

Plant–soil associations in a lower montane tropical forest: physiological acclimation and herbivore-mediated responses to nitrogen addition

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Summary

1. Soil nutrients influence plant productivity and community composition in tropical forests. In lower montane tropical forests in western Panama, the distribution of understory palm species over a scale of 1–20 km correlates with differences in soil nitrogen (N). We hypothesized that soil N determines seedling performance in the forest understory, and, may therefore influence species distributions along the soil N gradient.

2. We explored the potential for N availability to generate species-habitat associations through species-specific differences in biomass allocation, photosynthetic capacity, N use-efficiency, and susceptibility to herbivory. Seedlings of nine palm species from two sub-families and four habitat types were transplanted into N-addition and control plots at a low N site. Growth, mortality, biomass allocation, photosynthesis, foliar N content and herbivory were measured over 21 months.

3. Foliar N increased for all species (15–68%) following N addition. Most species showed strong (20–200%) increases in photosynthetic rates with N addition except two species with marginal decreases in photosynthetic rates (5–15%). However, shifts in physiological traits did not increase relative growth rate or change in biomass allocation for any species or N treatment combination. Rather, increased leaf quality contributed to greater levels of herbivory in species associated with soils of intermediate and high inorganic N availability.

4. Thus, potential increases in overall growth with N addition were masked by herbivory, resulting in no apparent growth response with increased N. We suggest that for understory palms, and potentially other montane forest plants, distribution patterns are driven by a combination of physiological and herbivore-mediated responses to soil nutrient availability.

Key-words: Arecaceae, fertilization, growth trade-offs, habitat association, Panama, seedling transplant experiment

Introduction

Nitrogen (N) and phosphorus (P) can limit net primary productivity in terrestrial ecosystems (Vitousek & Howarth 1991; Lebauer & Treseder 2008). For tropical forests, P supply is often assumed to limit productivity on highly weathered soils in the lowlands (Walker & Syers 1976; Vitousek & Sanford 1986), whereas at higher elevations, where climate is similar to temperate forests and soils may be pedogenically young, evidence for nutrient limitation is varied (Tanner *et al.* 1990; Vitousek & Farrington 1997; Tanner, Vitousek

& Cuevas 1998; Adamek, Corre & Holscher 2009). Narrow N : P ratios in leaves from tropical montane forest trees suggest N limitation (Tanner, Vitousek & Cuevas 1998; Soethe, Lehmann & Engels 2008; Wilcke *et al.* 2008), whereas fertilization studies in montane forests of Hawaii, Jamaica and Venezuela indicate that tree growth is limited by either N or N and P together (reviewed by Tanner, Vitousek & Cuevas 1998). No experiments have examined N limitation of seedling establishment in tropical montane forests.

Habitat specialization with respect to soil nutrients is commonly documented, but rarely examined experimentally. Recent experimental studies in lowland tropical forests have suggested that three trade-offs influence habitat specialization

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(Fine, Mesones & Coley 2004; Palmiotto *et al.* 2004; Baltzer *et al.* 2005). First, habitat associations may be determined by a trade-off between investment in aboveground biomass to achieve a higher relative growth rate and belowground biomass to acquire limiting nutrients (Chapin 1980; Aerts, Boot & van der Aart 1991; Wilson & Tilman 1993; Aerts & Chapin 2000; Palmiotto *et al.* 2004). Secondly, habitat associations may be determined by a trade-off between growth and the efficiency with which limiting soil resources are used (Chapin 1980; Chapin, Autumn & Pugnaire 1993; Aerts & Chapin 2000; Baltzer *et al.* 2005). At sites where nutrients are limiting, resource-use efficiency (RUE) can be increased by increasing leaf longevity and decreasing foliar nutrient concentration. Collectively, these traits enhance nutrient use efficiency by increasing carbon gain per unit of nutrient uptake (Aerts & Chapin 2000). Thirdly, habitat associations may arise from trade-offs between growth and allocation to defense against herbivores. The level of investment in anti-herbivore defense should increase as plant growth rates and resources available to replace leaf tissue lost to herbivory decrease (Coley, Bryant & Chapin 1985). Thus, different sets of trade-offs between growth and allocation to resource acquisition, use, or defense may determine species distributions along soil gradients.

We used an experimental approach to explore mechanisms underlying observed habitat partitioning of plant species across a soil fertility gradient in a lower montane forest in western Panama. High landscape-level diversity in these forests is associated with variability in soil nutrients. Total inorganic N availability ranges from <1 to 8 $\mu\text{g N cm}^{-3}$ within the Fortuna Forest Reserve and surrounding protected areas (Andersen, Turner & Dalling 2010). Multivariate analyses of soil nutrients and understory palm communities identified three palm–soil associations: (i) species associated with soils developed on rhyolite, characterized by an organic surface horizon and low nutrient availability; (ii) species associated with soils developed on andesite, characterized by mineral soils of intermediate nutrient availability; and (iii) species associated with soils developed on porphyritic dacite, characterized by an organic surface horizon and high nutrient availability (Andersen, Turner & Dalling 2010). Variation in understory palm community composition among sites was most strongly correlated with differences in inorganic N, although experimental tests are necessary to link species distribution patterns to individual nutrients and to provide support for mechanisms underlying palm–soil associations. Note that identification of the geology of the third group of soils as developed on dacite replaces the previous description (granodiorite; Andersen, Turner & Dalling 2010) following more detailed geological investigation of the site.

