THE EFFECTS OF SPATIALLY HETEROGENEOUS IRRADIANCE AND SOIL RESOURCES ON NEOTROPICAL SEEDLING GROWTH

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ABSTRACT

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Plant growth responses to resources may be an important mechanism that influences species coexistence and community structure. While irradiance is regarded as the most important resource for seedling growth in wet tropical forests, the spatial variation of multiple soil resources have yet to be evaluated across a range of species and at a fine seedling-appropriate scale. The objectives of this research were to compare soil resource availability among sites and characterize their spatial structure, determine the appropriate spatial scale to measure soil resources to understand seedling responses, and identify the resources that best predicted Neotropical seedling growth. We measured irradiance and an array of soil resources over a fine spatial scale (1 m^2) in 5 sites of an old-growth, wet tropical forest at La Selva Biological Station, Costa Rica. Soil resource availability and heterogeneity appeared to correlate with soil type and their importance in plant-nutrient cycles, thus to understand seedling responses soil resources, essential plant nutrients, such as inorganic nitrogen, phosphorus, and base cations, should be measured at a seedling-level spatial scale, while other resources, such as total nitrogen and carbon may be measured at coarse spatial scales (>10 m). Light limitation in the forest understory also did not preclude seedling growth correlations with soil nutrients, which were equally prevalent and as strong as with irradiance. These results challenge the idea that soil resources are not important to seedling performance in the light-limited understory.

This work is dedicated to my family and friends who have always supported me through all my endeavors, the Guatemalan people who inspired me to study forest ecology, and Todd Robinson who is a constant source of support and understanding in my life.

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CHAPTER I

Introduction

Plant growth responses to resources may be an important mechanism that influences species' distributions, coexistence, and community structure. Yet responses to variation in the location and size of resource patches can differ between plants of different sizes and species. Gradients of abiotic resources can allow different species to specialize on different amounts of resources, thus permitting their cohabitation, while competition for resources within a particular patch may influence whether certain individuals are destined to be dominant or subordinate within a population (Casper et al. 1999). Tropical forest understories, in particular, are extremely spatially heterogeneous in both irradiance (Nicotra et al. 1999) and soil resources (Holste et al., in prep), yet estimates of seedling-appropriate resource availability and heterogeneity have yet to be examined for multiple soil nutrients and species as well as simultaneously with irradiance. Because the performance of individual plants depend upon their ability to compete for and capture resources, understanding the availability and spatial heterogeneity of abiotic resources is a prerequisite to understanding the effects of resources on seedling growth.

Resource patches can differ in scale and concentration of supply (Stuefer 1996), and the sessile nature of plants makes the spatial structure of resources especially important to the study of plant-resource interactions. The most relevant scale to understand resource effects on plant performance depends upon the organism of study. For example, limited rooting extent could makes forest soils extremely heterogeneous from a tree seedling perspective (Hutchings et al. 2003), but fine scale heterogeneity may be less relevant to a mature tree with a large root system. Thus, seedling responses to resource patches may be extremely variable depending upon the spatial heterogeneity of resources.

How plants respond to the availability and heterogeneity of resources within their environment also may differ depending upon the resource. Irradiance is considered the most limiting resource in wet tropical forests (Pearcy 2007). Canopy structure, topography, treefall gaps, and sunflecks all contribute to the understory light environment. Among seedlings of different species, there is tremendous variation in growth – irradiance relationships (Augspurger 1984, Lee et al. 1996, Poorter 1999). Likewise, variability in soil resources originates from multiple biotic and abiotic sources; parent material, climate, topography, organisms (such as plant-soil feedbacks), and the time over which organisms, climate and topography have affected the parent material all affect soil resource availability and heterogeneity. Although typically not considered to be as important as irradiance in seedling growth, soil nutrients also influence seedling growth rates, even in the deep shade of the forest understory (Hättenschwiler 2002, Yavitt and Wright 2008, Palow and Oberbauer 2009). Furthermore, interactions between irradiance and soil nutrients can modify seedling performance (Kobe 2006, Cai et al. 2008).

In this thesis, I examined the availability and spatial heterogeneity of soil resources in an old-growth, wet tropical forest at La Selva Biological Station, Costa Rica, as well as species-specific seedling responses to both irradiance and soil nutrients. Five sites, spanning a soil fertility gradient, were used to capture a broad array of soil resource levels. In addition, multiple soil resources (i.e. major nutrients and soil carbon) were measured, including sum of inorganic nitrogen (nitrate and ammonium), total nitrogen, phosphate, total phosphorus, base cations (potassium, magnesium, and calcium) and total carbon. By sampling across a fertility gradient, we included two soil types typical of wet tropical forests: alluvial and volcanic soils. Alluvial soils, commonly formed by recent deposition of fine silt and nutrients from nearby rivers, are considered moderately fertile sites (Vitousek and Sanford 1986). At La Selva, alluvial soils are those at the lowest elevations, so that these soils still flood periodically and their properties are thought to be still strongly affected by small differences in age and original texture (McDade and Hartshorn 1994). Volcanic soils are highly weathered of mineral-derived resources and typically range from moderately to severely infertile (Vitousek and Sanford 1986). At La Selva, volcanic soils are those found at higher elevations and on the oldest terraces. I expected these soil types to be very different in resource availability and spatial heterogeneity due to their dissimilarities in topographic position and relative age.

In Chapter II, I compared soil resource availability among sites, characterized spatial autocorrelation of resources, and examined whether adult trees imposed a pattern of fine-scale soil resource availability and heterogeneity in wet tropical forests. I also determined an appropriate spatial scale to measure soil resources to understand seedling responses. In Chapter III, I examined the growth responses of 94 species of woody seedlings to irradiance and soil nutrients, measured over a presumed seedling-appropriate spatial scale (1 m^2), to identify the resources that best predicted Neotropical seedling growth.

The research presented in this thesis contributes to previous studies examining seedling growth responses along a resource gradient, because it incorporated both irradiance and soil resources, quantified soil fertility in terms of specific soil resources, methodologically examined whether the scale at which soil resources were measured corresponded to the scale of the studied organism, and examined a broad range of Neotropical species. Based upon findings of this thesis, predictions of species-specific seedling growth responses may be used to understand forest dynamics and promote ecology-based forest management and restoration.

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CHAPTER II

Spatial heterogeneity of soil resources in a wet tropical forest: influences of substrate and plant-nutrient cycles

ABSTRACT

Spatial heterogeneity in soil resources may contribute to tree species distributions, species coexistence, and population persistence. Yet responses to variation in the location and size of resource patches can differ between plants of different sizes. For this reason, estimates of resource availability and heterogeneity are strongly dependent upon the spatial scale at which they are measured and the organism of study. The objectives of this research were to compare soil resource availability (i.e. major nutrients and soil carbon) among sites differing in soil type, characterize spatial autocorrelation of resources, examine whether adult trees imposed a pattern of fine-scale soil resource availability and heterogeneity in wet tropical forests, and determine appropriate spatial scales to measure resources in order to understand individual seedling responses. Five study sites (three volcanic and two alluvial soils) were sampled in an old growth, wet tropical forest at La Selva Biological Station, Costa Rica. An array of soil resources were measured including sum of inorganic nitrogen (inorganic N), total nitrogen (total N), phosphate (PO_4^-), total phosphorus (P), total carbon (C), and base cations (potassium, magnesium, and calcium). Soil type was only weakly correlated with mean resource availability, but the spatial heterogeneity of soil resources was related to both soil type and type of mineral nutrient cycle (source and biological mediation). Over half of the total variance in most resources was spatially structured, indicating a high degree of

spatial autocorrelation, and the spatial structure of resources appeared to be related to soil type. Total C and total N had long effective ranges between 27-174 m, base cations, PO_4^- and total P between 16 and 97 m, and inorganic N between 14 and 32 m. Patch size (defined as points within a distance having $\geq$50% correlation) were 10-40 m for total C and total N and 3-16 m for base cations, P, PO_4^- and inorganic N. Adult tree functional groups did not create patches of similar resource availability and impose of pattern of spatial heterogeneity in this wet tropical forest. These results suggest that to understand seedling responses to soil resources in a wet tropical forest, essential plant nutrients, such as inorganic N, P, and base cations, should be measured at a seedling-level spatial scale, while other resources, such as total N and C may be measured at coarser scales (>10 m).

INTRODUCTION

Spatial heterogeneity in resources can strongly influence local species abundances (Tilman 1994), distributions (Li et al. 2009), coexistence (Fargione and Tilman 2005), and overall community structure (Wilson et al. 1995, Finzi et al. 1998). Gradients of abiotic resources allow species to specialize on different amounts of resources, thus permitting their cohabitation. Tree species can aggregate on patches that provide suitable resources for their regeneration, while competition for soil nutrients within a resource patch may influence whether particular individuals are destined to be dominant or subordinate within a population (Casper et al. 1999). Because the performance of individual plants depend upon their ability to compete for and capture resources, understanding the spatial heterogeneity of abiotic resources is a prerequisite to understanding their effects on community structure.

Resource patches can differ in scale and concentration of supply (Stuefer 1996), thus the sessile nature of plants makes the spatial structure of resources especially important to the study of plant-resource interactions. Responses to variation in the location and size of nutrient patches would differ between plants of different sizes. For example, limited rooting extent could make forest soils extremely heterogeneous from a tree seedling perspective (Hutchings et al. 2003), but fine scale heterogeneity may be less relevant to a mature tree with a root system large enough to explore both nutrient rich and poor patches. For this reason, the most relevant scale to characterize resource heterogeneity depends upon the questions being asked and the studied organism.

Since the size and distribution of resource patches is very important to tree seedlings, seedling performance may be extremely variable depending upon the spatial heterogeneity of resources. Especially in natural forests, soil nutrients are heterogeneously distributed (Lechowicz and Bell 1991, Mou et al. 1997, Farley and Fitter 1999). Heterogeneity in soil resources originates from both abiotic and biotic sources. Parent material, climate, topography, organisms (such as plant-soil feedbacks), and the time over which organisms, climate and topography have affected the parent material all create heterogeneity in soil resources (Jenny 1941). Abiotically, the physical properties of the surrounding environment and chemical properties of soil resources typically create heterogeneity (see Table 1). Mineral-derived resources such as base cations, phosphorus, and many micronutrients originate from parent material. Weathering and erosion release these resources into the soil where they may be occluded (i.e. bound) to other chemicals or soil colloids, leached through the soil, or taken up by plants. Topographic gradients and the relative mobility of resources also can influence their spatial heterogeneity across a landscape.

Heterogeneity also originates from biotic sources, including soil microorganisms, herbivores, or resource uptake and release by plants (see Table 2.1). Plants create spatial heterogeneity in soil resources by creating zones of depletion around roots, incorporating nutrients into foliage and other plant components, and depositing senesced tissues on or in the soil in another location (Stark 1994). Individuals of different species and functional types may cause patches of similar resource levels, likely mediated through senesced tissue chemistry and possibly other plant-soil feedbacks (e.g. McCarthy-Neumann and Kobe 2010, Ushio et al. 2010). For example, the presence of N-fixing microorganisms associated with leguminous species may change the availability of nitrogen (N) by creating patches of higher N (Vitousek et al. 1987, Rodriguez et al.

2009), whereas other species could elevate phosphorus (P) availability or the depletion of other resources (Chen et al. 2003, Phillips and Fahey 2006). Fungi and bacteria also may colonize and break down organic materials, making nutrients available. Biologically-derived resources, such as nitrogen and carbon, often arise from the accumulation and decomposition of organic residues (e.g. decaying plant material) and/or through biological N fixation by microorganisms.

Plant growth can increase resource heterogeneity by creating and maintaining nutrient patches, but the scale of resource distribution has depended upon the ecosystem (e.g. grasslands vs. shrublands; Schlesinger et al. 1996) and the biotic and abiotic processes acting upon those resources (Gallardo and Parama 2007). Since inorganic nitrogen, base cations (potassium, magnesium, and calcium), and phosphate are essential plant nutrients needed in plant growth and survival, I expected the cycling of these nutrients to create finer-scale, spatial heterogeneity than total carbon and total nitrogen (Hinsinger et al 2005). Furthermore, I expected the composition of forest species to impose a broad-scale pattern of soil resource availability and heterogeneity across the landscape.

In this study, soils were sampled along a fertility and substrate age gradient in a wet tropical forest at La Selva Biological Station, Costa Rica. La Selva soils range from relatively fertile entisols and inceptisols of alluvial origin to large areas of low fertility ultisols developed on old lava flows (McDade and Hartshorn 1994). By sampling across a fertility gradient, I included two soil types typical of wet tropical forests: alluvial and volcanic-origin, residual soils. Topographic position and age are the two dominant factors thought to determine soil type at La Selva. Alluvial soils are commonly formed by recent deposition of fine silt and nutrients from nearby rivers and are considered moderately fertile sites (Vitousek and Sanford 1986). At La Selva, alluvial soils are those at the lowest elevations. These soils still flood periodically and their properties are thought to be still strongly affected by small differences in age and original texture (McDade and Hartshorn 1994). Volcanic-origin residual soils are highly weathered of mineral-derived resources; these soils typically range from moderately to severely infertile (Vitousek and Sanford 1986). At La Selva, volcanic soils are those found at higher elevations. These soils are regarded as Pleistocene in age but the actual dates are lacking (McDade and Hartshorn 1994). Due to the differences in topographic position and relative age, I expected soil resources to differ in availability according to soil type.

Comparisons of the spatial heterogeneity of particular soil resources have received little attention in tropical forests, despite the fact that nutrient patches may be highly variable due to biotic feedbacks through high tree species diversity. The specific questions address by this study were: 1) Do major soil nutrients and carbon levels differ across sites that presumably stratify a soil fertility gradient?, 2) How does spatial structure vary across sites and among different resources?, 3) If adult trees imposed a pattern of fine-scale soil resource availability and heterogeneity in wet tropical forests?, and 4) What is an appropriate, or biologically meaningful, spatial scale to measure soil resources for understanding individual tree seedling responses? I expected soil resources to differ in availability and spatial heterogeneity according to soil type, their respective physical, chemical and biological properties (e.g. mobility, occlusion, biological fixation), as well as their relative importance in plant processes. Capturing the availability and heterogeneity of soil resources is essential to the study of tropical forest functioning at many scales (Townsend et al. 2008) but is especially important in understanding seedling performance and future forest dynamics.

METHODS

Site Description and Sampling Design

Five study sites were sampled in a wet tropical forest (*sensu* Holdridge 1967) at La Selva Biological Station in the Atlantic lowlands of Costa Rica (10º 26’N, 84º 00’ W). La Selva is located at the convergence of the Sarapiqui and Puerto Viejo rivers; the mean annual rainfall is 4367 mm, and the mean monthly minimum is 124 mm (http://www.ots.ac.cr/meteoro/default.php?pestacion=2). To represent landscape-level occurrence of soils, three study sites on older, weathered volcanic soils and one site each on older and recent alluvial soils in mainly old growth forests were sampled; sites were established to span a presumed phosphorus gradient, since this resource is generally considered the most limiting in tropical ecosystems (Hedin et al. 2009). Soils from all five sites were fairly acidic (pH 3-5).

Each of the five sites was centered on a transect of 200 contiguous 1m^2 quadrats; along each of the five transects, three soil subsamples were composited from 16, 50 and 83 cm along the central axis of each 1m^2 quadrat (n=200 per transect, n=1000 in total). Each sample was taken with a corer (2 cm diameter) in the upper 20 cm of mineral soil. In addition, forty-six samples were collected around each transect every ten to twenty meters and fourteen “irregularly-spaced” samples at a random angle and distance from the regularly-spaced lattice design (n=60 per transect, n=300 in total); these additional samples were also a composite of three subsamples taken within a 1m^2 quadrat (Fig. 2.1).

The combination of forty-six regularly-spaced sampling locations around the transect and the fourteen “random” sampling points represented a compromise between the predictive accuracy under a regularly-spaced model versus better estimation of model parameters through a lattice plus close pairs design (Diggle and Lophaven 2006). Thus, to obtain a representative soil resource map of each site, a total of 260 soil samples were collected per site (Fig. 2.1).

Because there can be tremendous variability in points that are very close together, particularly related to micro-topography (e.g., old root channels, animal disturbance), I used composites of three subsamples within a 1 m^2 sampling unit. By compositing the samples, I averaged over any sub-meter scale heterogeneity and likely underestimated total variability, but I captured variability among mean conditions in 1 m^2 sampling units, a typical unit of many plant sampling studies.

Soil Methods

A broad array of soil resources were measured including inorganic nitrogen (summation of nitrate and ammonium pools), total nitrogen (total N), phosphorus (P), calcium (Ca^+), magnesium (Mg^+), potassium (K^+), and total carbon (total C) as an estimate of plant input. All samples were air-dried before being shipped to Michigan State University for analysis. Phosphorus, K^+, Ca^+, and Mg^+ ions were extracted with Mehlich III solution, which was originally designed as multi-element extractant (Monterroso et al. 1999, Loide et al. 2005) for acidic, highly weathered soils, such as those found in the Neotropics (Mehlich 1984). Calcium, K^+, Mg^+, and P concentrations were analyzed with an Optima 2100DV ICP Optical Emission Spectrometer (Perkin-Elmer, Shelton, CT); phosphorus was also analyzed colorimetrically with a continuous flow auto-analyzer (ELx808 Absorbance Microplate Reader, BioTek Instruments, Inc, Winooski, VT).

Mehlich III extractable P was measured with both the ICP and colorimetric methods using a reagent solution containing acid molybdate, antimony potassium tartrate, 70% sulfuric acid, and absorbic acid (Frank et al. 1998). Phosphorus measured with ICP analyses sometimes have up to 50% higher P concentrations than measured with the colorimetric method, suggesting organic forms of P in addition to the orthophosphate (plant available) P are being measured (Hylander et al. 1995). Measurements of ICP versus colorimetric P were correlated (r^2=0.49). Consistent with previous studies (Pittman et al. 2005, Nathan et al. 2002), I interpreted ICP-P concentrations as a measure of “total P” and colorimetric-P as “plant available” phosphorus, or PO_4^-.

Inorganic nitrogen (N) pools were extracted with potassium chloride and analyzed colorimetrically using an ammonium salicylate and ammonium cyanurate colorimetric method to detect ammonium (Sinsabaugh et al. 2000) and vanadium (III), sulfanilamide and N-(1-naphthyl)-ethylenediamine dihydrochloride (NED) to quantify nitrate (Doane and Horwath 2003). Total soil N and C were measured via the dry combustion method using an Elemental Combustion CHNS-O analyzer (ECS 4010, Costech Analytical Technologies, Valencia, CA).

Statistical Analysis and Model Description

Comparisons of soil resource availability among sites were tested with one way analysis of means with unequal variances and a Bonferroni correction for multiple comparisons (α=0.05) using the R project computing software (http://www.r-project.org). Soil type comparisons within soil resources were tested with a mixed model (R software package lme4), accounting for subsamples within the sites.

Using LiDAR data collected from aerial photographs at La Selva (see Kellner et al. 2009), maps of geographic variables (elevation, slope, aspect, flow direction, flow length and curvature) were created using Quantum GIS (QGIS Version 1.0.2-Kore, http://www.qgis.org) with a GRASS GIS interface (GRASS Version 6.2.3, http://grass.osgeo.org). Spatial autocorrelation of soil resources was analyzed with and without these geographic variables as potential covariates in linear univariate models using spBayes, a statistical package compatible with the R software. spBayes uses a hierarchical Bayesian approach for computing univariate and multivariate point-referenced spatial models (Finley et al. 2007). This statistical approach allowed us to specify prior distributions on the parameters and build hierarchical models that were estimated using a Gibbs sampler, with Metropolis-Hastings updates (as required), to fit spatial models. I used empirical variograms to estimate the starting values (i.e. informative priors) for model parameters. Variance parameter priors followed an inverse-gamma distribution, while the spatial range priors followed uniform distributions. I transformed soil resource concentrations to more closely approximate Gaussian distributions, which is an assumption of the linear model.

Four candidate models were used to characterize and predict soil resources: 1) a null model containing non-informative priors and only soil resources, 2) a model with non-informative priors, geographic variables and soil resources, 3) a model with informative priors and only soil resources, and 4) a model containing informative priors, geographic variables and soil resources. Models were compared according to their DIC (Deviation information criterion) values. DIC sums the Bayesian deviance as a measure of model fit and the effective number of parameters as a penalty for model complexity; thus, lower DIC values indicate preferred models, and in cases of similar DIC values, the least complex model would be chosen. For each preferred univariate model, three MCMC (Markov chain Monte Carlo) chains were run for 100,000 iterations each; summaries were generated from these three chains.

I calculated ninety-five percent credible intervals for each parameter in the model, including the semivariogram values of nugget (τ^2), partial sill (σ^2), lag distance (ϕ) and effective range ($-\ln(0.05)/\phi$) (Fig 2.2). The nugget (τ^2) represents the random variation that cannot be explained by the model. The partial sill (σ^2), the variation that can be attributed to autocorrelated spatial effects, provides an index of the spatial dependence of soil resources. Following Li and Reynolds (1995), the proportion of variance due to spatial dependence (% structural variance) of each resource was calculated as:

$$\%\ \text{structural variance (SV)} = \sigma^2 / (\sigma^2 + \tau^2)$$

High % SV values indicate a greater degree of spatial autocorrelation (Wang et al. 2007), whereas high % nugget variance suggests a lack of spatial dependence for the studied scale:

$$\% \text{ nugget variance (NV)} = \tau^2 / (\sigma^2 + \tau^2).$$

The semivariogram effective range is the distance beyond which correlation between sampling points decreases to < 0.05 and was calculated as $-\ln(0.05)/\phi$. To identify an effective range at which the correlation between points is $\geq 50\%$, a level that would indicate ecologically meaningful similarity and provide a measure of resource patch size, I calculated a 50% correlation distance as: $d_{50\%} = -\ln(0.5)/\phi$.

