to understanding forest dynamics and regeneration. Although irradiance has been regarded as the primary determinant of seedling growth in wet tropical forests, growth correlations with soil nutrients were equally as important. Even though we cannot directly evaluate if the different species’ responses to irradiance and soil nutrients contributes to niche diversification and diversity maintenance in wet tropical forests, our study does demonstrate tremendous variation among species in which resources influenced growth and the magnitude and direction of those resource effects. This interspecific variation satisfies important prerequisites for niche partitioning along gradients of resources (Kobe 1999). Moreover, the positive correlation among species’ growth responsiveness to resources and survival at low light is consistent with a general species’ trade-off between low-resource survival vs. high-resource growth. Both irradiance and soil nutrients were correlated with

Fig. 5. Species-specific shade tolerance (mortality at 1% full sun) vs. growth responsiveness to resources (expressed as height growth at maximum resource level [mm/month] per unit initial seedling height [mm]). Statistics for individual resources: (A) irradiance, $F_{1,48} = 12.30$, $P = 0.001$, $r = 0.45$; (B) SBC, $F_{1,35} = 18.79$, $P = 0.0001$, $r = 0.59$; (C) NO$_3^-$, $F_{1,28} = 5.13$, $P = 0.03$, $r = 0.39$; (D) NH$_4^+$, $F_{1,31} = 4.84$, $P = 0.04$, $r = 0.37$; (E) PO$_4^{3-}$, $F_{1,27} = 3.42$, $P = 0.08$, $r = 0.34$; and (F) total N, $F_{1,44} = 0.17$, $P = 0.07$, $r = 0.68$. 
seeding growth in the light-limited forest understory, and therefore must be examined simultaneously across a broad array of species with different life-history traits in order to begin to understand potential mechanisms of species coexistence and diversity in wet tropical forests.

Acknowledgments

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APPENDIX A

APPENDIX B
Spatial dependence of seedlings with residual growth variance per species and transect (Ecological Archives E092-153-A2).

APPENDIX C
Resource parameters of seedling growth rate, by species (Ecological Archives E092-153-A3).

APPENDIX D
Maximum magnitude of resource effects on the final height of seedling growth, by species (Ecological Archives E092-153-A4).

APPENDIX E
Correlations between species’ magnitude of responses and initial seedling size (Ecological Archives E092-153-A5).