Palms are a major component of the understory in tropical forests, modifying microsite conditions for seedling establishment (Farris-Lopez *et al.* 2004; Wang & Augspurger 2004). Therefore, information on palm ecology and processes influencing palm species distributions has direct implications for understanding regeneration within tropical forests. Both *Chamaedorea* (tribe Chamaedoreae) and Geonomoid

(Geonomateae) palms of the Arecoide subfamily are common elements of the understory of montane forests, with most species reaching < 5 m in height at reproductive maturity. Chamaedoroid and Geonomoid palms share similar vegetative morphologies and habitat requirements, but are estimated to have diverged 70 million years ago (Cuenca, Asmussen-Lange & Borchsenius 2008). Given the ecological similarities between the groups, we examined whether there was a phylogenetic component to seedling response to soil N availability.

To test whether soil N availability determines palm species distribution patterns, we compared the response to N addition of palms from the three species–soil groups and from an additional group of generalist species that showed no habitat preference. We conducted a field transplant experiment in the forest understory to address the following hypotheses: (i) if habitat specialization arises directly from differences in the biomass allocated to acquire soil N, then species with greater allocation to aboveground biomass will have a growth advantage with N addition; (ii) if habitat specialization is determined by nutrient use efficiency (NUE), then species with lower NUE or higher foliar N concentrations and higher photosynthetic capacity will achieve greater growth with N addition; and (iii) if habitat specialization is mediated by herbivores through a trade-off between allocation to growth versus defense, then species with the strongest growth response to N addition will also experience the highest herbivory rates and/or decreased growth.

Materials and methods

SITE DESCRIPTION

To examine the effect of soil N availability on seedling performance, we conducted a field transplant experiment nested within a larger N fertilization experiment (the NITROF project; Koehler *et al.* 2009; Adamek, Corre & Holscher 2009; Corre *et al.* 2010, in press). The study area is located within the Quebrada Honda watershed (8°45'40"N, 82°14'22"W; elevation 1200–1300 m a.s.l.) with soil developed on rhyolitic tuff at the low end of the N gradient (based on total inorganic N) found in Fortuna Reserve (Chiriqui province, Republic of Panama; Table 1). The soil is derived from volcanic ash

Table 1. Site environmental characteristics measured in May 2007 from control and nitrogen addition plots (starting in January 2006)

Environmental variable	Control	N addition
pH _{water}	3.97 ± 0.10	3.88 ± 0.11
NH ₄ ($\mu\text{g N cm}^{-3}$)	2.28 ± 0.19	2.66 ± 0.53
NO ₃ ($\mu\text{g N cm}^{-3}$)	0.51 ± 0.13	1.01 ± 0.26
Al ($\mu\text{g Al cm}^{-3}$)	144 ± 11.1	129 ± 22.5
Ca ($\mu\text{g Ca cm}^{-3}$)	71.4 ± 11.9	101 ± 22.0
K ($\mu\text{g K cm}^{-3}$)	19.0 ± 1.49	28.1 ± 6.79
Mg ($\mu\text{g Mg cm}^{-3}$)	23.4 ± 3.51	36.9 ± 13.1
P ($\mu\text{g P cm}^{-3}$)	0.94 ± 0.14	1.74 ± 0.57
Zn ($\mu\text{g Zn cm}^{-3}$)	0.43 ± 0.07	0.61 ± 0.18
Red : Far red ratio	0.23 ± 0.03	0.32 ± 0.02
Canopy openness (%)	5.37 ± 0.54	6.55 ± 0.54

Values represent mean ($n = 4$) with standard errors.

deposits, has a sandy loam texture, and is classified as Alic Hapludand (Koehler *et al.* 2009). Soils are continually moist, with an average annual rainfall for 2007 and 2008 of 7800 mm year⁻¹ (Andersen, Turner & Dalling 2010) and a mean annual temperature of 19 °C (Cavelier, Solis & Jaramillo 1996). The area is classified as lower montane rain forest in the Holdridge life zone system and consists of mature forest with a closed canopy with a mean height of 20 m (Adamek, Corre & Holscher 2009). *Oreomunnea mexicana* (Juglandaceae), *Vochysia guatemalensis* (Vochysiaceae), *Colpothrinax aphanopetala* (Arecaceae) and *Podocarpus oleifolius* (Podocarpaceae) are common canopy species within the study area (Fig. 1).

FERTILIZATION EXPERIMENT

The fertilization experiment consisted of four 40 × 40 m paired control and N addition (N+) plots with 40 m separating paired plots and 100 m separating pairs of plots. Nitrogen addition plots received 125 kg urea-N ha⁻¹ year⁻¹ applied in four intervals per year beginning in January 2006. Gross rates of soil N cycling and microbial biomass were initially low and increased in the first year of N addition (Corre *et al.* 2010, in press). Annual fine litterfall also increased during the 2 years of N addition compared to the control (Adamek, Corre & Holscher 2009). These responses to N addition indicate that canopy trees at the study site were N-limited.