Adult trees versus soil resources

Adult woody species > 5 cm in diameter were mapped within a 40 m buffer zone around each transect. Diameter at breast height (DBH) measurements were taken between September 2008 and March 2009. Adult species were characterized into leguminous and non-leguminous species to test whether adult trees impose a pattern of fine-scale availability and heterogeneity upon soil nutrients. Nearest neighbor analyses (R software package yaImpute) were used to calculate soil nutrient availability under adult trees. Essential soil nutrients (e.g. inorganic N, total P, K^+, Ca^+, and Mg^+) were used to test this relationship, since these resources may be the most affected by plant-nutrient cycling.

RESULTS

Site differences

Mean availability of soil resources differed among sites and were generally associated with soil type (Table 2.2). Not surprisingly, phosphate (PO_4^-) and total phosphorus (total P) concentrations were greatest on alluvial soils since sites were chosen to stratify a presumed phosphorus gradient (Table 2.3, 2.4; Fig. 2.3A, B). Potassium values also had greater concentrations on alluvial soils (Table 2.3, 2.4; Fig. 2.3C), while Ca^+ and Mg^+ availability were not associated with soil type (Table 2.3, 2.4; Fig. 2.3D, E). On the other hand, inorganic N concentrations were greatest on volcanic soils (Table 2.3, 2.4; Fig. 2.3F), but neither total N nor total C were associated with soil type (Table 2.3, 2.4; Fig. 2.3G-H). Interestingly, even though alluvial sites are considered to be "nutrient rich", these sites generally had resource concentrations as low as the assumed "infertile" or volcanic sites for all resources (Fig. 2.3). Variability of soil resources also differed among sites. The coefficient of variation (% CV) in all soil resources ranged from 18-190%, with a mean value of ~70% (Table 2.4), suggesting moderate to high variability for all soil nutrients (per Wilding (1985)).

Resource spatial structure, range of autocorrelation, and patch size

Of the four candidate models that were tested to explain spatial patterns and site differences in soil resources, the informative models with or without geographic variables provided the best fit. No geographic variables were significant, probably due to the small land areas that the transects encompassed (only 240m x 40m). Thus I used only measured resource levels to characterize spatial structure in resources.

Over half of the total variance in most of the soil resources was spatially structured (% structural variance; Table 2.5), indicating a high degree of spatial autocorrelation. The spatial structure (% SV) of resources was site-specific (Fig. 2.4). Generally the recent alluvial site (transect 5) had the least structural variance ~58% SV (with the exception of total N where transect 2 had a high % NV), while two of the volcanic sites (transects 1 and 2) had the highest spatial structure ~72% SV. The spatial heterogeneity of PO_4^- , total P, base cations (calcium, potassium, and magnesium), and total C all had a mean % SV between 60-75% (Table 2.5). For total N, four of the five sites had over 70% SV for total N; the fifth site (transect 2) had 11% SV (Table 2.5), suggesting its variance could be attributed more to random noise in the data or unmeasured variables in the site. On the other hand, inorganic N had the lowest % SV (less than half of the total variance) and highest % NV (Table 2.5), indicating its heterogeneity was due to unmeasured factors, occurred at finer than the measured 1 m spatial scale, or arose from random noise in the data.

The range of autocorrelation was analogous within each resource across all sites and fell into three categories: total C and total N had long effective ranges between 27-174 m, the base cations (Ca^+, K^+, and Mg^+), PO_4^- and total P between 16 and 97 m, and inorganic N ranged between 14 and 32 m (Table 2.6). Similarly, the 50% correlation distances (approximating patch sizes), of total C and total N were generally long, varying between 6 (transect 2, total N) to 40 m across sites, between 7 and 22 m for base cations, PO_4^- and total P, and the resource with the highest % NV, inorganic N, had the smallest patch size varying between 3-7 m (Table 2.6, Fig. 2.5).

Leguminous species not correlative with soil resources

The availability of soil nutrients did not differ between locations occupied by leguminous versus non-leguminous trees (Fig. 2.6). A few soil nutrients were correlated with tree size when divided by functional group (leguminous vs. non-leguminous; Table 2.7, Fig. 2.7), but these relationships were very weak.

DISCUSSION

Summary

Substrate type and type of mineral nutrient cycle (source and biological mediation) influenced soil resource availability and heterogeneity in this wet tropical forest. Soil resource availability overlapped across sites yet weakly corresponded to soil type, while the spatial structure of resource heterogeneity was similar across sites but differed among resources. Contrary to expectation, adult tree functional groups (leguminous vs. non-leguminous) did not create patches of similar resource availability or heterogeneity. In general, resource patch sizes were larger than the mean root length of most tropical seedlings, so that seedlings would find a range of favorable to unfavorable habitats. The tremendous fine scale variability of these soil resources calls into question the use of site-level mean nutrient levels to approximate seedling nutrient availability. Thus, in order to capture the variability in resources that seedling are actually experiencing, it is especially important to sample resources according to the type of nutrient cycle and intrinsic physical and chemical properties to make sure that the perceived resource environment, or patch size, is estimated appropriately.

Resource availability

In this study, the availability of soil resources was associated with soil type in about half of the resources. Inorganic N levels were highest on the older, volcanic sites, while PO_4^-, total P, and K^+ were highest on alluvial sites. The high N and low P concentrations found in the volcanic sites are consistent with previous studies at La Selva Biological Station that found high rates of N mineralization and highly efficient P cycling (Robertson 1984, Vitousek 1984, Vitousek and Denslow 1986). This study suggests that the alluvial soils could be N-limited because readily weatherable minerals, such as mineral-derived P and base cations, are in relatively greater supply than on older, volcanic soils (Hedin et al. 2009, Townsend et al. 2008). Although not specifically tested in this study, these results are consistent with a global nutrient limitation hypothesis of P-limitation on older sites and N-limitation on younger sites (Walker and Syers 1976, Vitousek 1984, Hedin 2003, Vitousek 2004). Under this hypothesis, P availability decreases with time as weathering dissolves phosphates from newly exposed rock, while N may be more available in older sites due to the biologically renewable capacity of soil N. In the alluvial sites, the constant flooding and disturbance by nearby rivers may have replenished weatherable minerals by depositing mineral-derived resources such as soil P and base cations and washed away mobile N ions, whereas volcanic soils could have experienced P and base cation losses from weathering and occlusion, without replenishment, and the long-term accumulation of N.

Spatial heterogeneity

Spatial heterogeneity of the soil resources appeared to be related to not only soil type but also to the type of mineral nutrient cycles. Because spatial heterogeneity can be the result of the physical, chemical, and biological processes in a system, similar degrees of structural variances of these resources could indicate that similar environmental factors are acting on these resources. Consistent with this view, the spatial dependence of resources appeared to be correlated with the relative age of the soils, with the recent alluvial site having the least structural variance whereas the “older” volcanic sites had the most spatial structure in soil resources. This suggests that the time over which climate, topography and organisms had to affect soil resources is important to spatial patterns in these sites.

Recent biotic processes also may influence the spatial heterogeneity of soil resources. The range of autocorrelation for total C and total N were similar, while base cations, PO_4^-, total P, and inorganic N demonstrated their own autocorrelative patterns (Table 2.8). Individual plants and species can influence nutrient distributions (Zheng et al. 2008, Diekmann et al 2007). Townsend et al. (2008) proposed that in highly diverse tropical forests, such as these La Selva sites, individual species may create tree-specific ‘biogeochemical footprints’ that extend from the canopy to the soil, and significant associations between local-scale variation in soil chemistry and tree species composition have been found in the forests of Panama, Colombia and Ecuador (John et al. 2007). However, somewhat surprisingly, soil nutrients were not associated with the presence of leguminous species in this study. Thus, whole tree inputs may not be influencing the fine scale heterogeneity of essential soil nutrients. Yet, the lack of correlation also may be a result of the fast and tight cycling of soil nutrients in wet tropical forests. Due to the dynamic nature of these nutrients, there is still the possibility that a relationship could be found with more dynamic measures of resource estimation (e.g., N mineralization) rather than simple standing pools.

The similar spatial structure and ranges of all mineral-derived soil nutrients suggest that they are influenced by similar factors. The short ranges of the base cations, PO_4^-, total P, and inorganic N also support this hypothesis. Furthermore, the short range but highly variable structure of biologically-derived inorganic N suggests finer scale controls, such as localized microbial transformations and immobilization (Wang et al 2002, Jackson and Caldwell 1993). On the other hand, total C and total N are not derived from minerals and are directly taken up by plants. The long effective ranges of total C and total N suggest similar inputs of organic matter across fairly broad areas, perhaps due to leaf litter dispersal (Ferrari 1999). Mean crown diameters of La Selva canopy trees are ~24 m (Clark et al. 2005), which correspond to the long ranges of total C and total N. Thus, the type of mineral nutrient cycle may explain the different autocorrelative patterns in soil resources.

These results generally correspond to a similar study conducted in an old growth, wet tropical forest in Panama (Yavitt et al. 2009). Established on highly weathered soil, the Panamanian study measured soil resources from 87 base points, sampled at 0, 2, 8 and 20 m along a transect, to quantify spatial patterns of soil resources from 2 to ~500m. Yavitt et al.'s study had a spatial dependence scale of 10-100 m for most soil properties, and the effective ranges of the base cations and PO_4^- were around 50-60 m, which was on the high end of the La Selva ranges. On the other hand, inorganic N's spatial heterogeneity differed between the studies. Although the Panamanian study had similar % NV for inorganic N, the resource also showed long effective ranges (74.2 m and 111.3 m for nitrate and ammonium, respectively) compared to La Selva's short inorganic N range. Yet in support of a short range for inorganic N, several studies in other ecosystems, with similar fine scale sampling designs to this study, found comparable effective ranges consistent with these results (Gallardo et al. 2005, Gross et al. 1995).

Implications of patch size on seedlings

Patch size of a resource may be equally important to its availability for seedlings, which have limited rooting extent. The long range of total C and total N indicated that similar concentrations of these resources occurred in large, smoothly continuous patches (Fig. 2.5). The effective ranges of the base cations, PO_4^- and total P indicated finer scale heterogeneity, as illustrated by steeper semivariogram functions as they approached the sill; these nutrient patches were smaller and more sharply discontinuous (Fig. 2.5). The short effective range of inorganic N indicated the smallest, most frequent and discontinuous patches of all the resources (Fig. 2.5).

Since the spatial distribution of forest soil nutrients is highly heterogeneous and soil nutrients are frequently a growth-limiting factor, plasticity in seedling rooting length is important to understand the implications of resource heterogeneity on plant performance. In this study, I examined horizontal, spatial heterogeneity of soil resources across the La Selva sites, since the sampling depth was uniform. Patch size varied depending upon the soil resource of interest; 50% correlation distances for total C and total N was on average between 10-40 m, 4-16 m for base cations, PO_4^-, and total P, and 3-7 m for inorganic N. A study examining the roots of 37 species from a Bolivian lowland wet tropical forest found 1st year (mean seedling height = 14 cm, range mean seedling height of species = 5-29 cm) seedling root length varied between 0.07-1.86 m with a mean length of ~0.5 m (not distinguished as either vertical or horizontal, Markesteijn and Poorter 2009). By comparing the patch size of soil resources with mean rooting length of tropical seedlings, it appears that resource patch sizes may be larger than the mean root length of most 1st year tropical seedlings. Therefore, seedlings may be experiencing "hot" and "cold" patches of nutrients that exist independent of soil type, as proposed by Townsend et al. (2008), which is especially important since establishment within the first year of growth is important to seedling growth and survival. In the La Selva soils, many of the "fertile" alluvial sites had similarly low levels of soil resources as the "infertile" volcanic sites, creating islands of infertility. Therefore, in contrast to a mature tree that can explore both the nutrient rich and poor habitats, tropical seedlings may find a range of habitats from favorable to unfavorable (Hutchings et al. 2003, Gallardo et al. 2006).

By not measuring soil resources at levels commensurate with seedlings, studies may not be capturing the variation in resources that seedling growth and survivorship are dependent upon. Studies that measured soil resources at fine scales found significant effects of resources on seedlings (Baraloto and Goldberg 2004), while those studies that measured coarse, stand-level resources did not find effects (Valdecantos 2005, Vargas-Rodriguez et al. 2005). Thus, it is especially important to sample resources at the seedling-appropriate scale to make sure that the perceived resource environment, or patch size, is estimated appropriately.

Conclusions

The scale at which heterogeneity emerges is especially important when compared to plant size. If samples are taken at a larger spatial scale than what seedlings may have access to, studies may not capture those equally low nutrient levels that seedlings are actually experiencing. Despite differences among resources' spatial autocorrelation and effective ranges, fine scale sampling is important with respect to most soil nutrients. Therefore, to understand seedling responses to soil resources and by extension, the potential for species to partition gradients of soil resource availability in wet tropical forests, essential plant nutrients, such as inorganic N, P, and base cations, should be measured at a seedling-level spatial scale, while other soil resources, such as total N and total C could be measured at coarser spatial scales (>10 m).

TABLE 2.1. Chemical, physical and biological properties that could affect the spatial heterogeneity of resources. Source: M = Mineral-derived, originated from parent material; B = Biological-derived. Plant Uptake: Y = Yes; N = No.

Resource	Source	Processes affecting availability	Plant Uptake	Mobility in tropical soils
PO_4^-	M	Weathering, erosion, occlusion	Y	Mainly immobile
Total P	M	Weathering, erosion, occlusion	Y/N	Mainly immobile
K^+	M	Weathering, erosion, leaching	Y	Somewhat mobile
Ca^+	M	Weathering, erosion, occlusion	Y	Mainly immobile, held fairly tight to soil colloids
Mg^+	M	Weathering, erosion, occlusion	Y	Mainly immobile, held fairly tight to soil colloids
Inorganic N	B	Biological fixation, decomposition of organic residues by bacteria/fungi	Y	Immobile as ammonium form, but more mobile as nitrate form
Total N	B	Accumulation/decomposition of organic residues, biological fixation	Y/N	See inorganic N; organic N is bound in organic material
Total C	B	Accumulation of organic residues	N	Bound in organic material

TABLE 2.2. Comparison of soil resources among sites (one way analysis of means with unequal variances and a Bonferroni correction for multiple comparisons, $p<0.05$).

Resource	**F statistic**	**df**	***P***
PO_4^-	85.87	4, 621.35	< 0.001
Total P	49.92	4, 622.14	<0.001
K^+	58.31	4, 619.57	<0.001
Ca^+	55.95	4, 621.21	<0.001
Mg^+	61.36	4, 620.66	<0.001
Inorganic N	62.98	4, 577.72	<0.001
Total N	121.89	4, 564.72	<0.001
Total C	134.89	4, 573.59	<0.001

TABLE 2.3. Comparison of soil resources among alluvial versus volcanic sites.

Resource	**F statistic**	**df**	***P***
PO_4^-	141.16	1, 3	0.001
Total P	7.57	1, 3	0.071
K^+	11.53	1, 3	0.043
Ca^+	0.22	1, 3	0.67
Mg^+	0.00	1, 3	0.96
Inorganic N	11.02	1, 3	0.045
Total N	0.67	1, 3	0.47
Total C	0.80	1, 3	0.44

TABLE 2.4. Summary of resource values per site (Transect 1, 2, 3 = volcanic sites, Transect 4 = alluvial site, Transect 5 = recent alluvial site). Letters denote differences ($p<0.05$, one-way analysis of means with unequal variances and a Bonferroni correction) among soil resources, SD = standard deviation, and % CV = coefficient of variation.

Transect	**PO_4^- (µg/g)**	**Total P (µg/g)**	**Ca^+ (µg/g)**	**K^+ (µg/g)**	**Mg^+ (µg/g)**	**Inorganic N (µg/g)**	**Total N (%)**	**Total C (%)**
Transect 1								
mean	3.06 *a*	4.45 *a*	207.26 *d*	103.64 *c*	76.92 *c*	341.87 *b*	0.39 *b*	4.91 *b*
SD	4.05	4.86	192.26	61.5	58.09	181.21	0.15	1.92
Median	1.76	3.01	139.6	87.63	61.25	315.60	0.38	4.61
% CV	132.52	109.29	92.77	59.34	75.52	53.01	38.46	39.10
Transect 2								
mean	3.06 *ab*	4.64 *a*	130.52 *b*	78.50 *a*	61.09 *b*	440.57 *c*	3.62 *e*	4.77 *b*
SD	3.25	3.85	160.73	43.20	55.80	262.18	6.88	2.77
Median	2.08	4.15	93.98	71.21	49.90	410.09	0.38	4.38
% CV	106.51	83.06	123.15	55.04	91.35	59.51	190.06	58.07
Transect 3								
mean	3.51 *b*	4.61 *a*	93.91 *a*	87.97 *b*	48.28 *ab*	341.69 *b*	0.49 *d*	6.13 *d*
SD	3.07	3.89	138.34	34.39	22.27	220.97	0.09	1.26
Median	2.97	3.79	77.46	83.91	45.09	257.09	0.47	6.00
% CV	87.55	84.31	147.30	39.10	46.12	64.67	18.37	20.55
Transect 4								
mean	8.75 *c*	9.67 *c*	192.62 *d*	119.63 *d*	77.67 *c*	203.74 *a*	0.43 *c*	5.29 *c*
SD	9.91	5.90	140.42	54.15	42.90	119.07	0.10	1.33
Median	6.17	9.55	153.19	111.4	70.04	173.40	0.45	5.14
% CV	113.25	61.04	72.90	45.26	55.23	58.44	23.26	25.14
Transect 5								
mean	7.74 *c*	6.33 *b*	139.94 *c*	133.06 *d*	44.96 *a*	245.25 *a*	0.32 *a*	3.87 *a*
SD	5.19	4.11	94.61	61.81	23.34	158.83	0.09	1.03
Median	6.90	5.81	119.78	118.74	39.73	202.76	0.34	3.70
% CV	67.09	6.90	67.61	46.45	51.91	64.76	28.13	26.61

TABLE 2.5. Structural and nugget variances for each soil resource by site (Transect 1, 2, 3 = volcanic sites, Transect 4 = alluvial site, Transect 5 = recent alluvial site). Letters denote differences (no overlap in 95% credible intervals) across a resource.

Nutrient	**Transect 1**	**Transect 2**	**Transect 3**	**Transect 4**	**Transect 5**
PO_4^-					
% Structural variance	71.80 *c*	70.49 *b*	46.24 *a*	84.15 *d*	35.29 *a*
(95% credible interval)	(72.21, 73.20)	(70.68, 71.84)	(24.19, 44.34)	(80.60, 88.48)	(27.21, 46.50)
% Nugget variance	28.20	29.51	53.76	15.85	64.71
(95% credible interval)	(26.80, 27.79)	(28.16, 29.32)	(55.66, 75.81)	(11.52, 19.40)	(53.50, 72.79)
Total P					
% Structural variance	51.56 *a*	76.20 *b*	55.55 *a*	84.82 *c*	48.25 *a*
(95% credible interval)	(45.50, 59.07)	(76.14, 77.94)	(48.96, 65.62)	(83.57, 89.15)	(40.64, 56.08)
% Nugget variance	48.44	23.80	44.45	15.18	51.75
(95% credible interval)	(40.93, 54.50)	(22.06, 23.86)	(34.38, 51.04)	(10.85, 16.43)	(43.92, 59.36)
Ca^+					
% Structural variance	86.93 *d*	81.38 *c*	43.72 *a*	68.88 *b*	68.88 *b*
(95% credible interval)	(84.99, 91.28)	(80.73, 84.49)	(38.27, 51.66)	(68.36, 72.28)	(38.27, 51.66)
% Nugget variance	13.07	18.62	56.28	31.12	56.28
(95% credible interval)	(8.72, 15.01)	(15.51, 19.27)	(48.34, 61.73)	(27.72, 31.64)	(48.34, 61.73)
K^+					
% Structural variance	73.38 *b*	90.77 *c*	64.97 *ab*	63.00 *ab*	50.55 *a*
(95% credible interval)	(67.86, 82.79)	(89.48, 93.64)	(56.09, 76.54)	(58.83, 74.78)	(47.04, 63.40)
% Nugget variance	26.62	9.23	35.03	37.00	49.45
(95% credible interval)	(17.21, 32.14)	(6.36, 10.52)	(23.46, 43.91)	(25.22, 41.17)	(36.60, 52.96)

TABLE 2.5 (cont). Structural and nugget variances for each soil resource by site (Transect 1, 2, 3 = volcanic sites, Transect 4 = alluvial site, Transect 5 = recent alluvial site). Letters denote differences (no overlap in 95% credible intervals) across a resource.