SEEDLING TRANSPLANT EXPERIMENT

We selected nine understory palm species based on their distribution patterns at Fortuna, including at least one *Chamaedorea* and one Geonomoid species belonging to each of three palm–soil association groups as well as a fourth group of generalists that includes species found across the soil nutrient gradient (Table 2). Seeds were collected from the Fortuna Reserve in May 2005 and seed mass was recorded on a subset of 10 seeds per species. Seeds were germinated in a growing house at the Smithsonian Tropical Research Institute Fortuna Station in a 50 : 50 mix of washed sand and soil. The soil was collected from forests at the NITROF site.

In January 2006, we transplanted seedlings into common gardens (75 × 75 cm) in the forest understory (closed canopy) within each of four paired control and N addition plots prior to the first fertilization. Hence, the experimental design was a split plot with four replicate blocks, with N treatment as the whole-plot and species as the subplot.



Fig. 1. Photograph of the field site in the Honda watershed.

Each garden consisted of two seedlings of each of nine species planted 25 cm apart to avoid shading and belowground competition. Seedlings had one fully expanded leaf at the time of transplantation and showed no sign of transplant stress and overall mortality rates were low throughout the experiment.

Seedlings were monitored for survival, leaf number, leaf area and leaf damage in bimonthly censuses beginning in February 2006. After 20 months, we measured maximum photosynthetic rates at 400 µmol m⁻² s⁻¹ on a subset of individuals for each species × N treatment combination. The most recently expanded fully mature leaf was chosen for physiological and foliar nutrient measurements. Photosynthetic rates (A_{max}), stomatal conductance, and transpiration rates were assessed in the field using a portable gas exchange system (LI-6400; LiCor, Lincoln, NE, USA). Instantaneous water use efficiency (WUE) was calculated from A_{max} and transpiration. Foliar N concentration was determined by dry combustion using an elemental analyzer (Costech Analytical Technologies Inc, Valencia, CA, USA). Foliar P concentration was determined by ignition at 550 °C and extraction in 1 M H₂SO₄, with P detected by molybdate colorimetry using a flow injection analyzer (Lachat QuikChem 8500; Hach Ltd., Loveland, CO, USA). Photosynthetic N use efficiency (PNUE) was calculated from A_{max} and foliar N concentrations. Photosynthetic P use efficiency (PPUE) was calculated from A_{max} and foliar P concentrations. Seedlings were harvested to assess relative growth rates, biomass allocation, and foliar nutrient contents. Seedlings were separated into root, shoot, and leaf components to weigh and measure leaf toughness and leaf area prior to drying. Leaves were digitally scanned to quantify leaf area and herbivory damage using ImageJ software (Rasband 2008). Leaf toughness was measured as fracture toughness using a 516-1000MRP push-pull gauge ‘penetrometer’ (Chatillon/Amtek, Largo, FL, USA). The following growth parameters were calculated following Hunt (1982): relative growth rate (RGR), net assimilation rate (NAR), leaf area ratio (LAR), specific leaf area (SLA), root mass ratio (RMR), and leaf mass ratio (LMR).

We characterized the environmental conditions of paired common gardens in May 2007. Hemispherical photographs were taken at the center of each experimental garden to measure canopy openness. Red : far-red ratios were taken above each seedling. Soil chemical properties (extractable NH₄, NO₃, P, Ca, K, Mg, Al, Fe) were measured in May 2007. Phosphorus and cations were extracted in Mehlich III solution and determined by inductively coupled plasma (ICP) optical-emission spectrometry on an Optima 2100 spectrometer (Perkin Elmer Inc., Waltham, MA, USA). Nitrogen was extracted in 2 M KCl directly in the field and analysed using continuous flow injection colorimetry on a Lachat QuikChem 8500 (Hach Company, Loveland, CO, USA).

DATA ANALYSIS

Growth, biomass allocation, physiological parameters and herbivory were analysed using analysis of variance with N treatment, palm–soil association groups, genera and species as fixed effects, and the blocking structure as a random effect. The blocking structure consisted of N addition treatment nested within four blocks. We tested the main effects and interactions using linear mixed-effect models and conducted post-hoc tests for significant effects after Bonferroni corrections (Proc mixed; SAS Institute, Cary, NC, USA). Initial biomass was used as a covariate in the ANCOVA for RGR. Values for RGR and biomass were log transformed and values of proportion leaf area missing were arcsine square root transformed prior to analyses to meet assumptions for ANOVA. Leaf area damage was analysed in two parts to control for non-normality. First, we tested for differences in

Table 2. List of species for the species–soil association groups used in the study. Nomenclature is based on Henderson, Galeano & Bernal (1995), Hodel (1997) and Henderson (2005). Soil associations were based on Andersen, Turner & Dalling (2010). Nutrient (Mehlich III extractable base cations and phosphorus), and inorganic nitrogen availability (2 M KCl extractable) increases from rhyolitic to andesitic to dacitic soils (Andersen, Turner & Dalling 2010)