Nutrient	**Transect 1**	**Transect 2**	**Transect 3**	**Transect 4**	**Transect 5**
Mg^{+}					
% Structural variance	74.59 *bc*	79.75 *c*	67.63 *ab*	69.29 *b*	51.18 *a*
(95% credible interval)	(69.09, 83.00)	(77.86, 84.56)	(59.88, 78.71)	(67.02, 75.79)	(44.56, 65.72)
% Nugget variance	25.41	20.25	32.37	30.71	48.82
(95% credible interval)	(17.00, 30.91)	(15.44, 22.14)	(21.29, 40.12)	(24.21, 32.98)	(34.28, 55.44)
Inorganic N					
% Structural variance	57.74 *b*	54.26 *b*	22.85 *a*	55.50 *b*	28.51 *a*
(95% credible interval)	(55.94, 60.80)	(49.63, 60.41)	(14.42, 33.72)	(48.89, 65.55)	(20.34, 36.50)
% Nugget variance	42.26	45.74	77.15	44.42	71.49
(95% credible interval)	(39.20, 44.06)	(39.59, 50.37)	(66.28, 85.58)	(34.45, 51.11)	(63.50, 79.66)
Total N					
% Structural variance	77.27 *b*	11.04 *a*	79.52 *b*	75.11 *b*	77.54 *b*
(95% credible interval)	(71.97, 86.10)	(6.64, 19.23)	(74.52, 83.18)	(70.27, 79.35)	(70.66, 82.43)
% Nugget variance	22.73	88.96	20.48	24.89	22.46
(95% credible interval)	(13.90, 28.03)	(80.77, 93.36)	(16.82, 25.48)	(20.65, 29.73)	(17.57, 29.34)
Total C					
% Structural variance	76.78 *ab*	63.95 *a*	81.01 *b*	78.13 *b*	7625 *ab*
(95% credible interval)	(72.44, 85.95)	(56.06, 72.78)	(75.89, 84.39)	(73.37, 82.09)	(68.23, 81.71)
% Nugget variance	23.22	36.05	18.99	21.87	23.75
(95% credible interval)	(14.05, 27.56)	(27.22, 43.94)	(15.61, 24.11)	(17.91, 26.63)	(18.29, 31.77)

TABLE 2.6. Effective range and 50% correlation distance (patch size) for each soil resource by site (Transect 1, 2, 3 = volcanic sites, Transect 4 = alluvial site, Transect 5 = recent alluvial site).

Nutrient	**Transect 1**	**Transect 2**	**Transect 3**	**Transect 4**	**Transect 5**
PO_4^-					
Range (m)	15.91	20.67	32.64	97.40	26.22
(95% credible interval)	(9.33, 30.09)	(11.98, 41.55)	(11.98, 198.68)	(49.75, 189.87)	(10.79, 123.46)
50% correlation distance (m)	3.68	4.78	7.54	22.50	6.06
(95% credible interval)	(2.16, 6.95)	(2.77, 9.60)	(2.77, 45.90)	(11.50, 43.87)	(2.49, 28.52)
Total P					
Range (m)	23.95	18.82	33.98	49.51	20.63
(95% credible interval)	(12.43, 59.88)	(11.50, 36.28)	(17.08, 92.88)	(27.45, 122.95)	(10.88, 56.29)
50% correlation distance (m)	5.53	4.35	7.85	11.44	4.77
(95% credible interval)	(2.87, 13.84)	(2.66, 8.38)	(3.95, 21.46)	(6.34, 28.41)	(2.51, 13.00)
Ca^+					
Range (m)	58.03	35.76	19.17	18.37	19.17
(95% credible interval)	(30.83, 147.73)	(20.83, 79.58)	(10.62, 61.22)	(8.99, 56.18)	(10.62, 61.22)
50% correlation distance (m)	13.41	8.26	4.43	4.24	4.43
(95% credible interval)	(7.12, 34.13)	(4.81, 18.39)	(2.45, 14.14)	(2.08, 12.98)	(2.45, 14.14)
K^+					
Range (m)	53.57	52.08	69.28	37.36	19.34
(95% credible interval)	(23.08, 158.73)	(27.68, 128.21)	(19.32, 185.19)	(11.64, 184.05)	(9.49, 154.64)
50% correlation distance (m)	12.38	12.03	16.01	8.63	4.47
(95% credible interval)	(5.34, 36.67)	(6.39, 29.62)	(4.46, 42.79)	(2.69, 42.52)	(2.19, 35.73)

TABLE 2.6 (cont). Effective range and 50% correlation distance (patch size) for each soil resource by site (Transect 1, 2, 3 = volcanic sites, Transect 4 = alluvial site, Transect 5 = recent alluvial site).

Nutrient	**Transect 1**	**Transect 2**	**Transect 3**	**Transect 4**	**Transect 5**
Mg^+					
Range (m)	60.73	37.22	62.24	24.86	37.31
(95% credible interval)	(27.52, 161.29)	(21.51, 85.23)	(22.69, 174.42)	(10.41, 90.36)	(12.68, 153.06)
50% correlation distance (m)	14.03	8.60	14.38	5.74	8.62
(95% credible interval)	(6.36, 37.27)	(4.97, 19.69)	(5.24, 40.30)	(2.41, 20.88)	(2.93, 35.36)
Inorganic N					
Range (m)	14.28	25.84	32.19	32.33	13.85
(95% credible interval)	(10.22, 29.53)	(12.60, 64.24)	(12.39, 116.73)	(13.84, 104.90)	(10.14, 38.86)
50% correlation distance (m)	3.27	5.97	7.44	7.47	3.20
(95% credible interval)	(2.36, 6.82)	(2.91, 14.84)	(2.86, 26.97)	(3.20, 24.24)	(2.34, 8.98)
Total N					
Range (m)	53.38	26.88	167.60	174.42	149.25
(95% credible interval)	(22.16, 165.75)	(10.29, 171.43)	(89.02, 198.68)	(103.81, 198.68)	(62.50, 197.37)
50% correlation distance (m)	12.28	6.18	38.55	40.12	34.32
(95% credible interval)	(5.10, 38.12)	(2.36, 39.43)	(20.47, 45.70)	(23.88, 45.70)	(14.38, 45.39)
Total C					
Range (m)	45.18	136.36	164.04	167.60	144.23
(95% credible interval)	(19.57, 153.85)	(24.94, 197.37)	(79.58, 198.68)	(85.71, 198.68)	(49.10, 197.37)
50% correlation distance (m)	10.39	31.36	37.50	38.55	33.17
(95% credible interval)	(4.50, 35.38)	(5.74, 45.39)	(18.30, 45.70)	(19.71, 45.70)	(11.29, 45.39)

TABLE 2.7. Responsiveness of soil nutrient availability to tree size by species type.

Resource	**Size of leguminous species**				**Size of non-leguminous species**			
	F	***P***	**r**	**(df = 1, 580)**	**F**	***P***	**r**	**(df = 1, 3520)**
Inorganic N	0.21	0.65	-0.019		3.92	0.048	-0.033	
Total P	1.55	0.21	-0.052		0.85	0.36	0.016	
K^+	0.27	0.61	-0.021		3.36	0.067	0.031	
Ca^+	5.63	0.018	-0.098		5.90	0.015	0.041	
Mg^+	9.82	0.002	-0.129		4.12	0.042	0.034	

TABLE 2.8. Mean resource estimates of patch sizes across all transects and the biological reasons supporting the ranges.

Resource	**Range of point estimates across transects (m) (“relative patch size”)**	**Biological reasoning for patch size**
PO_4^-	3.7 –22.5	Mineral weathering, plant uptake
Total P	4.4 - 11.4	Mineral weathering, plant uptake (includes both POand organic P forms)
K^+	4.4 - 16.0	Mineral weathering, plant uptake
Ca^+	4.2 - 13.4	Mineral weathering, plant uptake
Mg^+	5.7 - 14.0	Mineral weathering, plant uptake
Inorganic N	3.2 - 7.5	Biological-derived origin, microbial transformations, N immobilization, plant uptake
Total N	6.2 - 40.1	Biological-derived origin, litterfall inputs, driven by organic N forms
Total C	10.4 - 38.6	Biological-derived origin, litterfall inputs

FIGURE 2.1. Layout of sampling at each of five study sites (200 m transect) at La Selva Biological Station. (Filled-in circles = Regular lattice sampling points, Open circle = Random sampling points, Short arrows = 10 m, and Longer arrows = 20 m).

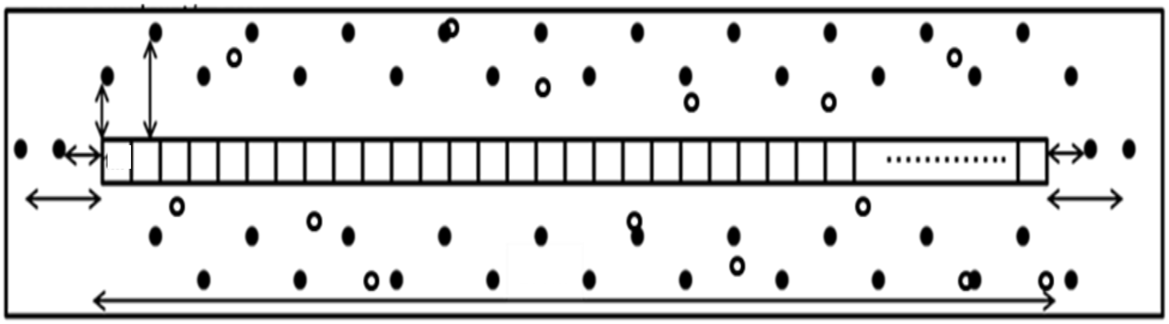


FIGURE 2.2. Example semivariogram illustrating the sill ($\sigma^2 + \tau^2$), partial sill (σ^2), nugget (τ^2) and effective range.

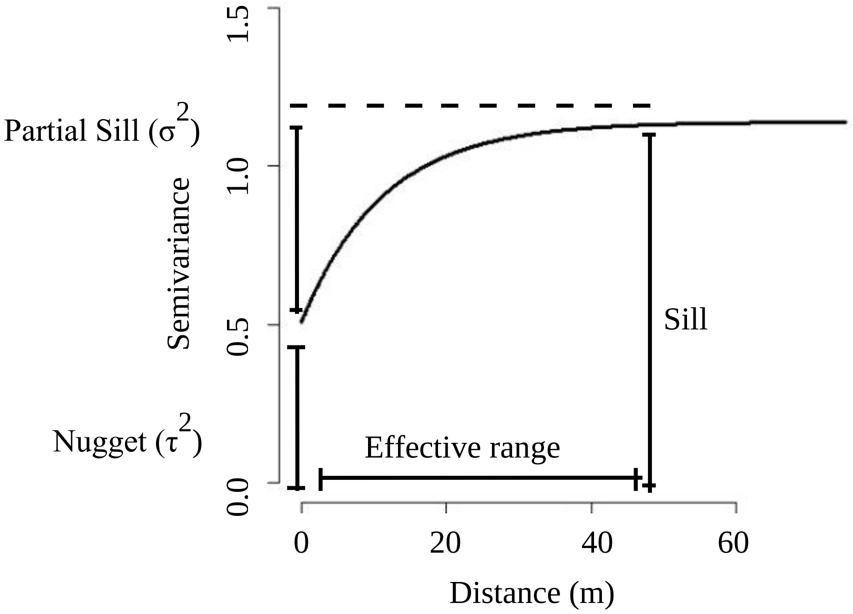


FIGURE 2.3. Distribution of soil resources by the proportion of cases. (A) Phosphate (B) Total phosphorus, (C) Potassium, (D) Calcium, (E) Magnesium, (F) Sum of inorganic nitrogen, (G) Total nitrogen, and (H) Total carbon (Transect 1/volcanic=solid, Transect 2/volcanic=dashed, Transect 3/volcanic=dotted, Transect 4/alluvial=dot-dash, Transect 5/recent alluvial=long-dash).

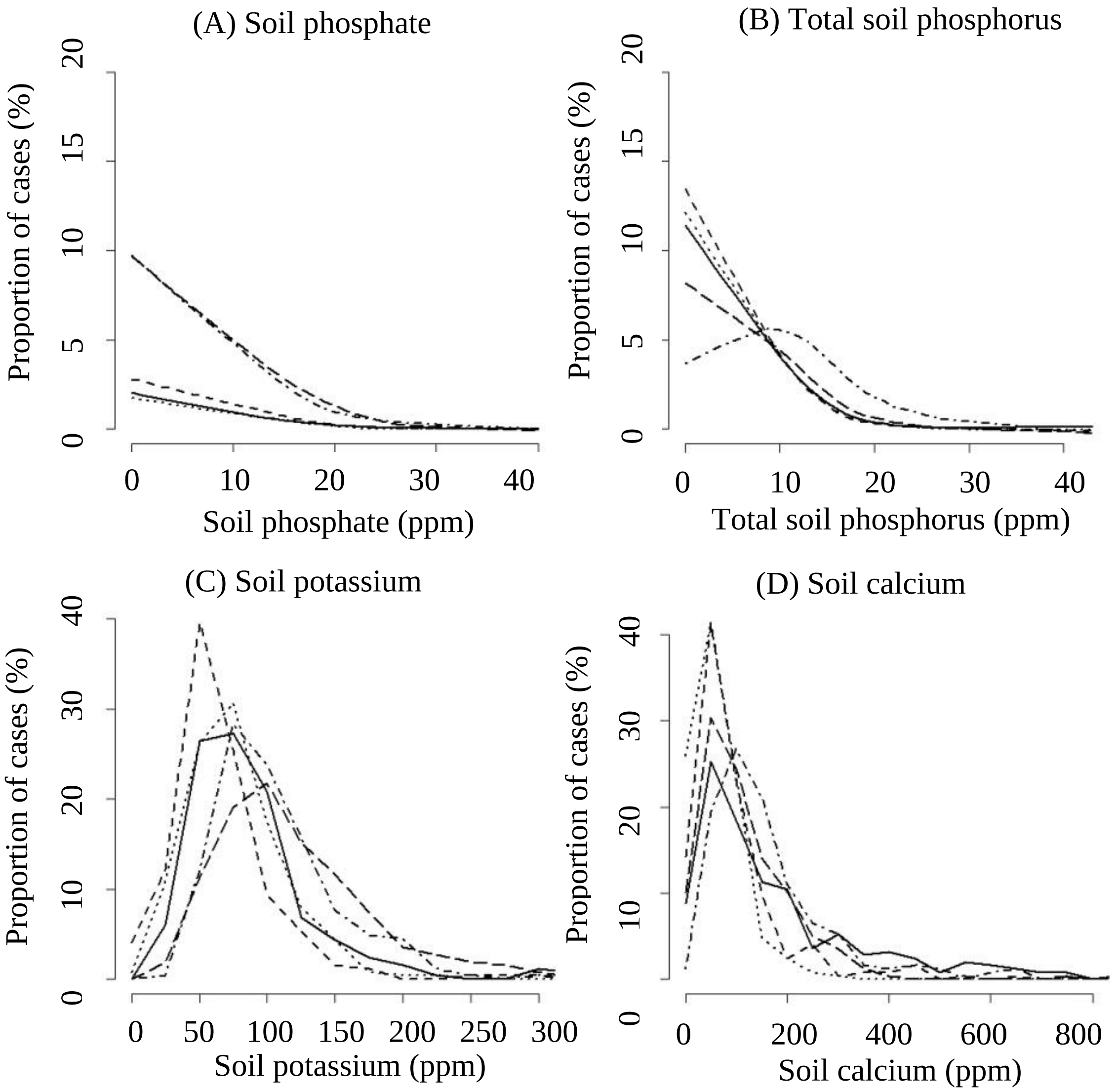
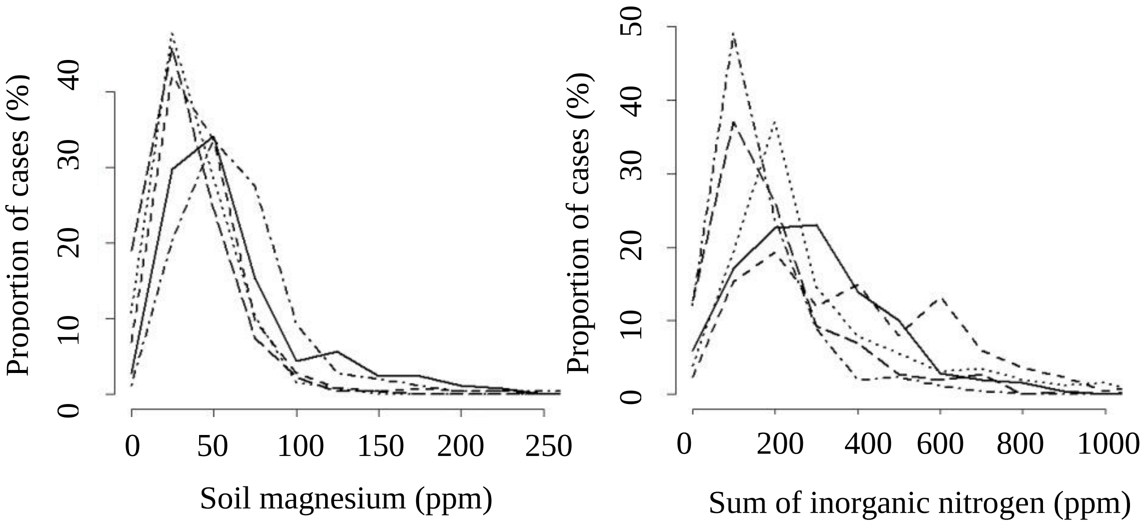
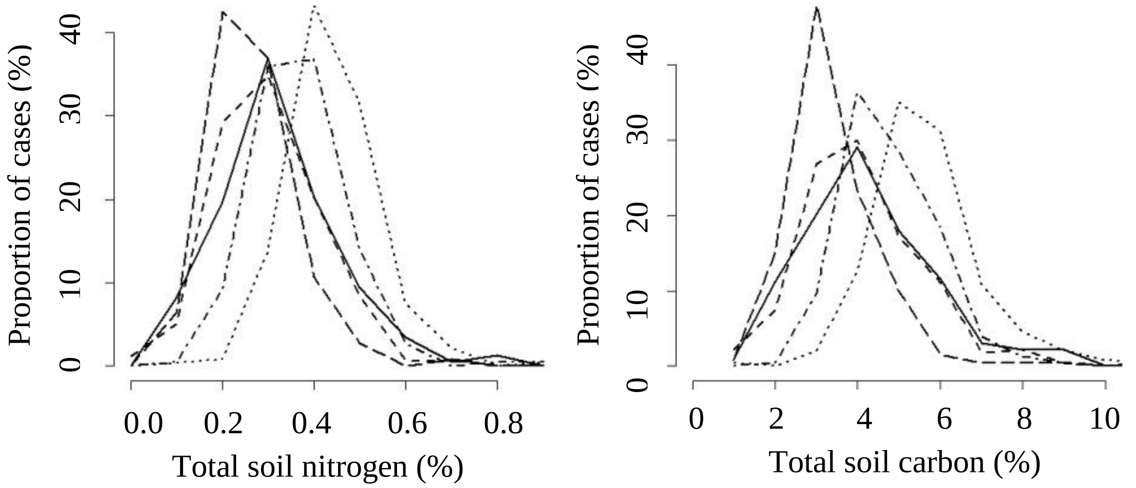


FIGURE 2.3 (cont). Distribution of soil resources by the proportion of cases. (A) Phosphate (B) Total phosphorus, (C) Potassium, (D) Calcium, (E) Magnesium, (F) Sum of inorganic nitrogen, (G) Total nitrogen, and (H)Total carbon (Transect 1/volcanic=solid, Transect 2/volcanic=dashed, Transect 3/volcanic=dotted, Transect 4/alluvial=dot-dash, Transect 5/recent alluvial=long-dash).



(E) Soil magnesium

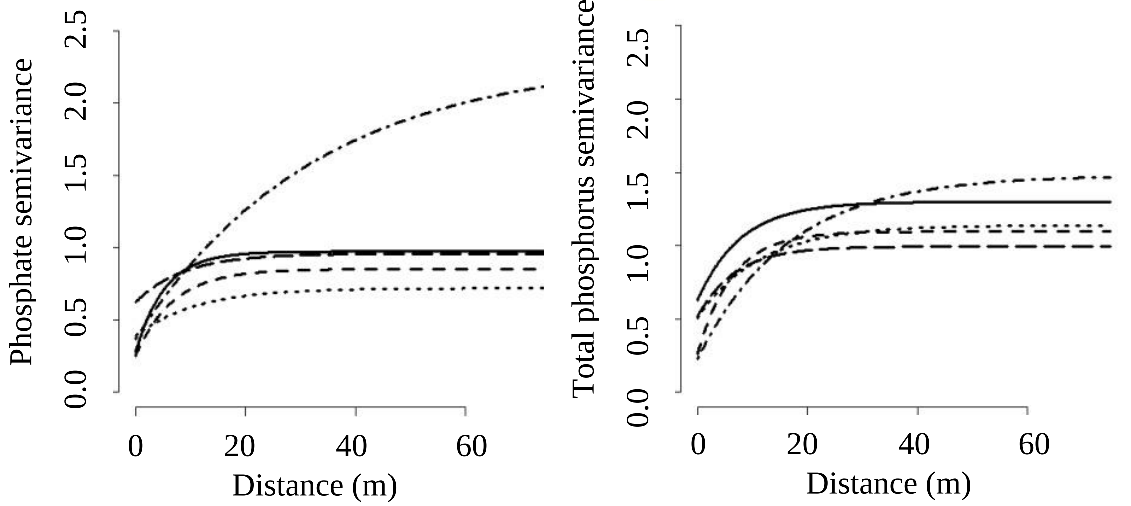
(F) Sum of inorganic nitrogen



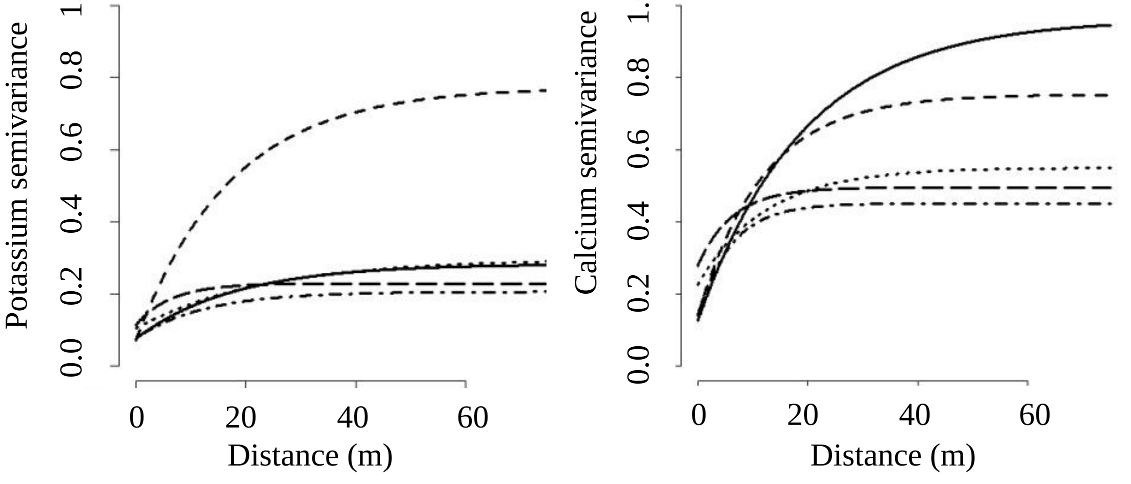
(G) Total soil nitrogen

(H) Total soil carbon

FIGURE 2.4. Semi-variograms of the 50% of the posterior estimate for each resource. (A) Phosphate (B) Total phosphorus, (C) Potassium, (D) Calcium, (E) Magnesium, (F) Sum of inorganic nitrogen, (G) Total nitrogen, and (H) Total carbon (Transect 1/volcanic=solid, Transect 2/volcanic=dashed, Transect 3/volcanic=dotted, Transect 4/alluvial=dot-dash, Transect 5/recent alluvial=long-dash).