Genus	Species	Code	Soil association	Growth form
Chamaedoreaceae				
<i>Chamaedorea</i>	<i>pinnatifrons</i> (Jacq.) Oerst.	CPI	Generalist	Arborescent
<i>Chamaedorea</i>	<i>recurvata</i> Hodel	CRE	Rhyolitic	Arborescent
<i>Chamaedorea</i>	<i>deckeriana</i> (Klotzsch) Hemsl.	CD	Andesitic	Arborescent
<i>Chamaedorea</i>	<i>tepejilote</i> Liebm.	CT	Andesitic	Arborescent
<i>Chamaedorea</i>	<i>woodsoniana</i> L. H. Bailey	CW	Dacitic	Arborescent
Geonomateae				
<i>Geonoma</i>	<i>cuneata</i> var. <i>cuneata</i> H. Wendl. ex Spruce	GC	Generalist	Decumbent
<i>Geonoma</i>	<i>cuneata</i> var. <i>gracilis</i> (H. Wendl. ex Spruce) Skov	GG	Rhyolitic	Arborescent
<i>Calyptrogyne</i>	<i>panamensis</i> var. <i>occidentalis</i> Henderson	CAG	Andesitic	Decumbent
<i>Geonoma</i>	<i>jussieuana</i> Mart.	GJ	Dacitic	Arborescent

the frequency of plants that encountered herbivory (incidence; 0 = no herbivory, 1 = herbivory) among treatments using proc glimmix (SAS Institute), with a binary distribution and a logit link function. Second, we tested for differences in the mean proportion of leaf area missing for plants with an incidence of herbivory (incidence = 1) among treatments using the lme function with a power variance function structure to fit the model (nlme package; Pinheiro & Bates 2008) in R (R Core Development Team 2008). A variance function was used to correct for heteroscedasticity among the within group errors (Pinheiro & Bates 2000).

To examine bivariate relationships we use standardized major axis (SMA), a type II regression technique (Warton *et al.* 2006). SMA regression techniques are more appropriate when examining variables with measurement error than standard linear regression (Sokal & Rolf 1995). Differences between slopes for the N addition treatment and control were tested. If a common slope was detected, differences in intercepts and shifts along the common axis were also tested following routines and procedures in the 'smatr' package available in the R statistical environment.

Results

RELATIVE GROWTH RATES

The understory palms in this study had inherently slow growth rates ranging from <0.50 to $2.45 \text{ mg g}^{-1} \text{ day}^{-1}$ (Table 3). Nitrogen addition did not affect on growth (Fig. 2a), although growth rates differed among species–soil associations ($F_{3,59} = 8.47$, $P < 0.0001$). Species associated with N-rich soils (andesitic and dacitic) had significantly lower growth rates than species associated with rhyolitic, N-poor soils (Fig. 2a). The RGR of generalist species did not differ from any of the species–soil association groups. The rhyolitic and generalist species and one andesitic species, *Calyptrogyne panamensis*, naturally occur at the study site, whereas the remaining andesitic and dacitic species are not found in the forests immediately surrounding the transplant experiment.

Species level differences in RGR were detectable even after controlling for differences in initial biomass ($F_{8,96} = 7.71$,

$P < 0.0001$). The small *Geonoma cuneata* var. *gracilis*, associated with N-poor soils achieved the highest RGR, whereas the large *Chamaedorea tepejilote* and *C. woodsoniana*, associated with N-rich soils, had the lowest RGR. Relative growth rate was negatively correlated with seed mass and initial biomass (Pearson's $r = -0.35$, $P < 0.0001$ and $r = -0.40$, $P < 0.0001$). Overall survival during the experiment was generally high, ranging from 80% to 100% survivorship, except for the two species from high nutrient soil, which had survival rates of 69% (*Chamaedorea woodsoniana*) and 75% (*Geonoma jussieuana*), distributed across both treatments.

BIOMASS ALLOCATION

Nitrogen addition did not affect on total biomass or biomass allocation (Table 3). However, several morphological traits varied with species–soil association. Rhyolitic species had lower RMR than species from higher nutrient soils (andesitic and dacitic), whereas generalist species did not differ from any of the species–soil groups ($F_{1,59} = 3.84$, $P < 0.05$). Dacitic species had lower LMR than rhyolitic and generalist species, whereas andesitic species did not differ from any of the species–soil groups ($F_{1,59} = 3.06$, $P < 0.05$). Andesitic species had significantly higher SLA and rhyolitic (low nutrient) species had significantly lower SLA than dacitic and generalist species ($F_{3,51} = 78.36$, $P < 0.0001$). There were no differences in LAR among the species–soil groups.

There were species level differences in specific leaf area, SLA ($F_{8,93.3} = 13.82$, $P < 0.0001$), and leaf area ratio, LAR ($F_{8,94.2} = 4.81$, $P < 0.0001$). *Chamaedorea tepejilote*, with large, thin, papery leaves, had the highest SLA ($450 \text{ cm}^2 \text{ g}^{-1}$), whereas *C. recurvata*, with very thick, almost succulent leaves, had the lowest SLA ($280 \text{ cm}^2 \text{ g}^{-1}$). For most species, root biomass accounted for about 20% of the total plant biomass and did not significantly differ significantly among species. *Chamaedorea tepejilote* had the highest (0.24) and *Geonoma cuneata* var. *gracilis* had the lowest (0.15) root mass ratios (Table 3). However, species did differ in allocation to leaf

Table 3. Species values for total biomass (RMR), root mass ratio (LMR), leaf mass ratio (LMR), relative growth rate (RGR), net assimilation rate (NAR), leaf area ratio (LAR), specific leaf area (SLA), incidence of herbivory, leaf area damaged, foliar nitrogen, area- and mass-based photosynthetic rates. Species are grouped by soil association (Table 5.2)

Species*	n	Biomass (g)	RMR	LMR	RGR (mg g ⁻¹ day ⁻¹)	NAR (mg cm ² day ⁻¹)	LAR (cm ² g ⁻¹)	SLA (cm ² g ⁻¹)	Incidence (%)	Leaf area damage (%)	Foliar N (%)	A _{max} (μmol m ⁻² s ⁻¹)	A _{max} (nmol g ⁻¹ s ⁻¹)
Generalist													
CPI	14	0.24 ^{bcd} (0.03)	0.19 ^{abc} (0.03)	0.39 ^{abcd} (0.04)	1.91 ^{ab} (0.22)	5.04 ^{ab} (0.72)	1.50 ^{ab} (0.11)	355 ^{bc} (12.9)	71.4 (12.5)	16.0 (7.72)	2.23 ^{abc} (0.08)	1.27 (0.26)	52.7 (13.6)
GCU	14	0.17 ^d (0.03)	0.19 ^{abc} (0.02)	0.48 ^{ab} (0.02)	1.53 ^{abc} (0.28)	4.05 ^{ab} (0.71)	1.58 ^{ab} (0.07)	329 ^{cd} (6.4)	71.4 (12.5)	11.2 (4.49)	2.33 ^{abc} (0.17)	1.18 (0.20)	40.7 (7.6)
Rhyolitic													
CRE	15	0.35 ^b (0.02)	0.20 ^{abc} (0.01)	0.42 ^{abc} (0.01)	1.32 ^{bcd} (0.11)	4.55 ^{ab} (0.43)	1.19 ^{bc} (0.06)	280 ^d (6.7)	66.7 (12.6)	12.8 (4.40)	2.63 ^a (0.15)	1.61 (0.19)	48.9 (6.5)
GG	13	0.15 ^{cd} (0.01)	0.15 ^c (0.01)	0.49 ^{ab} (0.02)	2.45 ^b (0.13)	6.36 ^a (0.42)	1.50 ^{ab} (0.09)	306 ^{cd} (9.8)	76.9 (12.2)	9.2 (3.67)	2.03 ^{bc} (0.15)	1.28 (0.19)	41.8 (6.9)
Andesitic													
CD	13	0.28 ^{bc} (0.03)	0.21 ^{abc} (0.02)	0.36 ^{bcd} (0.04)	1.43 ^{abc} (0.23)	3.43 ^{abc} (0.47)	1.55 ^{ab} (0.11)	401 ^{ab} (12.4)	92.3 (7.7)	26.8 (9.33)	2.50 ^{ab} (0.19)	1.17 (0.17)	48.2 (7.3)
CT	13	0.40 ^b (0.05)	0.24 ^b (0.03)	0.27 ^d (0.02)	0.41 ^d (0.25)	1.55 ^c (0.56)	1.30 ^{abc} (0.10)	449 ^a (8.9)	92.3 (7.7)	36.6 (9.55)	2.56 ^{abc} (0.40)	1.22 (0.32)	57.0 (15.4)
CAG	16	0.25 ^{bcd} (0.03)	0.20 ^b (0.02)	0.50 ^a (0.03)	1.84 ^{ab} (0.24)	5.08 ^{ab} (0.64)	1.61 ^a (0.09)	328 ^{cd} (11.4)	68.8 (12.0)	11.8 (5.53)	1.91 ^c (0.11)	1.33 (0.20)	45.1 (5.1)
Dacitic													
CW	11	1.24 ^a (0.14)	0.18 ^{abc} (0.02)	0.33 ^{cd} (0.04)	0.71 ^{cd} (0.21)	3.13 ^{bc} (0.73)	1.02 ^c (0.19)	312 ^{cd} (43.7)	90.9 (9.1)	24.9 (8.68)	2.95 ^a (0.23)	1.98 (0.30)	62.1 (8.7)
GJ	12	0.11 ^d (0.01)	0.23 ^{ab} (0.02)	0.44 ^{abc} (0.02)	1.02 ^{bcd} (0.18)	3.11 ^{bc} (0.53)	1.51 ^{ab} (0.06)	345 ^{bc} (6.1)	83.3 (11.2)	16.4 (5.76)	2.59 ^{ab} (0.17)	1.66 (0.25)	61.4 (11.5)

Mean (± standard error) followed by different letters indicate significantly differences among species (linear mixed-effects models with Bonferroni corrections at $P \leq 0.05$).

*Species abbreviations as listed in Table 2.

biomass ($F_{8,100} = 7.93$, $P < 0.0001$): *Calyptrogyne panamensis* allocated 50% of its biomass to leaves, whereas *Chamaedorea tepejilote* allocated only 24% of its biomass to leaves. Leaf mass ratio was positively correlated with RGR ($r = 0.57$, $P < 0.0001$). Seed mass was negatively correlated with both LMR ($r = -0.33$, $P < 0.0005$) and LAR ($r = -0.42$, $P < 0.0001$) for log-transformed data, but was not related to RMR or SLA.