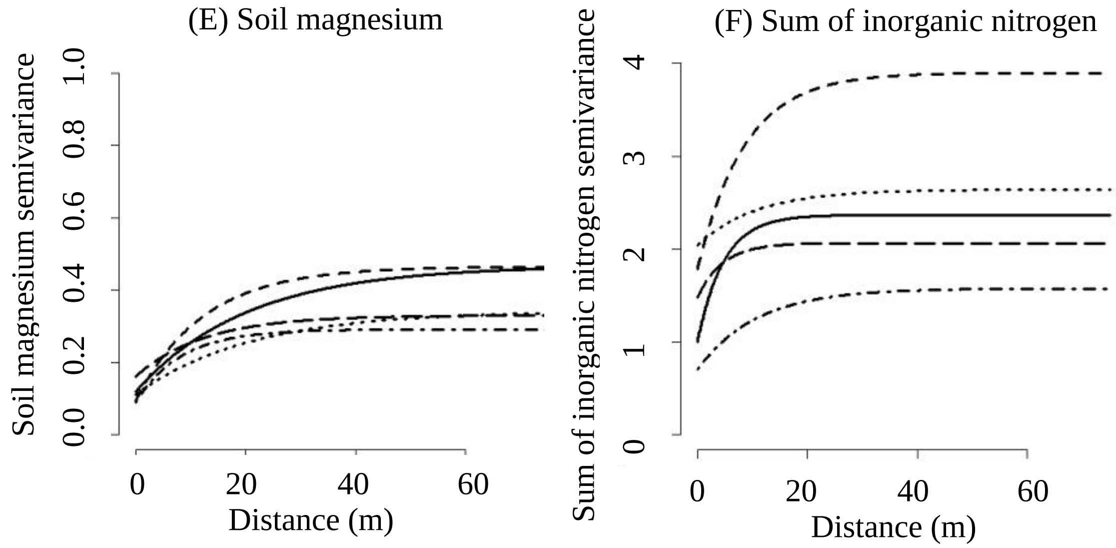

(A) Soil phosphate

(B) Total soil phosphorus

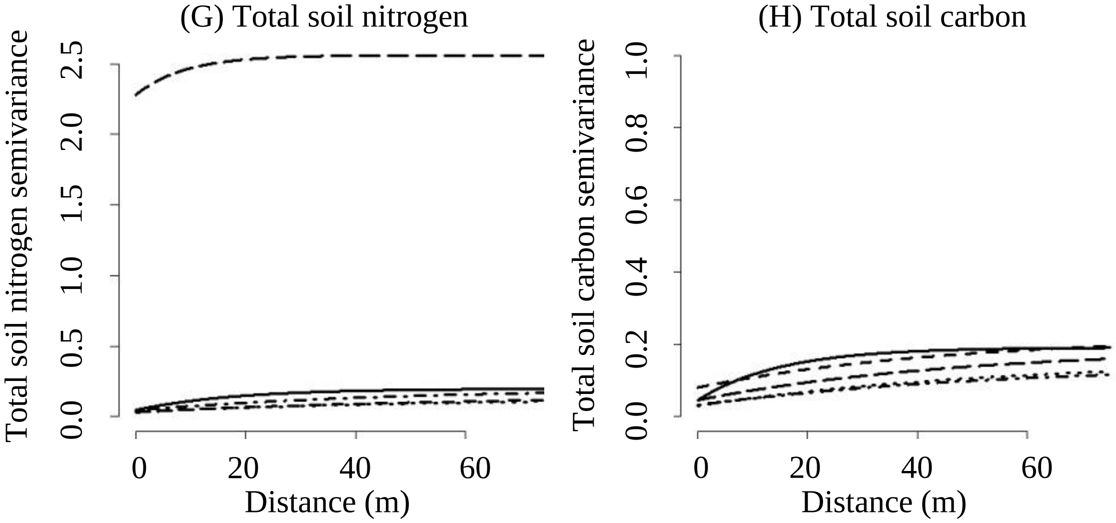

(C) Soil potassium

(D) Soil calcium

FIGURE 2.4 (cont). Semi-variograms of the 50% of the posterior estimate for each resource. (A) Phosphate (B) Total phosphorus, (C) Potassium, (D) Calcium, (E) Magnesium, (F) Sum of inorganic nitrogen, (G) Total nitrogen, and (H) Total carbon (Transect 1/volcanic=solid, Transect 2/volcanic=dashed, Transect 3/volcanic=dotted, Transect 4/alluvial=dot-dash, Transect 5/recent alluvial=long-dash).

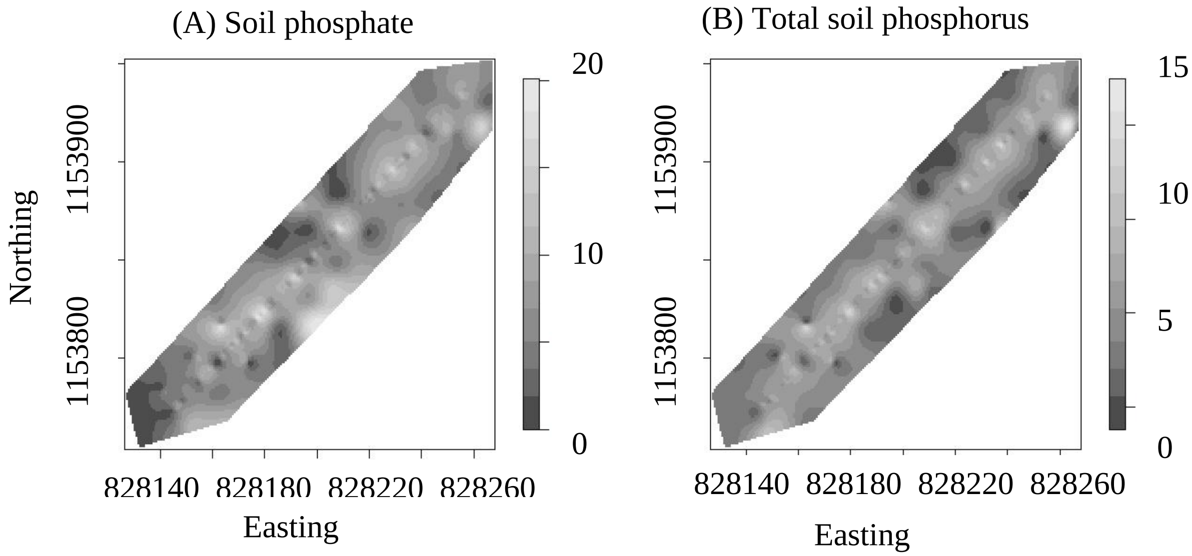

(E) Soil magnesium

(F) Sum of inorganic nitrogen


(G) Total soil nitrogen

(H) Total soil carbon

FIGURE 2.5. Example surface approximation of patch sizes for each resource across site 5 (alluvial soil). (A) Phosphate, (B) Total Phosphorus, (C) Calcium, (D) Potassium, (E) Magnesium, (F) Sum of Inorganic Nitrogen, (G) Total Nitrogen, and (H) Total Carbon.



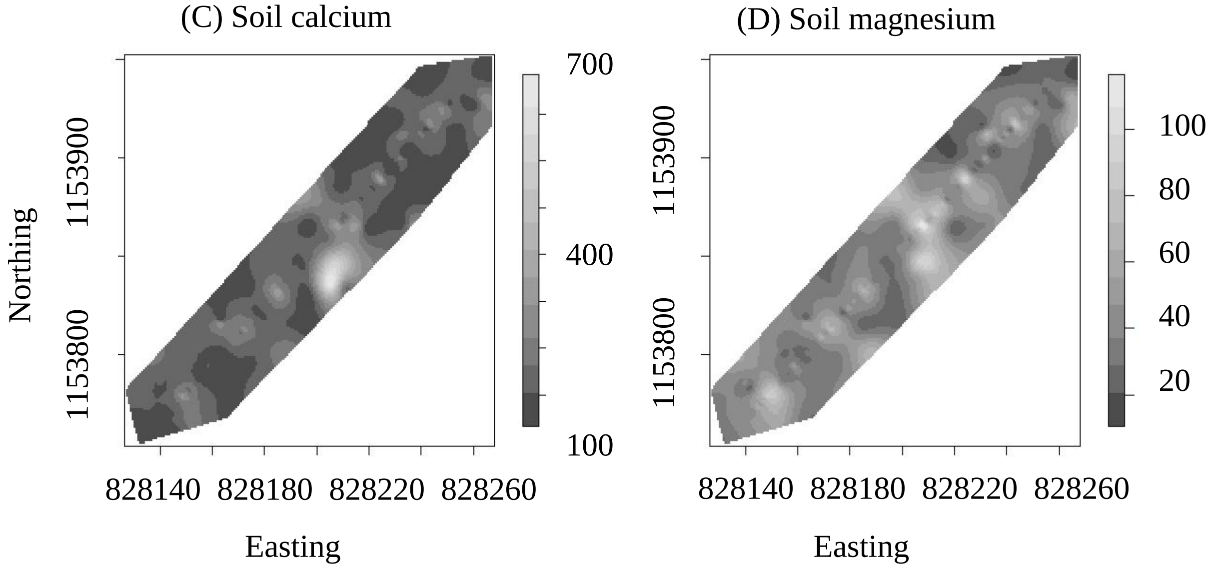
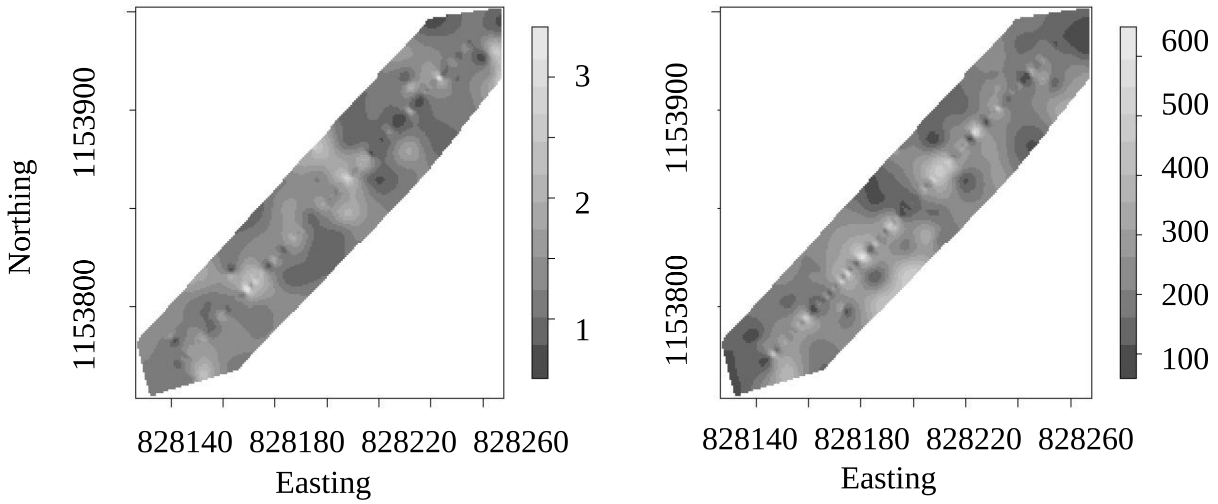
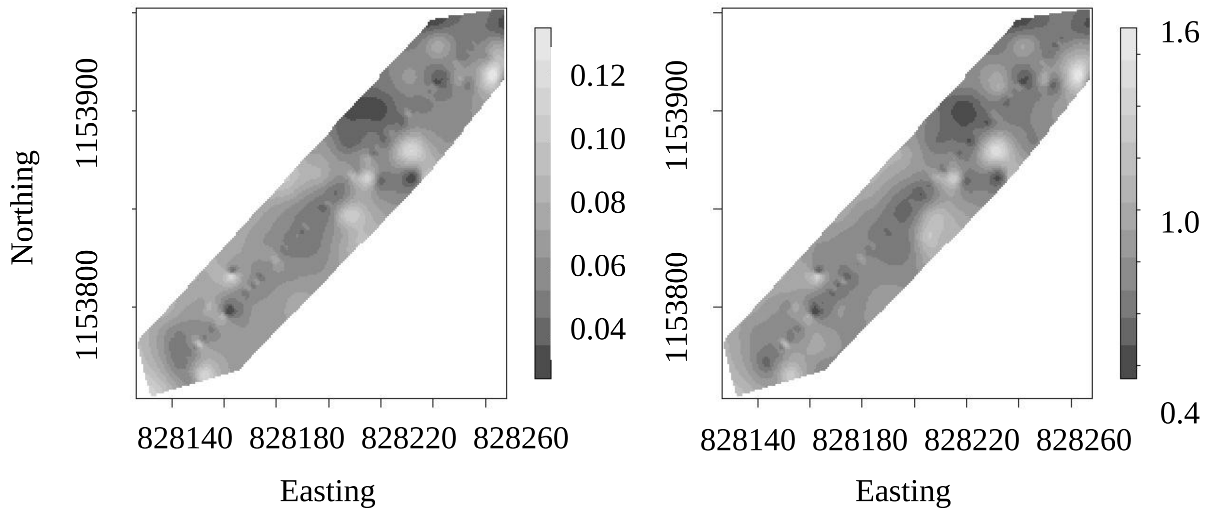


FIGURE 2.5 (cont). Example surface approximation of patch sizes for each resource across site 5 (alluvial soil). (A) Phosphate, (B) Total Phosphorus, (C) Calcium, (D) Potassium, (E) Magnesium, (F) Sum of Inorganic Nitrogen, (G) Total Nitrogen, and (H) Total Carbon.

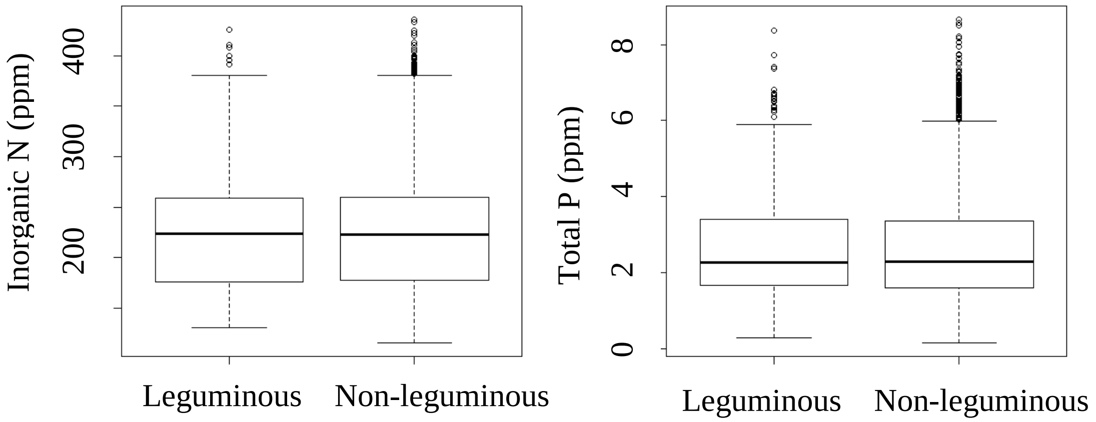

(E) Soil potassium

(F) Sum of inorganic nitrogen


(G) Total soil nitrogen

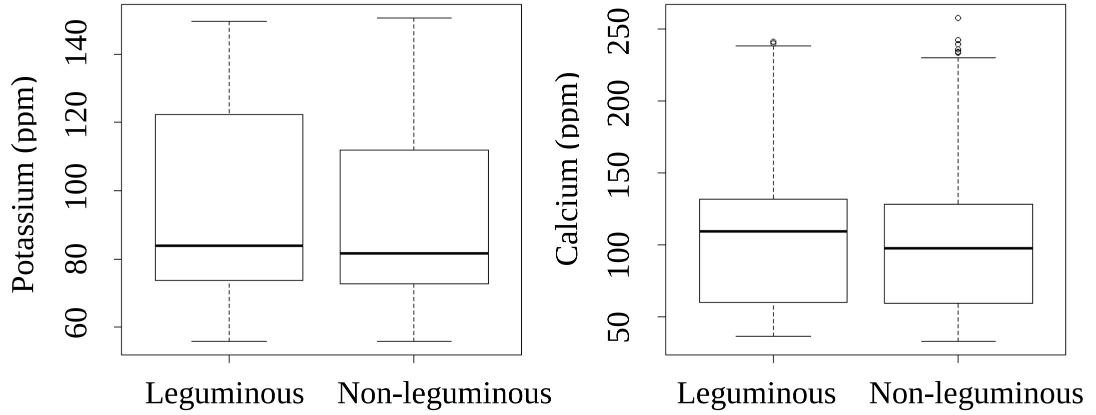
(H) Total soil carbon

FIGURE 2.6. Soil nutrient availability by species type. (A) Inorganic N by species type; (B) Total P by species type, (C) Potassium by species type, (D) Calcium by species type, (E) Magnesium by species type.



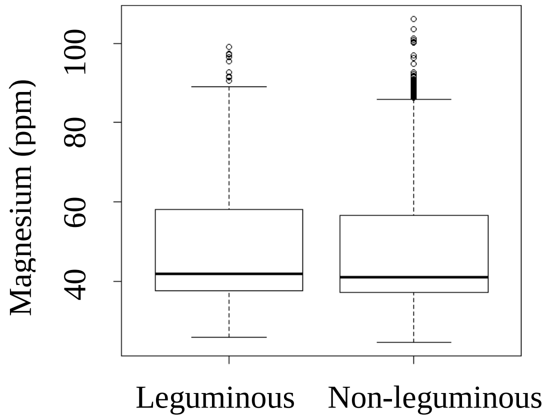
(A) Inorganic N by species type

(B) Total P by species type



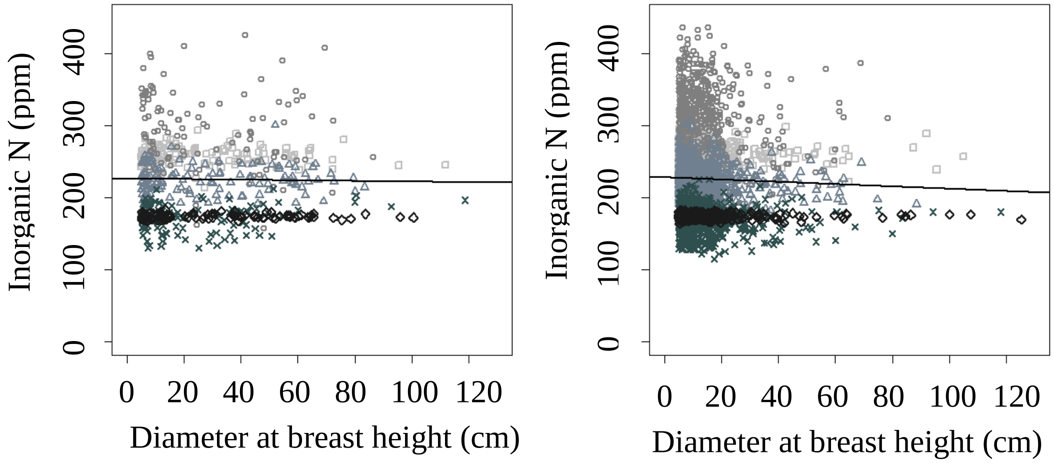
(C) Potassium by species type

(D) Calcium by species type

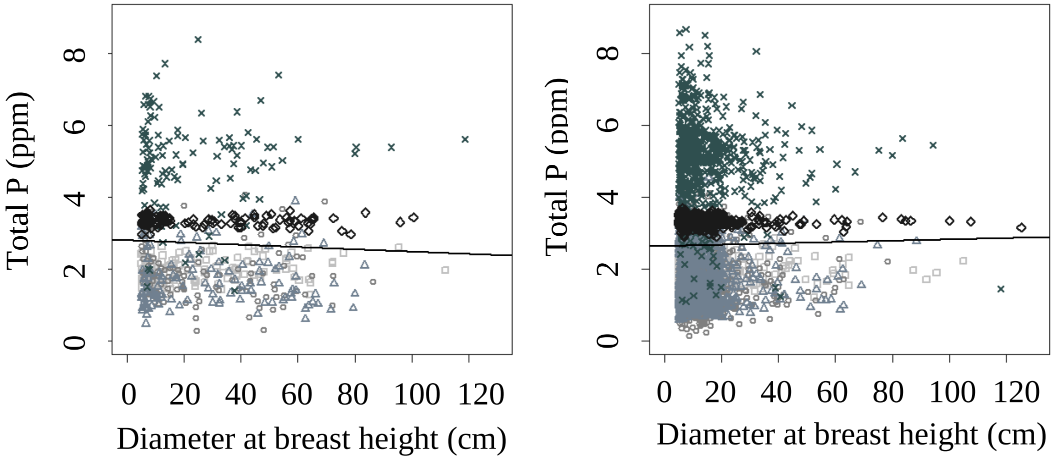


(E) Magnesium by species type

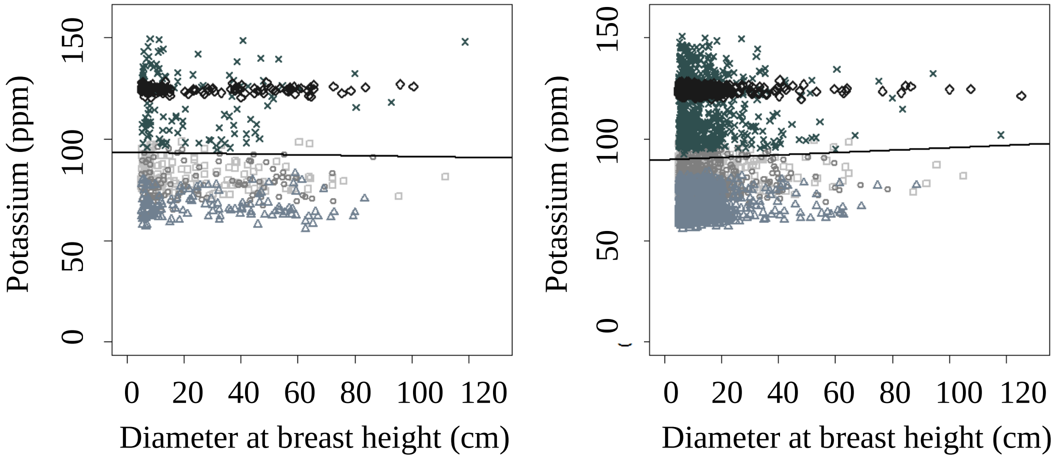
FIGURE 2.7. Responsiveness of soil nutrient availability to tree size by species type. (Transect 1 = square, Transect 2 = circle, Transect 3 = triangle, Transect 4 = X, Transect 5 = diamond.)