PHYSIOLOGICAL RESPONSES

Foliar nutrients

In contrast to biomass allocation, foliar N content responded strongly to N addition and differed among species–soil associations, being 30% higher in the N addition treatment compared to the control ($F_{1,3} = 14.61$, $P < 0.05$). Dacitic species had significantly higher foliar N content than species from the other soil groups ($F_{3,51} = 4.40$, $P < 0.01$; Fig. 2b). Foliar N content ranged from 1.7% in *G. cuneata* var. *gracilis* to 2.5% in *G. jussieumana* in the control treatment and from 2.1% in *Calyptrogyne panamensis* to 3.4% in *C. woodsoniana* in the N addition treatment.

Foliar N was linked to several important performance variables (Fig. 3). Foliar N was related to a decrease in RGR across both N addition and control treatments (Fig. 3a), with a common slope of -1.80 (95% CI: -2.50 to -1.31). However, seedlings in the N addition treatment had a higher RGR at a given foliar N content compared to species in the control treatment ($P < 0.0001$). Three species (*Chamaedorea tepejilote* in N addition and control; *C. woodsoniana* in control; *Geonoma juessiana* in N addition) had a mean of 20–50% leaf area damage. As a result, these values fell well below the common regression line between RGR and foliar N and were not included in the analysis. Leaf damage increased with increasing foliar N content (Fig. 3b) in both N addition and control treatment along a common slope of 4.84 (95% CI: 2.78–8.10). However, there was a shift along the common axis with higher foliar N and leaf area damage in seedlings in the N addition treatment compared to the control ($P < 0.01$). Mass-based photosynthesis increased with increasing foliar N content along a common slope of 1.85 (95% CI: 1.08–3.11). There was a shift along the common axis with higher photosynthetic rates and foliar N in the N addition treatment compared to the control treatment (Fig. 3c).

Foliar P content ranged from 0.073% in *G. gracilis* in the control treatment to 0.169% in *C. tepejilote* in the control treatment. There were no differences in foliar P content with N addition treatment. However, there were significant differences in foliar P at both the species–soil association ($F_{3,54} = 7.54$, $P < 0.0001$) and the species levels ($F_{8,49} = 7.52$, $P < 0.0001$). Foliar P increased with foliar N along a common slope of 0.94 (95% CI: 0.59–1.52) for both the control and N addition treatments (Fig. 4). However, foliar P content was lower at a given foliar N content in the N addition treatment compared to the control ($P < 0.01$).

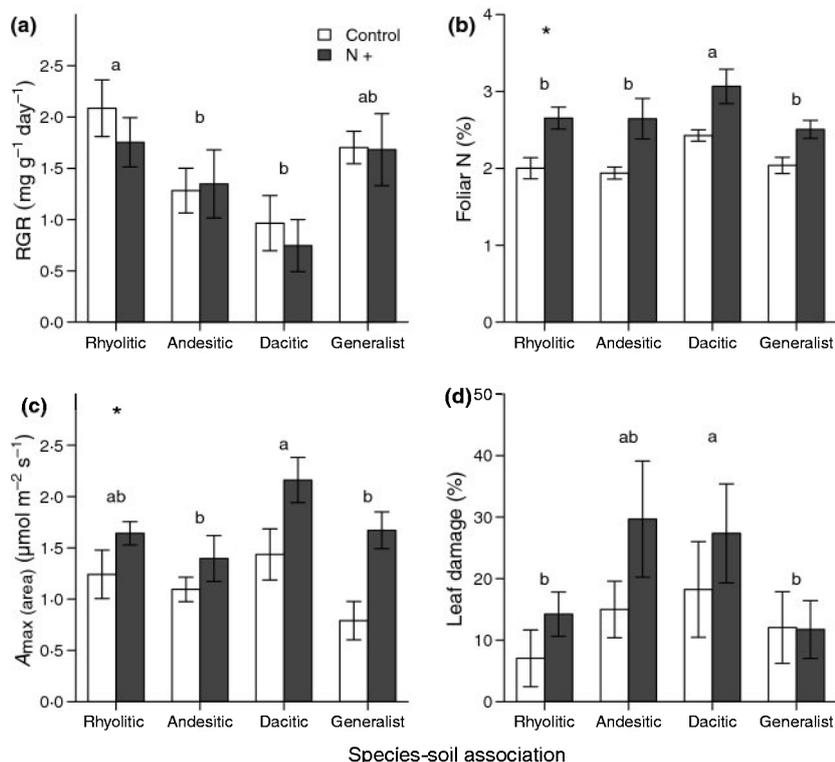


Fig. 2. Mean \pm standard error bar (a) relative growth rates (RGR), (b) foliar nitrogen content, (c) area-based maximum photosynthetic rate ($A_{\max(\text{area})}$), and (d) leaf area damage of the four species-soil association groups. Different letters indicate significant differences among species groups (linear mixed-effect model with Bonferroni corrections at $P < 0.05$). Note: *Variable with a significant difference between control and nitrogen addition plots.