(A) Leguminous size vs. Inorganic N

(B) Non-leguminous size vs. Inorganic N

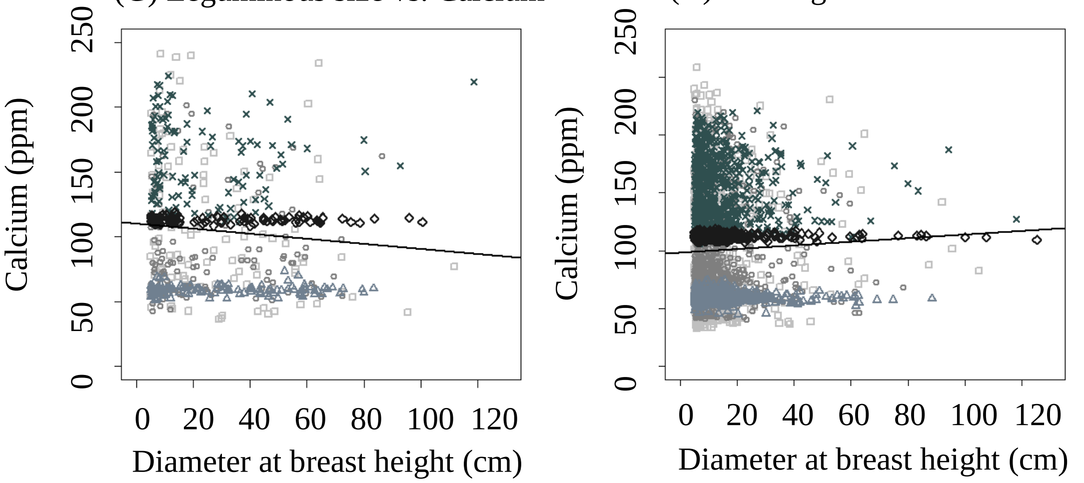

(C) Leguminous size vs. Total P

(D) Non-leguminous size vs. Total P

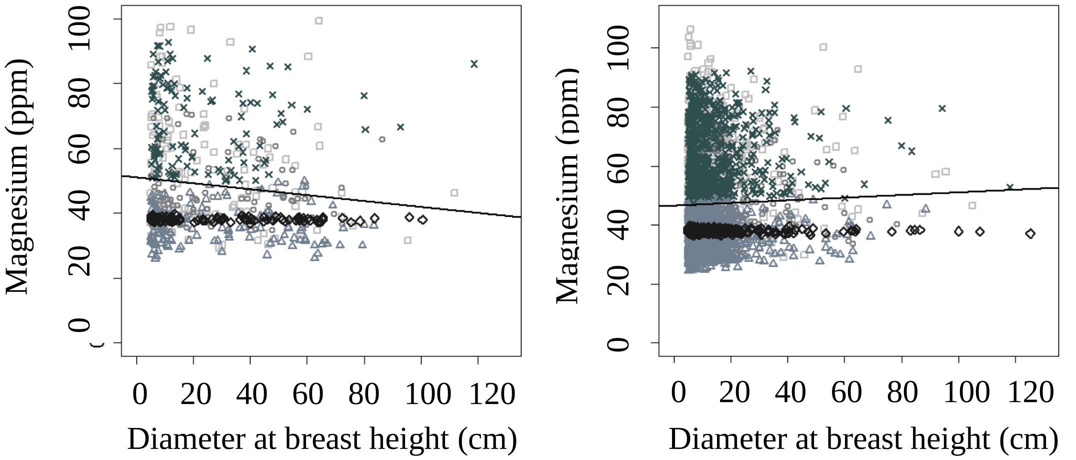

(E) Leguminous size vs. Potassium

(F) Non-leguminous size vs. Potassium

FIGURE 2.7 (cont). Responsiveness of soil nutrient availability to tree size by species type. (Transect 1 = square, Transect 2 = circle, Transect 3 = triangle, Transect 4 = X, Transect 5 = diamond.)


(G) Leguminous size vs. Calcium

(H) Non-leguminous size vs. Calcium


(I) Leguminous size vs. Magnesium

(J) Non-leguminous size vs. Magnesium

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CHAPTER III

Seedling responses to soil nutrients in the forest understory

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. To identify the resources that best predicted Neotropical tree seedling growth, irradiance and soil nutrients were measured over a seedling-appropriate spatial scale (1 m^2) in five sites, spanning a soil fertility gradient, in old-growth wet tropical forests at La Selva Biological Station, Costa Rica. An array of soil nutrients were measured including nitrate (NO_3^-), ammonium (NH_4^+), total nitrogen (total N), phosphate (PO_4^-), and sum of base cations (SBC; including potassium, magnesium, and calcium). Light limitation in the forest understory did not preclude seedling growth correlations with soil nutrients; growth was correlated with both irradiance and soil nutrients in about 45% of species, but in an additional 48% of species, growth was associated with only soil nutrients. Irradiance was a significant predictor of growth in 52% of the species, total N in 47%, SBC in 39%, NO_3^- in 32%, NH_4^+ in 34%, and PO_4^- in 29%. Contrary to expectations, the realized magnitudes of growth effects, assessed as the maximum growth response 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 first SBC, followed by PO_4^- and N (total N, NO_3^- and NH_4^+). Species' growth responsiveness (i.e. magnitudes of effect) to irradiance, SBC, NO_3^-, NH_4^+, and PO_4^- 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 challenges the idea that soil nutrients are less important than irradiance in the light-limited understory of wet tropical forests.

INTRODUCTION

Tropical forest understories are spatially heterogeneous in irradiance (Nicotra et al. 1999) and soil resources (Holste et al., in prep), and species-specific seedling growth and survivorship responses to resource levels could influence community structure. In both temperate and tropical forests, there is an inter-specific trade-off between survivorship under low light (i.e. shade-tolerant species) versus growth under high light (i.e. light-demanding species) that could promote species coexistence across light gradients (Kobe et al.1995, Kobe 1999). Similarly, inter-specific trade-offs between growth and survivorship also 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, Denslow 1980), 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 and promoting ecology-based forest management and restoration.

In tropical forests, irradiance is considered to be "the single-most limiting resource" (Pearcy 2007), with sometimes less than 1% of above canopy radiation transmitted to the forest floor (Chazdon and Fetcher 1984). Wet tropical forest seedlings exhibit inter-specific 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 with light availability (Montgomery and Chazdon 2002).

Soil nutrients also can influence tree growth (Burslem et al. 1995, Dent and Burslem 2009). In tropical forests, species differ in the direction and strength of growth responses to (Baraloto et al. 2006) and distributions with (John et al. 2007) soil factors.

Phosphorus (P) is widely thought to be more limiting than nitrogen (N) in mature 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, Ceccon et al. 2003). However, N also could alleviate P limitations by providing the substrate to construct extracellular phosphatases to acquire P (Treseder and Vitousek 2001). Based on reviews of tropical soils and plant-soil relations, Sollins (1998) proposed (in decreasing order of importance) that P, base cations (potassium, calcium, and magnesium), and N could influence species' performance in lowland wet tropical forests.

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), while shade-tolerant species 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 shade-tolerant and light-demanding 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). Despite presumed lower nutrient demand under low irradiance, soil nutrients influence seedling growth even in the deep shade of the forest understory (Yavitt and Wright 2008, Palow and Oberbauer 2009). 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). Yet seedlings in the shaded understory could benefit from increased soil nutrient availability via improved light capture (Fahey et al.

1998). Thus, I expect light-demanding species to be more dependent upon soil resources during seedling growth than more shade-tolerant species. I also expect growth-irradiance correlations to be more prevalent and to have a greater effect than soil nutrients on seedling growth in the shaded forest understory.

In this study, I examined the growth responses of 94 species of woody seedlings (represented by 12,800 individuals) to irradiance and soil nutrients to better understand species-specific seedling performance and implications for forest dynamics. I hypothesized that:

H1: Irradiance limitations to seedling growth are more prevalent among species and are of a greater magnitude than soil resource limitations to seedling growth.

H2: 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.

H3: The effect of irradiance and soil nutrients on species-specific seedling growth is negatively correlated with a species shade tolerance.

METHODS

Site description

Irradiance and soil nutrients were measured over a seedling-appropriate spatial scale (1 m^2) within five sites in mainly old-growth wet tropical forest at La Selva Biological Station, Costa Rica. A portion of one site contained secondary forest, which was associated with higher ecosystem productivity (T.W. Baribault, personal communication) but not higher seedling growth. La Selva is located in the Atlantic lowlands, at the convergence of the Sarapiqui and Puerto Viejo rivers (10º 26’N, 84º 00’

W) and receives a mean annual rainfall of 3859 mm with a mean monthly minimum of 100 mm. La Selva soils span a fertility gradient from relatively fertile entisols and inceptisols of alluvial origin to low fertility 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 1m^2 quadrats. In each transect, seedlings were identified and monitored, with height measurements taken every six weeks from February 2000 to September 2009.

Resource measurements

Light availability was measured in Fall 2000, July 2004, 2006, and 2007, and February and July 2008 as percent canopy openness. A hemispherical photograph was taken at the center of each 1 m^2 quadrat with a digital camera (Nikon Coolpix 950) and fish-eye lens (Nikon FC-E8). All photos were taken at 0.25 m height (+/- 0.05m) during uniformly overcast or twilight conditions. To increase contrast between sky and vegetation in the images, the 2000 and 2004 photos were under-exposed and for subsequent photos the automatic exposure level was locked based on spot metering of open sky (Ishida 2004). For 2000 through 2006 images, thresholds for images were set manually to classify pixels as sky or vegetation and percent canopy openness was calculated using Gap Light Analyzer (Gap Light Analyzer 2.0, Frazer et al. 1999). Later images were taken in black and white, classified with an edge detection algorithm (Sidelook 1.1, Nobis 2005), and resulting binary images were analyzed with Gap Light Analyzer to estimate percent canopy openness. I used percent canopy openness rather than irradiance metrics that include direct beam radiation, because percent canopy openness is a better predictor of seedling / sapling performance (Kobe and Hogarth 2007, Kobe and Vriesendorp, in review).

Because the 2000-2006 images were analyzed differently, measurements from these years were disproportionately higher in canopy openness compared to later years. Thus, canopy openness for individual quadrats was normalized across years (i.e. proportionately adjusted to result in the same mean percent canopy openness for each year). Because there were strong correlations of canopy openness through time (transect 1, $\bar{r}$ between measurements = 0.40; transect 2, $\bar{r}$ = 0.64; transect 3, $\bar{r}$ = 0.54; transect 4, $\bar{r}$ = 0.40; transect 5, $\bar{r}$ = 0.36), I approximated the light environment experienced by each seedling by calculating mean canopy openness over each individual's lifespan. I assumed that a single measurement of percent canopy openness applied to half of the interval between the preceding and subsequent measurements.

Along each of the five, 200 m transects, three soil subsamples from 16, 50 and 83 cm along the central axis of each 1 m^2 seedling quadrat (n=200 per transect, n=1000 in total) were taken with a corer (2 cm diameter) in the upper 20 cm of mineral soil in June 2008. Soil subsamples were composited, homogenized, air-dried for one week and shipped to Michigan State University for analysis. An array of soil resources were measured including nitrate (NO_3^-), ammonium (NH_4^+), total nitrogen (total N), potential net N mineralization rate (Nmin), phosphate (PO_4^-), potassium (K^+), calcium (Ca^+), and magnesium (Mg^+).

Plant available inorganic N (NO_3^- and NH_4^+) pools were extracted with potassium chloride and analyzed colorimetrically with an absorbance microplate reader

(ELx808 Absorbance Microplate Reader, BioTek Instruments, Inc, Winooski, VT). I used an ammonium salicylate and ammonium cyanurate colorimetric method to detect NH_4^+ (Sinsabaugh et al. 2000) and vanadium (III), sulfanilamide and N-(1-naphthyl)-ethylenediamine dihydrochloride (NED) to colorimetrically quantify NO_3^- (Doane and Horwath 2003). I calculated Nmin as the difference between final and initial pools of inorganic N after a 28 day incubation period. However, Nmin was correlated with NO_3^- ($P < 0.001$, r = -0.36) and led to similar species' growth responses to resources as NO_3^- and NH_4^+. Some Nmin rates also were negative. To avoid redundant independent variables and multicollinearity, I used initial NO_3^- and NH_4^+ pools in the analyses. Total soil N, which included both organic and inorganic N forms, was also measured via the dry combustion method using an Elemental Combustion CHNS-O analyzer (ECS 4010, Costech Analytical Technologies, Valencia, CA).

Phosphate, K^+, Ca^+, and Mg^+ ions were extracted with Mehlich III solution, a multi-element extractant (Monterroso et al. 1999) for acidic, highly weathered soils, such as those found at La Selva (Mehlich 1984). Potassium, Ca^+, and Mg^+ were analyzed with an Optima 2100DV ICP Optical Emission Spectrometer (Perkin-Elmer, Shelton, CT). Since previous studies found colorimetrically analyzed PO_4^- correlated more closely to "plant available" P (Pittman et al. 2005), PO_4^- was analyzed colorimetrically with a reagent solution containing acid molybdate, antimony potassium tartrate, 70% sulfuric acid, and absorbic acid (Frank et al. 1998). Total P was also analyzed (ICP analyzed P; Hylander et al. 1995), but since total P and PO_4^- were correlated, only PO_4^- was used to avoid multicollinearity in estimating seedling growth. Extractable K^+, Ca^+, and Mg^+ also were highly correlated; these elements were combined into a composite metric of sum of base cations expressed in charge equivalents (SBC).

Because soil texture can potentially alter nutrient availability (Neill et al 1997) and influence drainage, water-holding capacity, and species composition (Sollins 1998), I estimated soil texture as the percent sand, silt and clay in the soil using the hydrometer texture classification method. However, since I did not find differences within or across sites, soil texture was not likely to influence seedling growth, and thus was not considered as a factor.

Data analyses

Across all five sites, the entire dataset encompassed 522 woody species (including lianas and canopy, subcanopy, and understory trees) and 14,000 individuals. Seedlings were included if they were alive for at least two censuses so that height growth over an interval could be calculated (i.e., $\Delta\text{Height} = \text{Height}_{\text{final}} - \text{Height}_{\text{initial}}$). Twelve species contained 50% of the individuals, and 5 of those species (*Colubrina spinosa, Pentaclethra macroloba, Coussarea hondensis, Parathesis trichogyne,* and *Welfia regia*) had over 500 seedlings and made up 33% of the individuals. *C. spinosa* had the most individuals (n=1432) and was more abundant than *P. macroloba*, the most common adult species in La Selva (Hartshorn 1983).

Among the 522 potential species, only 95 species (represented by 12,800 individuals) had sample sizes of $\geq$ 20 individuals; one of the 95 species was excluded from analyses because all individuals were found in only two quadrats. In general, seedlings of a given species were broadly distributed across transects and quadrats (also see Kobe and Vriesendorp 2009). Species with the most clumped spatial distribution occupied at least 4 seedling quadrats in 2 transects. Thus, I tested for spatial dependence of seedlings with semivariograms of residual growth variance. For most species, the lowest model semivariance occurred at a lag distance other than zero, meaning that seedlings located in the same plot or in close proximity were not more similar in residual growth variance than seedlings located farther away. The lack of spatial structure in residual growth likely was due to the generally good fit of the models in which spatial variation in growth was accounted for in the resource measurements and models. Thus, seedlings were treated as independent units.

Measurements of $\text{Height}_{\text{final}}$ 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), I determined $\text{Height}_{\text{final}}$ as the last census at which ΔHeight for the most recent interval was zero or positive. Seedling growth can be characterized as a compound interest formula:

$$\text{Height}_{\text{final}} = \text{Height}_{\text{initial}} (1 + R)^{\text{lifespan}} \qquad \text{(equation1)}$$

In this equation, 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). Seedling growth rate may slow over time due to exhaustion of seed reserves, the accumulation of respiring non-photosynthetic tissue (e.g. MacFarlane and Kobe 2005), or cumulative effects of natural enemies. I tested whether growth rate declined over time by estimating an exponent (θ) on lifespan:

$$\mathrm{Height}_{\mathrm{final}} = \mathrm{Height}_{\mathrm{initial}}(1 + \mathrm{R})^{\mathrm{lifespan}^{\theta}} \quad \text{(equation 2)}$$

When $\theta = 1$, compounding of growth rate (R) is constant over seedlings of different lifespans; $\theta < 1$ indicates a diminishing while $\theta > 1$ indicates increasing compounding of R for longer-lived seedlings.

I 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 I used linear models to characterize the relationship between growth and irradiance.

Models were fit using maximum likelihood based non-linear regression in R-project computing software (http://www.r-project.org). The best 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 θ), 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 hold-out set seedlings, and r^2 values were calculated as above.

To express resource effects on a comparable scale, potential influence of a resource was calculated as the product of the maximum observed resource level for a species and the corresponding resource parameter estimate for that species. The absolute value of each maximum effect was compared across resources. To estimate the rank importance of soil nutrients and compare their effects on seedling growth with irradiance, resources effects were considered significantly different ($P \leq 0.05$) when their maximum effects had $\leq$ 29% overlap in 95% support (Austin and Hux 2002).

I characterized species' shade tolerance as the probability of seedling survival at 1% full sun and zero conspecific seedling density, calculated from mortality models that were calibrated with survival data from the same sites (Kobe and Vriesendorp, in review). Since shade-tolerant species generally have larger seed size (total seed mass), resulting in a proportionally larger initial seedling size than light-demanding species (e.g. Osunkoya et al. 1994), I obtained seed sizes for 31 of the species (KEW Seed Information Database, http://data.kew.org/sid/sidsearch.html) and calculated the mean initial seedling height for each species. To assess negative density dependence (Janzen 1970, Connell 1971), I tested for effects of both con- and heterospecific seedling density on growth for each species; neither con- nor heterospecific seedling densities were correlated with seedling growth rate for any species (mean $r = -0.01$, $r = 0.02$, respectively).

RESULTS

Summary

In this broad survey of species and resources, I found support for both soil nutrients and irradiance correlations with seedling growth in a wet tropical forest understory (Appendix A). 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. 3.1). On average, resources explained ~25% of the variation in growth (mean of differences in r^2 values between models containing initial height and resources versus only initial height) and initial height ~33% of growth variation. The holdout dataset 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, which were excluded for subsequent analyses.

Soil resources and irradiance influenced seedling growth

Contrary to expectation, irradiance was not the most prevalent or strongest correlate of seedling growth. With regards to prevalence, growth of 48% of the species was correlated with only soil nutrients, and an additional 45% were related to both soil nutrients and irradiance (see Appendix A). In 7% of species, growth was correlated with only irradiance. Among soil nutrients, total N was a significant predictor of growth in almost half (47%) of the species, SBC in 39% of species, NO_3^- in 32%, and NH_4^+ in 34%. 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 (for irradiance, z = 1.47, *P* = 0.14; for NO_3^-, z = 1.11, *P* = 0.27; for NH_4^+, z = 0.80, *P* = 0.42; for PO_4^-, 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 NO_3^- and NH_4^+, respectively, and 18% for PO_4^-; ~6-12% of species' resource-growth relationships were negative (Fig. 3.2).

Contrary to expectation, most soil nutrients (with the exception of NO_3^-, t = -2.06, df = 77.77, *P* = 0.04) had similar magnitudes of effect on seedling growth as irradiance (Fig. 3.3). Across the range of measured resources among species, irradiance's mean potential effect on growth was 0.10 mm/month. Mean potential magnitudes of effect for soil nutrients were 0.11 mm/ month for total N, 0.09 mm/month for PO_4^-, 0.08 mm/month for SBC, 0.08 mm/month for NH_4^+, and 0.06 mm/month for NO_3^- (see Appendix B). Among species for which both irradiance and a soil nutrient(s) 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 indistinguishable from irradiance in the other half of species (Table 3.1, e.g. Fig. 3.4A-C). Among species for which growth was correlated with soil nutrients, the rank importance of nutrients was first SBC, followed by PO_4^- and N (e.g. Fig. 3.4D-F); SBC affected 42-59% of species more than any other nutrient, PO_4^- had a greater effect on 0-39% of species, and total N, NO_3^- and NH_4^+ affected 7-43% of species more than other nutrients (Table 3.2). All N forms affected species similarly and had analogous effects as PO_4^- on species (Table 3.2).

Lifespan effects on compounding of growth

Of the 94 species, 24 species (27%) experienced diminishing compounding of growth ($\theta < 1$) and 7 species (8%) exper 70 ccelerating growth ($\theta > 1$) with increasing lifespan. Species estimates of θ were 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 I had seed size for only one-third of species, I used species mean initial height as a surrogate for seed size. As expected, species of smaller initial seedling height tended be less shade-tolerant ($F_{1,89} = 21.66$, $P < 0.001$, $r = -0.44$).

Across species, magnitude of growth responses to resources were negatively correlated with shade tolerance but not with initial seedling size, with the exception of larger seedlings affected less by NO_3^- (Appendix C). Shade tolerance was negatively correlated with species' responses to irradiance, SBC, NO_3^-, NH_4^+, and PO_4^- (Fig. 3.5A-E). Species' growth responsiveness to total N was similar for light-demanding and shade-tolerant species (Fig. 3.5F).

DISCUSSION

In wet tropical forest understories, both irradiance and growth rates of seedlings are generally very low (Clark and Clark 1992). Despite low light levels in this study, the results suggest that soil nutrients may be equally important as irradiance for understory seedling growth, which was frequently and strongly correlated with soil nutrients. Species' growth responsiveness to many soil nutrients was negatively correlated with shade tolerance, suggesting that faster growth by light-demanding species created a higher demand for soil nutrients. This study highlights the potential importance of both irradiance and soil nutrients to tropical seedling growth in low light and challenges the idea that soil nutrients are not important in the light-limited understory.

Contrary to H1, irradiance and soil nutrient correlations with seedling growth had similar prevalence and magnitudes of influence. 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^+ 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^+ additions (Burslem 1993). Therefore, irradiance and soil nutrients may be simultaneously limiting to seedling growth in the forest undestory and increased Mg^+ 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 (Augsburger 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 9 years. In contrast to other studies (e.g. Kobe 1999), I did not intentionally stratify variation in irradiance but wanted to represent typical conditions experienced by seedlings. I 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 intensity of light measurements early in study was not a strong influence.

Contrary to H2, base cations (SBC) had greater prevalence and greater magnitudes of effect than P, which is consistent with accumulating empirical evidence about the importance of calcium and magnesium (see Lawrence 2003). For example, *Antidesma cuspidatum* seedling growth responded to Mg^+ additions but not to any other macronutrient added singly, including P and N (Burslem et al. 1996). Base cation levels also were found to more strongly correlate with tree species distributions than either P or N (John et al. 2007). Base cations are more mobile than P and could be depleted more rapidly, especially in tropical ecosystems where high precipitation levels increase nutrient leaching (Chadwick et al. 1999). Base cations could influence seedling growth through: the structural role of Mg^+ in chlorophyll, Ca^+ as a constituent of woody tissue (Baribault et al. 2010) and correlate of photosynthetic rates (Reich et al. 1995), and role of K^+ and Ca^+ in signal transduction and nutrient uptake (Stevens et al. 1993). The availability of base cations also could limit mycorrhizal associated tropical tree seedling growth (Denslow et al. 1987, Burslem et al. 1994, Burslem et al. 1995) through an unknown mechanism. In temperate forest, base cation amendments increased mycorrhizal colonization and photosynthesis (St. Clair and Lynch 2005).

Even though N is generally more abundant than P in tropical forests (Hedin 2009), growth of about 50% of species were correlated with total N and another third with inorganic N (NO_3^- and NH_4^+), while growth correlations with PO_4^- were much less prevalent. Similarly, N fertilization increased tropical plant growth (Lewis and Tanner 2000). One possible explanation is that N may be used to alleviate P limitation through extracellular phosphatase production (Treseder and Vitousek 2001). Phosphatases hydrolyze the ester–phosphate bonds in soil organic P and release the phosphate into soil solution for uptake by nearby roots or microbes (Pant and Warman 2000). Phosphatases require a significant investment of N (N concentrations between 8% and 32%). Supporting this interpretation, N fertilization increased phosphatase activity in temperate soils under Norway spruce (Clarholm and Rosengren-Brinck 1995), while increased P availability reduced extracellular acid phosphatase activity (McLachlan 1980).

Instantaneous pools of available P (PO_4^-) and inorganic N (NO_3^- and NH_4^+) might have been too dynamic to provide an integrated estimate of long-term availability; thus, seedling growth responses to PO_4^-, NO_3^-, and NH_4^+ may have been underestimated. Under limitation, P would be quickly assimilated (Vandecar et al. 2009), and this study's one time measurement of PO_4^- may not have accounted for temporal heterogeneity Seedling growth correlated more with total N than inorganic N (NO_3^- and NH_4^+) perhaps because total N better approximates long-term N availability or provides an integrated measure of fertility. Since total P was highly correlated to PO_4^-, it was not included in predicting seedling growth, but similar to total N, total P may have provided a better estimate of P fertility.

Consistent with H3, the effects of most resources (except total N) were negatively correlated with shade tolerance. Of the 52 species for which seedling growth correlated with light availability, irradiance had greater effects on shade intolerant species. The growth of six shade tolerant species (*Borojoa panamensis, Byrsonima arthropoda, Coussarea talamancana, Doliocarpus multiflorus, Rauvolfia purpurascens,* and *Tetragastris panamensis*) was negatively correlated to irradiance. Shade-tolerant species may grow poorly under high irradiance due to inhibition of photosynthetic capacity (Krause et al. 2007). However, it is unlikely that irradiance levels encountered in the present study would have been high enough for photo inhibition. Nevertheless, this study's results are consistent with a broader species trade-off between low-resource survival and high resource-growth (Kobe et al.1995, Kobe 1999, Russo et al. 2008).

Of the 92 species for which growth correlated with a soil nutrient(s), effects of SBC, inorganic N, and PO_4^- affected light-demanding species more than shade-tolerant species. This result supports that species' demand for nutrients increases with average species growth, which is inversely correlated with low-light survival (shade tolerance). The inverse relationship between species shade tolerance and magnitude of growth responses to nutrients has not always been supported (Denslow et al. 1987, Lawrence et al. 2001). However, most nutrient studies have included only P and inorganic N; this study's examination of a broader array of nutrients and nutrient forms suggests relationships between shade tolerance /growth and growth responsiveness to resources.

Conclusions

As seedlings represent the next generation of forest individuals, understanding and predicting seedling growth 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 prevalent and as strong as growth correlations with irradiance. Seedling growth in these 94 species was generally affected more by SBC than any other soil nutrient, including P which is widely assumed to be most limiting. Furthermore, species' responses to resources may arise from covariance in life-history traits between shade tolerance and the demand for soil nutrients to achieve faster growth. Both irradiance and soil nutrients likely affect seedling growth under the low light conditions of the forest understory, and, therefore, must be simultaneously examined 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.

TABLE 3.1. Resource effect comparisons between irradiance and soil nutrients across species; percentages denote the portion of species that contained both irradiance and a particular soil nutrient. Resources effects are considered significantly different when $P \leq 0.05$ and there is $\leq$ 29% overlap in 95% support.

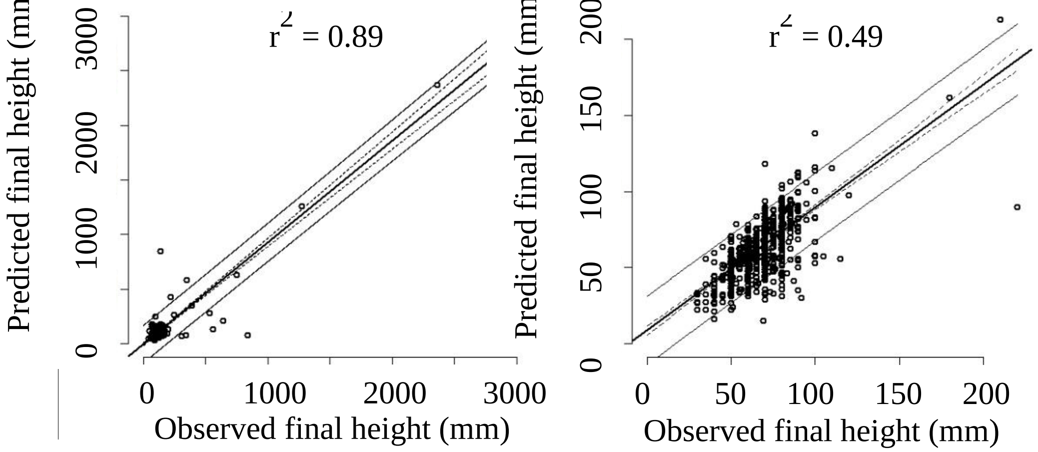
			Resource effects (%)		
Comparison	**SBC**	**PO_4^-**	**Total N**	**NO_3^-**	**NH_4^+**
Greater irradiance effect	35	39	45	54	55
Greater soil nutrient effect	35	28	5	8	5
Effects indistinguishable	30	33	50	38	40

TABLE 3.2. Resource effect comparisons among soil nutrients across species; percentages denote the portion of species that contained two particular soil nutrients (e.g. SBC and PO_4^-, or SBC and total N). Resources effects are considered significantly different when *P* $\leq$ 0.05 and there is $\leq$ 29% overlap in 95% support.

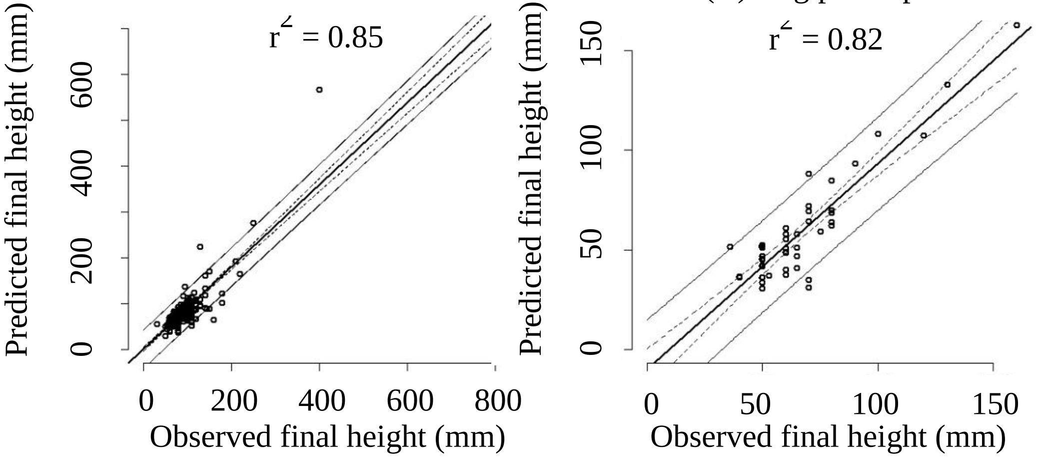
			Resource effects (%)		
Comparison	**SBC**	**PO_4^-**	**Total N**	**NO_3^-**	**NH_4^+**
Greater SBC effect	—	47	42	47	59
Lesser SBC effect	—	0	25	18	12
Greater PO_4^- effect	0	—	18	21	39
Lesser PO_4^- effect	47	—	27	43	11
Greater Total N effect	25	27	—	33	8
Lesser Total N effect	42	18	—	27	33
Greater NO_3^- effect	18	43	27	—	33
Lesser NO_3^- effect	47	21	33	—	7
Greater NH_4^+ effect	12	11	33	7	—
Lesser NH_4^+ effect	59	39	8	33	—

FIGURE 3.1. Model fit of representative species as assessed by r^2 values; 95% confidence intervals and prediction intervals are represented by dashed and solid lines, respectively.

(A) Hampea appendiculata (B) Colubrina spinosa



(C) Heteropterys laurifolia (D) Aegiphila sp.



(E) Virola koschnyi (F) Psychotria sp. 3

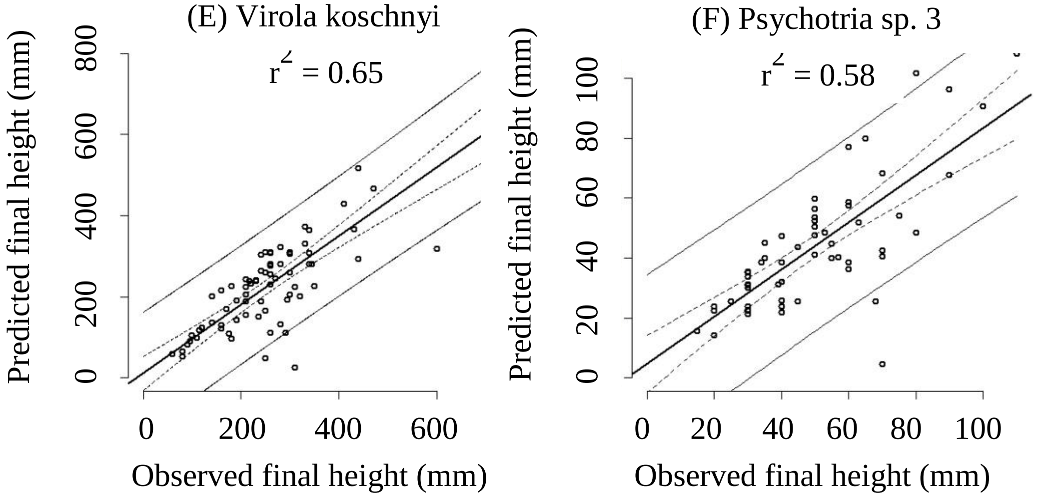


FIGURE 3.2. Proportion of species for which each resource is correlated with growth.

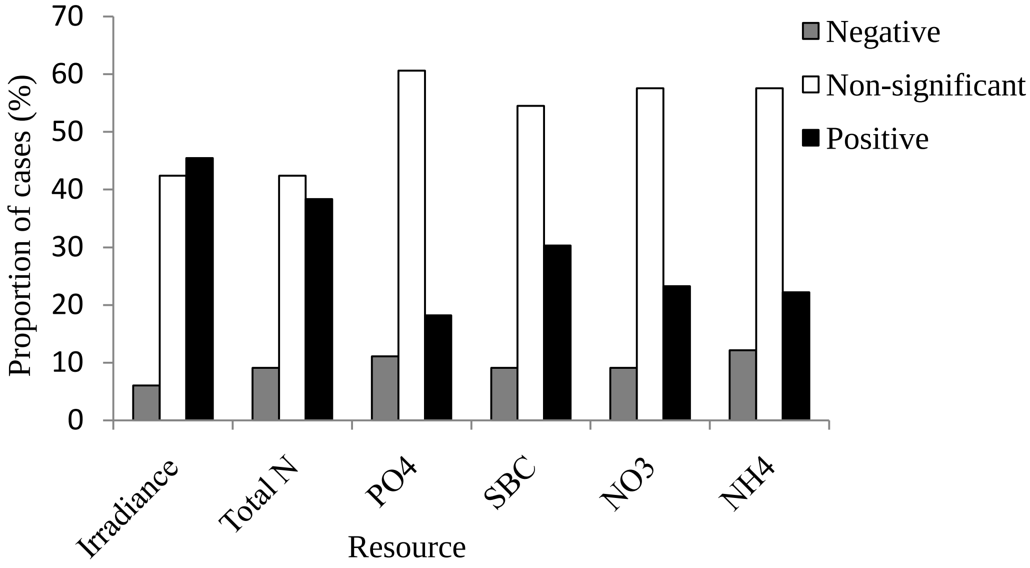


FIGURE 3.3. Mean absolute values of resource effects on seedling growth across species. Error bars denote standard error; letters represent significantly different pairwise comparisons at *P*=0.05.

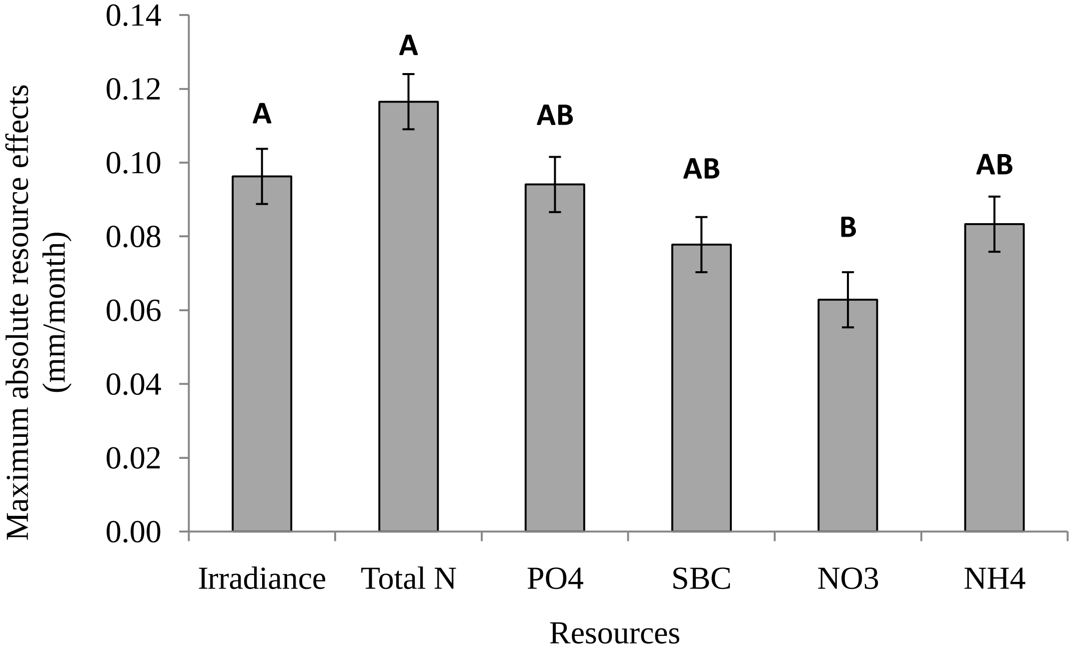


FIGURE 3.4. Representative models of height growth (mm/month) with respect to irradiance and soil nutrients.