Gas exchange

Understory palm photosynthetic rates were low overall ($< 2 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), but there were strong effects of N addition on gas exchange rates. Both area- and mass-based maximum photosynthetic rates were higher in N addition than control plots ($F_{1,3} = 33.0$, $P < 0.05$; and $F_{1,3} = 29.92$, $P < 0.05$ respectively). Mean area-based maximum photosynthetic rates ($A_{\max(\text{area})}$) increased from $1.12 \mu\text{mol CO}_2 \text{ cm}^{-2} \text{ s}^{-1}$ in the control plants to $1.63 \mu\text{mol CO}_2 \text{ cm}^{-2} \text{ s}^{-1}$ in plants receiving N addition. Dacitic species had higher area-based photosynthetic rates than species with other soil associations ($F_{3,58.7} = 3.38$, $P < 0.05$; Fig. 2c). There were also significant effects of species-soil group ($F_{3,48} = 7.10$, $P < 0.0001$) and interaction between N addition treatment and species-soil group ($F_{3,48} = 2.80$, $P < 0.05$) on mass-based photosynthetic rates, with dacitic species showing a greater response to N addition compared to andesitic and rhyolitic species and generalist species showing an intermediate response. Individual species did not differ in photosynthetic rates (Table 3). There were significant effects of N addition treatment ($F_{1,3} = 58.36$, $P < 0.01$) and an interaction between N addition treatment and species-soil group ($F_{3,48} = 4.73$, $P < 0.01$) on stomatal conductance, with generalist species showing a greater increase in conductance rates than species with soil associations. Among species, gas exchange was correlated with foliar N content on both a mass and area basis (mass-based N Pearson's correlation coefficient $r = 0.66$, $P < 0.005$; area-based N $r = 0.70$, $P < 0.005$). Despite increases in photosynthetic capacity and

foliar N concentrations, there were no differences in foliar respiration rates, WUE, PNUE, or PPUE among any of the treatment groups.

PLANT-HERBIVORE INTERACTIONS

The incidence of herbivory was similar between the N treatments with 72% of the plants in the control treatment and 85% of the plants in the N addition treatment having some level of herbivory. Andesitic and dacitic species had higher overall leaf area damage, 29 and 24% respectively, compared to generalists and species from N-poor soils with 19 and 16% respectively ($F_{1,51} = 2.76$, $P = 0.05$; Fig. 2d). Species differed in leaf area damage ($F_{8,55} = 7.16$, $P < 0.0001$), ranging from an average of 12% in *G. cuneata* var. *gracilis* to 40% in *C. tepejilote* across all treatments. Mean leaf area damage was 22% in the N addition treatment compared to 15% in the control treatment ($F_{1,3} = 14.3$, $P < 0.05$; arcsine square root data). There was a significant interaction between species and N addition on leaf area damage ($F_{8,55} = 2.83$, $P < 0.05$). *Geonoma jussieana*, a species associated with N-rich soils, suffered significantly more herbivory damage in the N addition treatment ($F_{1,3} = 10.53$, $P < 0.05$), whereas other species did not show significant differences between the N treatments.

Differences in leaf damage were not related to leaf toughness and there were no differences in leaf toughness between N treatments or among species-soil groups. However, species differed in leaf toughness ($F_{8,50} = 5.04$, $P < 0.001$) ranging from 30 to 188 g of force to penetrate a 3 mm rod through

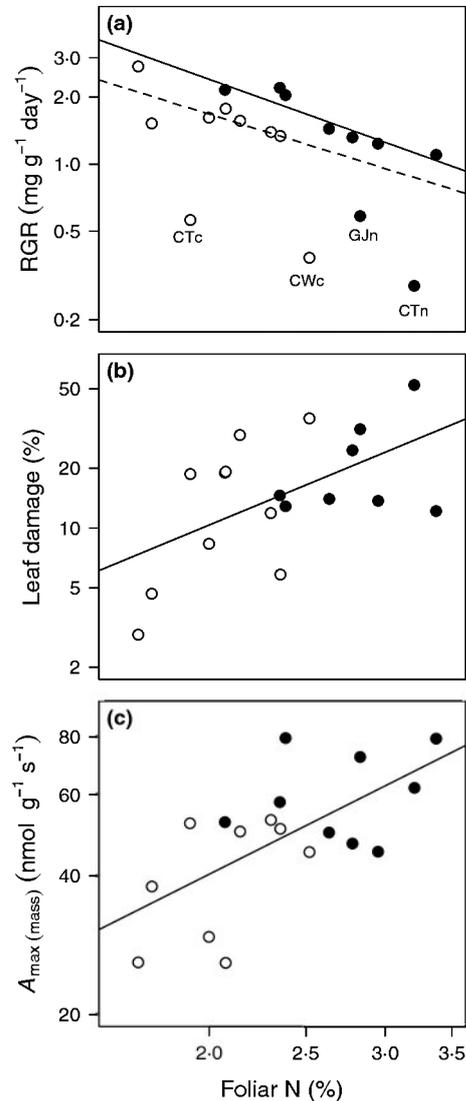


Fig. 3. The effect of nitrogen fertilization on the relationship between foliar nitrogen (%) and (a) relative growth rate (RGR), (b) leaf damage and (c) mass-based photosynthetic rate ($A_{\max(\text{mass})}$) for nine species of understory palm. Symbols represent species mean for the nitrogen addition (filled) and control (open) treatments. Note that the two very low RGR values in both control and nitrogen addition treatments are not included in the analysis.

the leaf lamina. Furthermore, leaf toughness increased with increasing foliar N content along a common slope of 4.22 (95% CI: 2.76–6.46) with higher foliar N content at a given leaf toughness for the plants in the N addition treatments ($P < 0.001$).