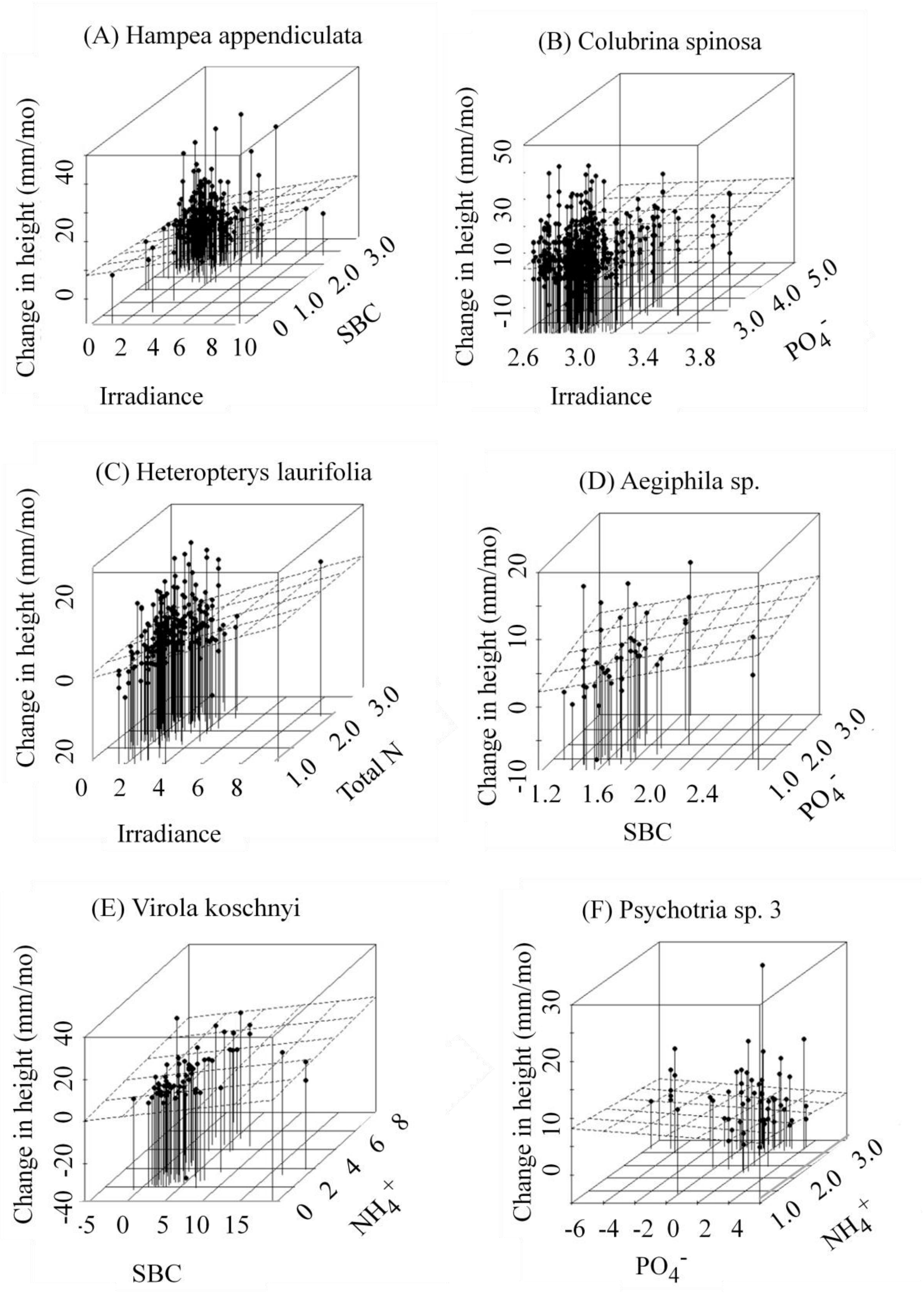
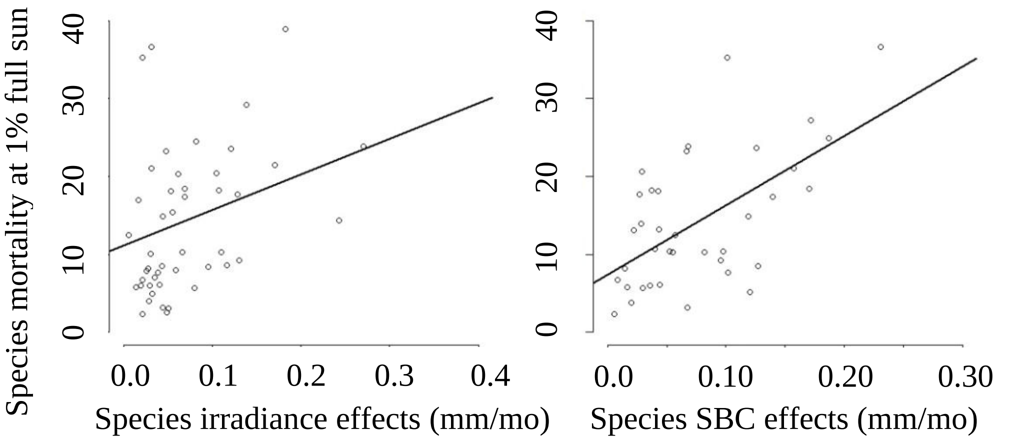
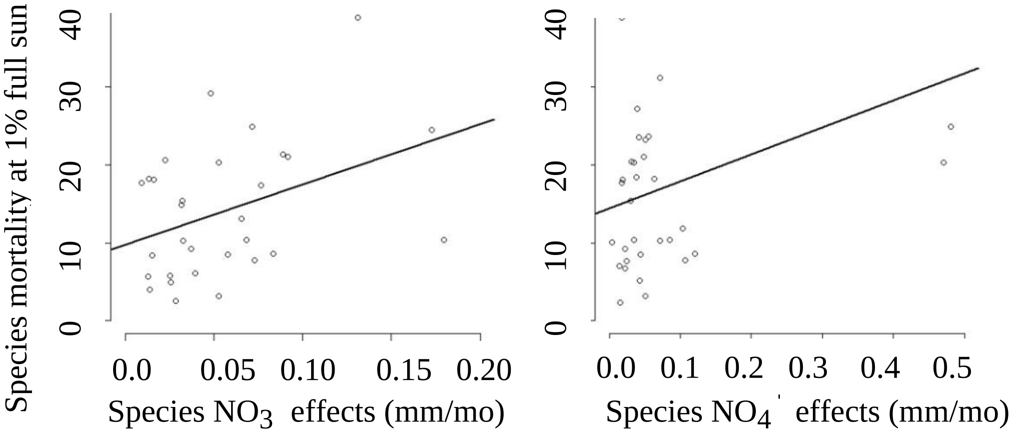


FIGURE 3.5. Species' responsiveness to irradiance and soil nutrients across a continuum of shade tolerance (for (A) irradiance, $F_{1,48}$ = 12.30, *P* = 0.001, r = 0.45; for (B) SBC, $F_{1,35}$ = 18.79, *P* = 0.0001, r = 0.59; for (C) NO_3^-, $F_{1,28}$ = 5.13, *P* = 0.03, r = 0.39; for (D) NH_4^+, $F_{1,31}$ = 4.84, *P* = 0.04, r = 0.37; for (E) PO_4^-, $F_{1,27}$ = 3.42, *P* = 0.08, r = 0.34; for (F) total N, $F_{1,44}$ = 0.17, *P* = 0.07, r = 0.68).

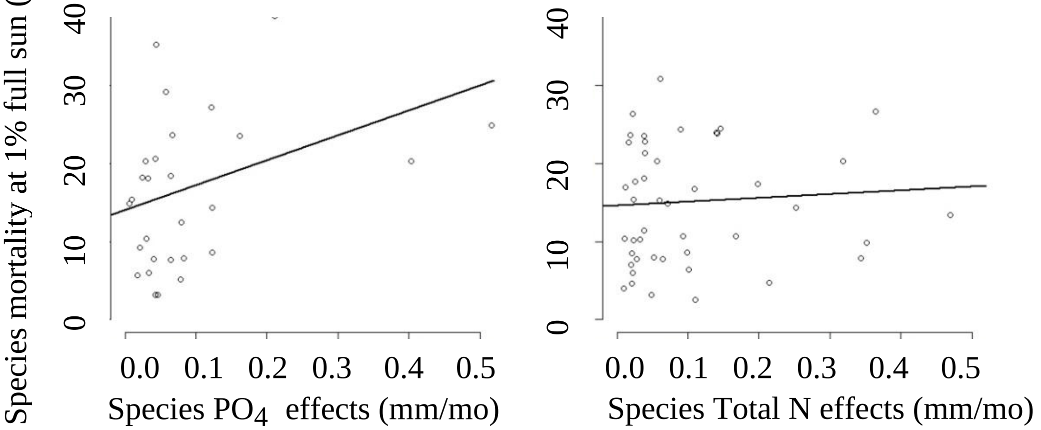
(A) Irradiance effects vs. shade tolerance (B) SBC effects vs. shade tolerance



(C) NO_3^- effects vs. shade tolerance (D) NO_4^+ effects vs. shade tolerance



(E) PO_4 effects vs. shade tolerance (F) Total N effects vs. shade tolerance



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CHAPTER IV

Conclusions

Understanding soil resource availability and heterogeneity within a system is critical to determining the factors that influence plant performance. In this research, soil type was weakly correlated with resource availability. Inorganic nitrogen (inorganic N) levels were lower on the younger sites (alluvial) and phosphate (PO_4^-), total phosphorus (total P), and potassium (K^+) were lower on older sites (volcanic), which is consistent with ideas of global patterns of nutrient limitation. Over half of the total variance in most soil resources was spatially structured, indicating a high degree of spatial autocorrelation, and the spatial structure of resources appeared to be based upon soil type. Adult tree functional groups did not create patches of similar resource availability and impose of pattern of spatial heterogeneity in this wet tropical forest. Patch size (defined as points within a distance having $\geq$50% correlation) were 10-40 m for total C and total N and 3-16 m for base cations, P, PO_4^- and inorganic N.

In general, resource patch sizes were larger than the mean root length of most tropical seedlings, so that seedlings would find a range of favorable to unfavorable habitats. The tremendous fine scale variability of these soil resources calls into question the use of site-level mean nutrient levels to approximate seedling nutrient availability. Thus, in order to capture the variability in resources that seedling are actually experiencing, it is especially important to sample resources according to the type of nutrient cycle and intrinsic physical and chemical properties to make sure that the perceived resource environment, or patch size, is estimated appropriately.

As seedlings represent the next generation of forest individuals, understanding and predicting seedling growth is important to future forest dynamics and regeneration. Through modeling 94 species, we were able to observe the overall resource trends affecting seedling growth in the light-limited understory. Based on the prevalence and the strength of soil nutrient correlations with growth, soil nutrients appeared to be equally important as irradiance to seedling growth in the forest understory. Across species, growth was correlated with both irradiance and soil nutrients in about 45% of species, but an additional 48% of species associated growth with only soil nutrients. Irradiance was a significant predictor of growth in 52% of the species, total N in 47%, SBC in 39%, NO_3^- in 32%, NH_4^+ in 34%, and PO_4^-, commonly considered the main limiting nutrient in many tropical systems, was significant in only in 29%. Contrary to expectation, the realized magnitudes of growth effects, assessed as the maximum growth response for each species, were similar for irradiance and most soil nutrients, and among species whose growth was correlated with soil resources, the rank importance of nutrient effects was first SBC, followed by PO_4^- and N (total N, NO_3^- and NH_4^+). Additionally, species' growth responsiveness (i.e. magnitudes of effect) to irradiance, SBC, inorganic N, and PO_4^- was negatively correlated with species' shade tolerance, assessed as survival under 1% full sun.

In this broad survey of species and soil resources, the nearly ubiquitous effects of soil nutrients on seedling growth challenges the idea that soil resources are less important than irradiance in the light-limited understory of wet tropical forests. This research has shown that irradiance and soil resources may both affect seedling growth and, therefore, must be simultaneously examined across a broad array of species and at a spatial scale commensurate with the soil environment experienced by seedlings in order to understand their effects on forest regeneration. Based upon these findings, seedling growth responses to resources could be used in understanding possible mechanisms of species coexistence and diversity in a wet tropical forest and to predict species-specific performance in ecology-based forest management and restoration.

APPENDICES

APPENDIX A

TABLE A1.1. Resource parameters (in mm/month per unit resource) of seedling growth rate by species. 95% confidence intervals are denoted by parentheses for each resource parameter.

Species	$\mathbf{r^2}$	**Irradiance (10e-2)**	**total N (10e-3)**	$\mathbf{PO_4^-}$ **(10e-3)**	**SBC**	$\mathbf{NO_3^-}$ **(10e-4)**	$\mathbf{NH_4^+}$ **(10e-5)**
Abuta panamensis	0.63		1.49 (0.60, 2.25)				
Aegiphila sp.	0.82			2.19 (0.47, 3.99)	0.53 (0.004, 0.94)	0.94 (0.03, 1.56)	
Anaxagorea crassipetala	0.89	2.85 (2.29, 3.36)	0.12 (0.07, 0.16)		0.70 (0.35, 1.04)	-0.38 (-0.69, -0.004)	-2.88 (-4.63, -1.23)
Apeiba membranacea	0.95	3.99 (3.43, 4.50)		-12.30 (-17.70, -6.14)		5.73 (3.80, 7.37)	-2.94 (-4.62, -1.00)
Ardisia fimbrillifera	0.04		0.49 (0.27, 0.65)				
Ardisia nigropunctata	0.53						67.0 (55.3, 77.6)
Ardisia sp.	0.74	1.12 (0.39, 1.81)					
Arisolochia sp.	0.55	6.44 (6.12, 6.78)					11.3 (3.43, 16.6)
Asterogyne martiana	0.35		6.43 (5.90, 6.90)				

TABLE A1.1 (cont.). Resource parameters (in mm/month per unit resource) of seedling growth rate by species. 95% confidence intervals are denoted by parentheses for each resource parameter.

Species	**r^2**	**Irradiance (10e-2)**	**total N (10e-3)**	**PO_4^- (10e-3)**	**SBC**	**NO_3^- (10e-4)**	**NH_4^+ (10e-5)**
Bauhinia guianensis	0.93		0.04 (0.01, 0.07)		2.10 (0.64, 3.33)	1.62 (0.69, 2.58)	-8.47 (-11.7, -5.34)
Bignoniaceae morph Model 1	0.82	1.67 (1.37, 1.91)					
Bignoniaceae morph Model 2	0.80		2.34 (1.91, 2.70)				
Borojoa panamensis	0.13	-34.7 (-44.3, -25.6)			3.77 (0.89, 6.41)	9.85 (7.44, 12.4)	
Brosimum lactescens	0.98	1.15 (0.80, 1.52)	7.28 (6.58, 8.03)	-0.42 (-0.83, -0.06)	-1.58 (-1.91, -1.27)	-1.33 (-1.82, -0.90)	
Byrosonima arthropoda	0.25	-0.12 (-0.22, -0.015)		6.30 (5.62, 6.97)	2.07 (1.89, 2.26)		
Callichlamys latifolia	0.28	0.59 0.48, 0.69)	1.09 (0.85, 1.32)				
Calyptrogyne ghiesbreghtiana	0.48		9.89 (7.77, 11.6)				
Capparis pittieri	0.47	0.61 (0.27, 0.88)			0.37 (0.15, 0.54)	0.77 (0.12, 1.28)	

TABLE A1.1 (cont.). Resource parameters (in mm/month per unit resource) of seedling growth rate by species. 95% confidence intervals are denoted by parentheses for each resource parameter.

Species	**r^2**	**Irradiance (10e-2)**	**total N (10e-3)**	**PO_4^- (10e-3)**	**SBC**	**NO_3^- (10e-4)**	**NH_4^+ (10e-5)**
Casearia corymbosa	0.83		2.72 (1.51, 3.82)				
Cassipourea elliptica	0.34					2.03 (1.45, 2.48)	
Castilla elastica	0.92	2.92 (2.34, 3.49)		3.63 (0.64, 6.40)		-2.33 (-3.67, -0.83)	
Colubrina spinosa	0.49	0.86 (0.13, 1.56)		3.08 (2.12, 4.02)	1.53 (1.30, 1.77)		
Cordia alliodora	0.32			6.25 (0.28, 12.2)			44.8 (3.34, 85.2)
Cordia bicolor	0.09	24.1 (10.5, 37.2)	-34.0 (-60.4, -11.2)				
Coussarea hondensis	0.06		0.17 (0.08, 0.24)				
Coussarea talamancana	0.92	-2.83 (-4.65, -0.96)	-0.05 (-0.08, -0.01)		2.33 (1.86, 2.78)	2.57 (1.41, 3.70)	-7.02 (-8.86, -5.05)
Cryosophila warscewiczii	0.98	1.82 (1.17, 2.35)	4.34 (1.82, 6.52)	2.34 (1.44, 3.07)	-1.64 (-2.63, -0.63)	-1.22 (-1.71, -0.72)	5.62 (2.11, 5.29)

TABLE A1.1 (cont.). Resource parameters (in mm/month per unit resource) of seedling growth rate by species. 95% confidence intervals are denoted by parentheses for each resource parameter.

Species	r^2	**Irradiance (10e-2)**	**total N (10e-3)**	**PO_4^- (10e-3)**	**SBC**	**NO_3^- (10e-4)**	**NH_4^+ (10e-5)**
Dendropanax arboreus	0.45				6.03 (3.80, 8.07)		
Dicranostyles ampla	0.85	1.38 (0.96, 1.80)			0.36 (0.04, 0.66)		
Doliocarpus multiflorus	0.34	-1.27 (-2.35, -0.21)			2.79 (1.78, 3.72	2.62 (1.62, 3.60)	-5.36 (-8.60, -2.10)
Eugenia sp.	0.74	13.7 (8.78, 18.8)	-14.3 (-22.9, -7.11)		-1.24 (-1.90, -0.53)		
Euterpe precatoria	0.89	3.67 (2.27, 4.85)			-1.71 (-2.64, -0.78)		10.7 (1.51, 18.8)
Faramea parvibractea	0.13				0.60 (0.23, 0.98)	1.66 (1.15, 2.14)	
Geonoma cuneata	0.13			2.49 (2.02, 3.01)		2.02 (1.48, 2.46)	-3.68 (-6.24, -1.47)
Geonoma cuneata (without outliers)	0.00005			1.44 (0.60, 2.28)	1.01 (0.23, 1.79)	1.64 (1.22, 2.06)	-4.11 (-5.53, -2.69)
Goethalsia meiantha	0.81	2.56 (1.53, 3.70)					46.2 (16.2, 71.8)

TABLE A1.1 (cont.). Resource parameters (in mm/month per unit resource) of seedling growth rate by species. 95% confidence intervals are denoted by parentheses for each resource parameter.

Species	**r^2**	**Irradiance (10e-2)**	**total N (10e-3)**	**PO_4^- (10e-3)**	**SBC**	**NO_3^- (10e-4)**	**NH_4^+ (10e-5)**
Guarea guidonia	0.02		1.73 (0.45, 1.93)				
Guatteria amplifolia	0.80	2.29 (1.69, 2.84)					3.18 (1.42, 4.70)
Gurania sp.	0.46		3.53 (1.49, 5.18)				
Hampea appendiculata	0.89	2.36 (2.17, 2.55)		-0.97 (-1.36, -0.61)	-0.57 (-0.68, -0.46)	0.42 (0.24, 0.59)	7.23 (6.10, 8.38)
Hernandia didymantha	0.76	1.28 (1.18, 1.38)				1.09 (0.96, 1.19)	
Herrania purpurea	0.23			11.2 (7.81, 13.4)			
Heteropterys laurifolia	0.85	2.55 (2.13, 3.00)	-4.03 (-6.12, -2.03)	6.42 (5.03, 7.76)			-6.29 (-8.58, -3.97)
Inga alba	0.72				0.78 (0.63, 0.90)		
Inga pezizifera	0.68	0.66 (0.46, 0.83)				0.60 (0.39, 0.79)	

TABLE A1.1 (cont.). Resource parameters (in mm/month per unit resource) of seedling growth rate by species. 95% confidence intervals are denoted by parentheses for each resource parameter.

Species	**r^2**	**Irradiance (10e-2)**	**total N (10e-3)**	**PO_4^- (10e-3)**	**SBC**	**NO_3^- (10e-4)**	**NH_4^+ (10e-5)**
Inga thibaudiana	0.84				0.47 (0.56, 0.76)		2.64 (0.48, 4.48)
Iriartea deltoidea	0.33	1.37 (0.71, 1.82)					
Jubelina wilburii	0.54		0.76 (0.02, 1.26)		1.74 (1.19, 2.27)		
Lacmellea panamensis	0.78	1.51 (1.26, 1.74)					0.46 (0.02, 0.89)
Laetia procera	0.84		-26.5 (-32.4, -20.5)	18.0 (13.3, 21.8)			85.8 (66.3, 102.0)
Machaerium seemannii	0.87				0.91 (0.51, 1.25)		
Maripa nicaraguensis	0.72		-1.99 (-3.22, -0.73)	2.52 (1.90, 3.13)		2.05 (1.39, 2.63)	
Mendoncia tonduzii	0.13	3.04 (1.95, 4.06)	0.15 (0.008, 0.27)			1.51 (0.96, 2.05)	-4.06 (-7.30, -0.86)
Mendoncia sp.	0.10		2.77 (0.88, 4.54)		1.13 (0.09, 2.07)		

TABLE A1.1 (cont.). Resource parameters (in mm/month per unit resource) of seedling growth rate by species. 95% confidence intervals are denoted by parentheses for each resource parameter.

Species	**r^2**	**Irradiance (10e-2)**	**total N (10e-3)**	**PO_4^- (10e-3)**	**SBC**	**NO_3^- (10e-4)**	**NH_4^+ (10e-5)**
Nectandra sp.	0.33		1.24 (0.46, 1.83)				
Neea elegans	0.80						14.7 (11.6, 17.3)
Neea sp.	0.15		9.90 (4.98, 14.1)				
Odontadenia macrantha	0.91	15.4 (3.74, 17.6)	-27.1 (-48.8, -5.45)	29.9 (7.47, 33.9)			
Paragonia pyramidata Model 1	0.76	2.02 (1.28, 2.63)					
Paragonia pyramidata Model 2	0.77				1.51 (0.96, 1.96)		
Paragonia pyramidata Model 3	0.77						7.57 (4.87, 9.82)
Parathesis trichogyne	0.25		0.04 (0.02, 0.07)	-5.01 (-7.06, -3.08)	5.22 (4.00, 6.34)		-7.64 (-10.2, -5.05)
Paullinia sp. A	0.93	2.09 (2.06, 2.11)				-0.39 (-0.56, -0.25)	

TABLE A1.1 (cont.). Resource parameters (in mm/month per unit resource) of seedling growth rate by species. 95% confidence intervals are denoted by parentheses for each resource parameter.

Species	**r^2**	**Irradiance (10e-2)**	**total N (10e-3)**	**PO_4^- (10e-3)**	**SBC**	**NO_3^- (10e-4)**	**NH_4^+ (10e-5)**
Paullinia fibrigera	0.0008		1.20 (0.82, 1.55)				
Pentaclethra macroloba	0.67	0.90 (0.69, 1.10)	0.09 (0.04, 0.13)	-0.43 (-0.65, -0.25)	0.42 (0.26, 0.58)	0.37 (0.22, 0.51)	-1.58 (-2.26, -0.93)
Perebea hispidula	0.79	3.92 (0.49, 5.19)	8.64 (2.71, 13.7)	-8.77 (-14.9, -2.20)		-2.80 (-5.15, -0.22)	13.4 (4.98, 22.1)
Pholidostachys pulchra	0.01	1.36 (6.45, 19.8)	1.06 (0.03, 1.56)	4.61 (3.15, 6.07)			
Pinzona coriacea	0.68		14.5 (12.4, 16.3)				
Plukenetia stipellata	0.78	10.4 (8.79, 13.5)		-24.5 (-39.7, -16.5)			48.2 (37.8, 58.7)
Pourouma bicolor	0.90	2.73 (2.59, 2.89)		0.82 (0.28, 1.40)	-1.74 (-2.11, -1.39)	0.88 (0.61, 1.14)	3.01 (1.94, 4.18)
Pourouma minor	0.44	1.61 (0.93, 2.19)			-1.68 (-3.32, -0.30)	1.46 (0.58, 2.48)	
Prestoea decurrens	0.01	7.17 (6.08, 8.48)		12.5 (11.1, 13.9)	-10.56 (-12.30, -9.03)	-3.06 (-4.07, -2.00)	12.9 (3.32, 19.9)

TABLE A1.1 (cont.). Resource parameters (in mm/month per unit resource) of seedling growth rate by species. 95% confidence intervals are denoted by parentheses for each resource parameter.

Species	**r^2**	**Irradiance (10e-2)**	**total N (10e-3)**	**PO_4^- (10e-3)**	**SBC**	**NO_3^- (10e-4)**	**NH_4^+ (10e-5)**
Prestoea decurrens (without outliers)	0.0003		2.13 (1.62, 2.58)				
Protium confusum Model 1	0.16	1.30 (0.05, 2.09)					
Protium confusum Model 2	0.19			1.82 (0.21, 3.43)			
Protium confusum Model 3	0.17				0.79 (0.13, 1.45)		
Protium panamense	0.96	1.29 (1.25, 1.32)	0.12 (0.11, 0.12)				
Psychotria panamensis	0.38	3.39 (1.93, 4.62)	0.35 (0.14, 0.50)			1.58 (0.74, 2.34)	
Psychotria sp.1	0.16	10.7 (2.90, 16.9)					
Psychotria sp.2	0.96		9.31 (8.97, 9.63)				
Psychotria sp.3	0.58			6.60 (4.73, 8.22)	3.04 (1.44, 4.47)		-4.60 (-8.63, -0.89)

TABLE A1.1 (cont.). Resource parameters (in mm/month per unit resource) of seedling growth rate by species. 95% confidence intervals are denoted by parentheses for each resource parameter.

Species	**r^2**	**Irradiance (10e-2)**	**total N (10e-3)**	**PO_4^- (10e-3)**	**SBC**	**NO_3^- (10e-4)**	**NH_4^+ (10e-5)**
Pterocarpus rohrii	0.32				1.56 (0.90, 2.07)		
Randia genipoides	0.87	3.18 (2.35, 3.90)	1.09 (0.20, 1.87)			-1.30 (-1.66, -0.90)	
Rauvolfia purpurascens	0.78	-2.75 (-5.14, -3.54)	0.66 (0.43, 0.90)		2.83 (2.07, 3.59)	-2.66 (-3.76, -1.64)	
Richeria obovata	0.12			1.84 (0.74, 2.81)			
Rinorea deflexiflora	0.08	1.44 (1.29, 1.58)	-2.79 (-3.91, -1.68)		1.22 (0.77, 1.66)	0.76 (0.55, 0.94)	
Securidaca diversifolia	0.41		1.95 (1.27, 2.54)				
Serjania sp.	0.86		-3.50 (-6.83, -0.33)			3.67 (1.89, 5.45)	
Simarouba amara	0.94	1.45 (1.04, 1.87)		-3.33 (-4.42, -2.27)	3.01 (2.40, 3.59)		-4.55 (-8.00, -1.17)
Socratea exorrhiza	0.85	1.57 (1.08, 1.99)			-0.18 (-0.31, -0.05)		1.87 (1.21, 2.49)

TABLE A1.1 (cont.). Resource parameters (in mm/month per unit resource) of seedling growth rate by species. 95% confidence intervals are denoted by parentheses for each resource parameter.

Species	**r^2**	**Irradiance (10e-2)**	**total N (10e-3)**	**PO_4^- (10e-3)**	**SBC**	**NO_3^- (10e-4)**	**NH_4^+ (10e-5)**
Synechanthus warscewiczianus	0.99		8.38 (8.28, 8.47)				
Tapiria guianensis	0.05		0.87 (0.42, 1.20)				
Tetragastris panamensis	0.88	-2.78 (-3.79, -1.76)		-4.81 (-6.81, -2.83)	4.23 (3.18, 5.25)		2.71 (0.50, 4.81)
Trophis racemosa	0.93					3.31 (2.06, 4.48)	6.89 (0.59, 13.0)
Unonopsis pittieri	0.66		5.26 (1.08, 9.12)				
Virola koschnyi	0.65			-3.34 (-4.67, -1.89)	1.86 (1.32, 2.36)		5.56 (3.00, 7.88)
Virola sebifera	0.94	2.21 (1.60, 2.74)		-0.68 (-1.23, -0.18)	-0.78 (-1.08, -0.45)	0.45 (0.19, 0.72)	
Vitex cooperi	0.99	0.58 (0.30, 0.87)			5.67 (4.76, 6.54)		

TABLE A1.1 (cont.). Resource parameters (in mm/month per unit resource) of seedling growth rate by species. 95% confidence intervals are denoted by parentheses for each resource parameter.

Species	**r^2**	**Irradiance (10e-2)**	**total N (10e-3)**	**PO_4^- (10e-3)**	**SBC**	**NO_3^- (10e-4)**	**NH_4^+ (10e-5)**
Vochysia ferruginea	0.79	3.70	0.06	0.55		-0.76	2.57
		(2.75, 4.59)	(0.03, 0.09)	(0.07, 1.01)		(-1.40, -0.12)	(1.16, 4.00)
Welfia regia	0.08	1.07	0.05				1.58

APPENDIX B

TABLE B1.1. Maximum magnitude of resource effects (in mm/month) on the final height of seedling growth by species. 95% confidence intervals are denoted by parentheses for each resource's magnitude of effect.

Species	**Irradiance (10e-1)**	**total N (10e-1)**	**PO_4^- (10e-1)**	**SBC (10e-1)**	**NO_3^- (10e-1)**	**NH_4^+ (10e-1)**
Abuta panamensis		0.21 (0.08, 0.32)				
Aegiphila sp.			0.43 (0.09, 0.78)	0.29 (0.02, 0.52)	0.22 (0.07, 0.37)	
Anaxagorea crassipetala	1.28 (1.03, 1.52)	0.25 (0.16, 0.34)		0.27 (0.13, 0.40)	-0.09 (-0.17, -0.01)	-0.18 (-0.29, -0.08)
Apeiba membranacea	1.82 (1.57, 2.06)		-2.11 (-3.02, -1.05)		1.31 (0.87, 1.68)	-0.18 (-0.28, -0.06)
Ardisia fimbrillifera		2.14 (1.21, 2.86)				
Ardisia nigropunctata						1.03 (0.85, 1.20
Ardisia sp.	0.22 (0.07, 0.33)					
Aristolochia sp.	4.33 (4.11, 4.56)					0.72 (0.22, 1.06)
Asterogyne martiana		0.65 (0.59, 0.69)				

TABLE B1.1 (cont.). Maximum magnitude of resource effects (in mm/month) on the final height of seedling growth by species. 95% confidence intervals are denoted by parentheses for each resource's magnitude of effect.

Species	**Irradiance (10e-1)**	**total N (10e-1)**	**PO_4^- (10e-1)**	**SBC (10e-1)**	**NO_3^- (10e-1)**	**NH_4^+ (10e-1)**
Bauhinia guianensis		0.10 (0.04, 0.18)		0.98 (0.30, 1.55)	0.69 (0.29, 1.09)	-0.85 (-1.17, -0.53)
Bignoniaceae morph Model 1	0.29 (0.24, 0.33)					
Bignoniaceae morph Model 2		0.22 (0.18, 0.26)				
Borojoa panamensis	-3.06 (-3.90, -2.25)			1.07 (0.25, 1.81)	2.38 (1.79, 2.99)	
Brosimum lactescens	0.44 (0.30, 0.58)	0.72 (0.65, 0.79)	-0.07 (-0.13, -0.009)	-1.19 (-1.44, -0.95)	-0.32 (-0.44, -0.22)	
Byrsonima arthropoda	-0.06 (-0.11, -0.007)		0.80 (0.71, 0.88)	0.57 (0.52, 0.63)		
Callichlamys latifolia	0.16 (0.13, 0.19)	0.12 (0.10, 0.15)				
Calyptrogyne ghiesbreghtiana		1.09 (0.86, 1.28)				
Capparis pittieri	0.14 (0.06, 0.20)			0.17 (0.07, 0.24)	0.25 (0.04, 0.42)	

TABLE B1.1 (cont.). Maximum magnitude of resource effects (in mm/month) on the final height of seedling growth by species. 95% confidence intervals are denoted by parentheses for each resource's magnitude of effect.

Species	**Irradiance (10e-1)**	**total N (10e-1)**	**PO_4^- (10e-1)**	**SBC (10e-1)**	**NO_3^- (10e-1)**	**NH_4^+ (10e-1)**
Casearia corymbosa		0.22				
		(0.12, 0.31)				
Cassipourea elliptica					0.72	
					(0.51, 0.88)	
Castilla elastica	1.39		0.58		-0.48	
	(1.11, 1.66)		(0.10, 1.03)		(-0.76, -0.17)	
Colubrina spinosa	0.21		0.44	1.01		
	(0.03, 0.38)		(0.31, 0.58)	(0.86, 1.17)		
Cordia alliodora			1.28			1.66
			(0.06, 2.50)			(0.12, 3.15)
Cordia bicolor	4.48	-3.64				
	(1.96, 6.93)	(-6.47, -1.20)				
Coussarea hondensis		0.60				
		(0.27, 0.82)				
Coussarea talamancana	-0.43	-0.21		1.27	0.58	-0.44
	(-0.71, -0.15)	(-0.37, -0.05)		(1.02, 1.51)	(0.32, 0.83)	(-0.55, -0.31)
Cryosophila warscewiczii	0.44	0.49	0.46	-0.67	-0.53	0.50
	(0.28, 0.57)	(0.21, 0.74)	(0.28, 0.60)	(-1.08, -0.26)	(-0.74, -0.31)	(0.19, 0.82)

TABLE B1.1 (cont.). Maximum magnitude of resource effects (in mm/month) on the final height of seedling growth by species. 95% confidence intervals are denoted by parentheses for each resource's magnitude of effect.

Species	**Irradiance (10e-1)**	**total N (10e-1)**	**PO_4^- (10e-1)**	**SBC (10e-1)**	**NO_3^- (10e-1)**	**NH_4^+ (10e-1)**
Dendropanax arboreus				1.87 (1.18, 2.50)		
Dicranostyles ampla	0.28 (0.19, 0.36)			0.15 (0.02, 0.27)		
Doliocarpus multiflorus	-0.31 (-0.58, -0.05)			1.57 (1.01, 2.10)	0.92 (0.57, 1.26)	-0.48 (-0.77, -0.19)
Eugenia sp.	2.70 (1.74, 3.71)	-1.42 (-2.27, -0.71)		-0.68 (-1.04, -0.29)		
Euterpe precatoria	1.10 (0.68, 1.45)			-0.82 (-1.26, -0.37)		0.72 (0.10, 1.26)
Faramea parvibractea				0.22 (0.09, 0.37)	0.66 (0.46, 0.85)	
Geonoma cuneata			0.53 (0.43, 0.64)		2.22 (1.62, 2.69)	-0.31 (-0.53, -0.12)
Geonoma cuneata (without outlier)			0.31 (0.13, 0.48)	0.52 (0.12, 0.92)	1.79 (1.33, 2.26)	-0.35 (-0.47, -0.23)
Goethalsia meiantha	1.15 (0.69, 1.67)					3.32 (1.16, 5.16)

TABLE B1.1 (cont.). Maximum magnitude of resource effects (in mm/month) on the final height of seedling growth by species. 95% confidence intervals are denoted by parentheses for each resource's magnitude of effect.

Species	**Irradiance (10e-1)**	**total N (10e-1)**	**PO_4^- (10e-1)**	**SBC (10e-1)**	**NO_3^- (10e-1)**	**NH_4^+ (10e-1)**
Guarea guidonia		3.51 (0.91, 3.93)				
Guatteria amplifolia	1.05 (0.77, 1.30)					0.32 (0.14, 0.47)
Gurania sp.		0.39 (0.17, 0.58)				
Hampea appendiculata	1.08 (0.99, 1.17)		-0.25 (-0.34, -0.15)	-0.37 (-0.45, -0.30)	0.14 (0.08, 0.19)	0.64 (0.54, 0.74)
Hernandia didymantha	0.32 (0.30, 0.35)				0.26 (0.23, 0.28)	
Herrania purpurea			0.43 (0.30, 0.52)			
Heteropterys laurifolia	1.21 (1.01, 1.43)	-0.38 (-0.58, -0.19)	1.61 (1.26, 1.95)			-0.42 (-0.57, -0.26)
Inga alba				0.20 (0.16, 0.24)		
Inga pezizifera	0.29 (0.20, 0.36)				0.14 (0.09, 0.19)	

TABLE B1.1 (cont.). Maximum magnitude of resource effects (in mm/month) on the final height of seedling growth by species. 95% confidence intervals are denoted by parentheses for each resource's magnitude of effect.

Species	**Irradiance (10e-1)**	**total N (10e-1)**	**PO_4^- (10e-1)**	**SBC (10e-1)**	**NO_3^- (10e-1)**	**NH_4^+ (10e-1)**
Inga thibaudiana				0.09 (0.05, 0.12)		0.22 (0.04, 0.38)
Iriatea deltoidea	0.50 (0.26, 0.67)					
Jubelina wilburii		1.67 (0.03, 2.76)		0.40 (0.27, 0.52)		
Lacmellea panamensis	0.31 (0.26, 0.36)					0.03 (0.002, 0.07)
Laetia procera		-3.18 (-3.89, -2.46)	4.03 (2.98, 4.88)			4.70 (3.63, 5.59)
Machaerium seemannii				0.28 (0.16, 0.39)		
Maripa nicaraguensis		-0.28 (-0.45, -0.10)	0.40 (0.30, 0.50)		0.73 (0.49, 0.94)	
Mendoncia tonduzii	0.61 (0.39, 0.82)	0.57 (0.03, 1.01)			0.53 (0.33, 0.72)	-0.34 (-0.62, -0.07)
Mendoncia sp.		6.11 (1.93, 10.00)		1.35 (0.11, 2.48)		

TABLE B1.1 (cont.). Maximum magnitude of resource effects (in mm/month) on the final height of seedling growth by species. 95% confidence intervals are denoted by parentheses for each resource's magnitude of effect.

Species	**Irradiance (10e-1)**	**total N (10e-1)**	**PO_4^- (10e-1)**	**SBC (10e-1)**	**NO_3^- (10e-1)**	**NH_4^+ (10e-1)**
Nectandra sp.		0.09 (0.03, 0.13)				
Neea elegans						1.07 (0.85, 1.26)
Neea psychotriodes		1.39 (1.17, 1.61)				
Neea sp.		0.89 (0.45, 1.27)				
Odontadenia macrantha	2.43 (0.59, 2.78)	-2.52 (-4.54, -0.51)	1.23 (0.31, 1.39)			
Paragonia pyramidata Model 1	0.48 (0.31, 0.63)					
Paragonia pyramidata Model 2				0.67 (0.43, 0.87)		
Paragonia pyramidata Model 3						0.51 (0.33, 0.66)
Parathesis trichogyne		0.19 (0.09, 0.29)	-0.67 (-0.94, -0.41)	1.26 (0.96, 1.53)		-0.56 (-0.74, -0.37)

TABLE B1.1 (cont.). Maximum magnitude of resource effects (in mm/month) on the final height of seedling growth by species. 95% confidence intervals are denoted by parentheses for each resource's magnitude of effect.

Species	**Irradiance (10e-1)**	**total N (10e-1)**	**PO_4^- (10e-1)**	**SBC (10e-1)**	**NO_3^- (10e-1)**	**NH_4^+ (10e-1)**
Paullinia sp. A	0.95 (0.94, 0.96)				-0.15 (-0.21, -0.10)	
Paullinia fibrigera		0.23 (0.16, 0.30)				
Pentaclethra macroloba	0.53 (0.41, 0.65)	0.38 (0.16, 0.55)	-0.33 (-0.50, -0.19)	0.43 (0.26, 0.59)	0.16 (0.10, 0.22)	-0.19 (-0.27, -0.11)
Perebea hispidula	1.16 (0.14, 1.54)	0.99 (0.31, 1.57)	-1.23 (-2.09, -0.31)		-0.83 (-1.53, -0.07)	1.20 (0.45, 1.98)
Pholidostachys pulchra	0.26 (0.12, 0.37)	3.43 (0.09, 5.05)	0.83 (0.57, 1.09)			
Pinzona coriacea		1.28 (1.10, 1.44)				
Plukenetia stipellata	4.20 (3.55, 5.45)		-5.17 (-8.37, -3.48)			4.81 (3.77, 5.86)
Pourouma bicolor	1.30 (1.23, 1.37)		0.21 (0.07, 0.35)	-0.96 (-1.16, -0.76)	0.37 (0.26, 0.48)	0.22 (0.14, 0.30)
Pourouma minor	0.41 (0.23, 0.55)			-0.44 (-0.87, -0.08)	0.40 (0.16, 0.67)	

TABLE B1.1 (cont.). Maximum magnitude of resource effects (in mm/month) on the final height of seedling growth by species. 95% confidence intervals are denoted by parentheses for each resource's magnitude of effect.

Species	**Irradiance (10e-1)**	**total N (10e-1)**	**PO_4^- (10e-1)**	**SBC (10e-1)**	**NO_3^- (10e-1)**	**NH_4^+ (10e-1)**
Prestoea decurrens	3.40 (2.88, 3.97)		3.45 (3.06, 3.83)	-5.96 (-6.94, -5.10)	-1.09 (-1.45, -0.71)	0.85 (0.22, 1.31)
Prestoea decurrens (without outlier)		4.69 (3.56, 5.69)				
Protium confusum Model 1	0.19 (0.008, 0.31)					
Protium confusum Model 2			0.34 (0.04, 0.64)			
Protium confusum Model 3				0.36 (0.06, 0.65)		
Protium panamense	0.59 (0.57, 0.60)	0.51 (0.48, 0.55)				
Psychotria panamensis	0.81 (0.46, 1.11)	1.46 (0.58, 2.07)			1.73 (0.81, 2.56)	
Psychotria sp.1	1.71 (0.46, 2.69)					
Psychotria sp.2		0.93 (0.90, 0.96)				

TABLE B1.1 (cont.). Maximum magnitude of resource effects (in mm/month) on the final height of seedling growth by species. 95% confidence intervals are denoted by parentheses for each resource's magnitude of effect.

Species	**Irradiance (10e-1)**	**total N (10e-1)**	**PO_4^- (10e-1)**	**SBC (10e-1)**	**NO_3^- (10e-1)**	**NH_4^+ (10e-1)**
Psychotria sp.3			1.22 (0.87, 1.52)	1.72 (0.81, 2.52)		-0.39 (-0.73, -0.08)
Pterocarpus rohrii				0.43 (0.25, 0.58)		
Randia genipoides	0.49 (0.36, 0.60)	1.11 (0.20, 1.89)			-0.29 (-0.37, -0.20)	
Rauvolfia purpurascens	-0.69 (-1.30, -0.09)	1.99 (1.28, 2.69)		1.39 (1.02, 1.77)	-0.77 (-1.08, -0.48)	
Richeria obovata			0.28 (0.12, 0.44)			
Rinorea deflexiflora	0.66 (0.59, 0.72)	-0.33 (-0.46, -0.20)		0.55 (0.35, 0.75)	0.33 (0.24, 0.41)	
Securidaca diversifolia		0.38 (0.25, 0.49)				
Serjania sp.		-0.39 (-0.76, -0.04)			0.89 (0.46, 1.32)	
Simarouba amara	0.69 (0.50, 0.89)		-0.65 (-0.86, -0.44)	1.70 (1.36, 2.03)		-0.38 (-0.67, -0.10)

TABLE B1.1 (cont.). Maximum magnitude of resource effects (in mm/month) on the final height of seedling growth by species. 95% confidence intervals are denoted by parentheses for each resource’s magnitude of effect.

Species	**Irradiance (10e-1)**	**total N (10e-1)**	**PO_4^- (10e-1)**	**SBC (10e-1)**	**NO_3^- (10e-1)**	**NH_4^+ (10e-1)**
Socratea exorrhiza	0.21 (0.15, 0.27)			-0.06 (-0.10, -0.02)		0.15 (0.10, 0.20)
Synechanthus warscewiczianus		1.01 (1.00, 1.02)				
Tapiria guianensis		0.17 (0.08, 0.23)				
Tetragastris panamensis	-0.39 (-0.53, -0.25)		-0.64 (-0.91, -0.38)	1.02 (0.77, 1.26)		0.24 (0.05, 0.43)
Trophis racemosa					0.55 (0.34, 0.74)	0.38 (0.03, 0.72)
Unonopsis pittieri		0.60 (0.12, 1.05)				
Virola koschnyi			-0.78 (-1.09, -0.44)	1.20 (0.85, 1.52)		0.43 (0.23, 0.60)
Virola sebifera	0.80 (0.58, 0.99)		-0.17 (-0.31, -0.04)	-0.30 (-0.41, -0.17)	0.13 (0.06, 0.21)	
Vitex cooperi	0.32 (0.17, 0.480			2.31 (1.94, 2.66)		

TABLE B1.1 (cont.). Maximum magnitude of resource effects (in mm/month) on the final height of seedling growth by species. 95% confidence intervals are denoted by parentheses for each resource's magnitude of effect.

Species	**Irradiance (10e-1)**	**total N (10e-1)**	**PO_4^- (10e-1)**	**SBC (10e-1)**	**NO_3^- (10e-1)**	**NH_4^+ (10e-1)**
Vochysia ferruginea	0.55 (0.41, 0.69)	0.23 (0.12, 0.34)	0.10 (0.01, 0.18)		-0.32 (-0.59, -0.05)	0.30 (0.14, 0.47)
Welfia regia	0.35 (0.30, 0.40)	0.19 (0.10, 0.26)				0.14 (0.08, 0.21)

APPENDIX C

TABLE C1.1. Correlations between species' magnitude of responses and initial seedling size.

Resource	**r**	**F**	**df**	***P***
Irradiance	-0.20	1.98	1, 49	0.17
SBC	-0.27	2.88	1, 37	0.10
PO_4^-	-0.14	0.53	1, 27	0.47
Total N	-0.26	3.37	1, 45	0.07
NH_4^+	-0.18	1.05	1, 32	0.31
NO_3^-	-0.45	7.53	1, 30	0.01