Differences in leaf area damage may have masked the anticipated increase in RGR with N addition. Relative growth rate decreased with increased leaf area damage along a common slope of -0.85 (95% CI: -0.58 to -1.26) for both the control and N addition treatments (Fig. 5). There were no differences in elevation between the N treatments or shifts along the common axis. Thus, the higher leaf area damage in the N treatment resulted in RGR values similar to those in the control.

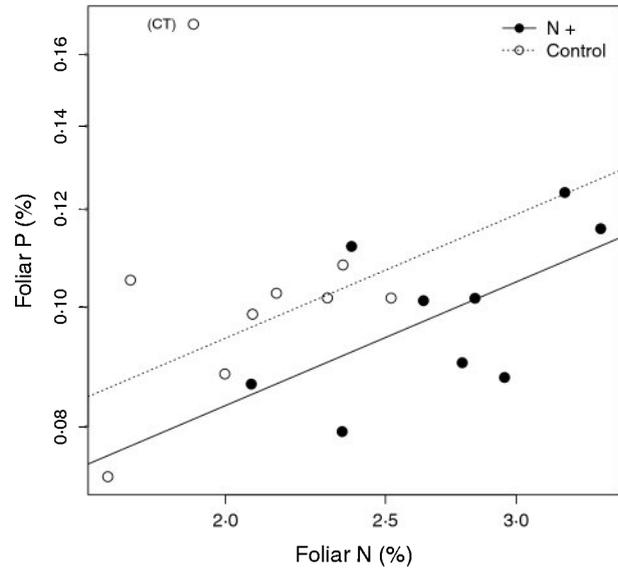


Fig. 4. Relationship between foliar nitrogen and phosphorus in seedlings growing in control (open symbol) and nitrogen addition (filled symbol) treatments in a field experiment. Symbols represent species means per treatment. The lines represent the SMA regressions between foliar phosphorus and foliar nitrogen for seedlings in the nitrogen addition (solid line) and control (dashed line) treatments. Foliar phosphorus increased with foliar nitrogen along a common slope of 0.94 (95% CI: 0.59–1.52), with a lower foliar phosphorus at a given foliar nitrogen content for the seedlings in nitrogen addition treatment ($P < 0.01$). Note that the outlier in the control treatment is *Chamaedorea tepejilote*, indicated by CT, and is not included in the regression analysis.

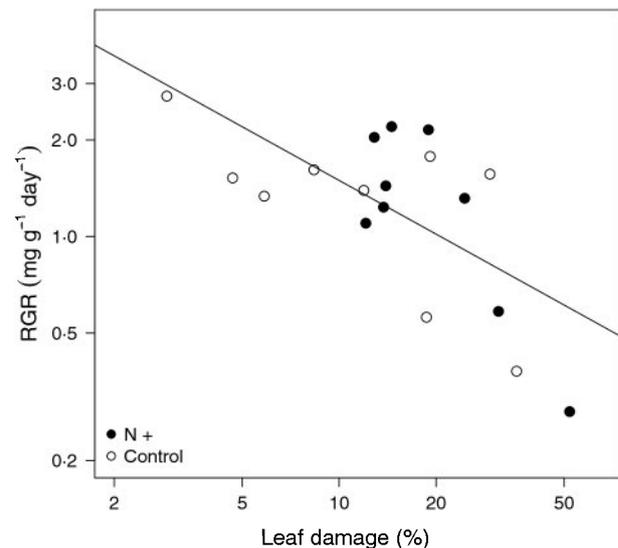


Fig. 5. The relationship between leaf area damage (%) and relative growth rate (RGR) for nine species of understory palm growing in nitrogen addition (filled) and control (open) treatments.

PHYLOGENETIC COMPARISONS

Despite morphological and ecological similarities, we detected several differences between *Chamaedorea* and *Geonomoid* palms. *Chamaedorea* species had significantly lower

growth rates than Geonomoid species ($F_{1,61} = 46.46$, $P < 0.0001$) and significantly lower leaf mass ratios ($F_{1,61} = 19.43$, $P < 0.0001$), but there were no differences in allocation to root biomass between the genera. *Chamaedorea* species had overall lower LAR than Geonomoid species ($F_{1,61} = 12.87$, $P < 0.001$), but *Chamaedorea* species had a higher SLA than Geonomoid species ($F_{1,61} = 10.20$, $P < 0.005$). *Chamaedorea* species also had higher foliar N contents (2.55%) than Geonomoid species (2.23%) ($F_{1,61} = 41.34$, $P < 0.0001$). *Chamaedorea* seedlings had significantly higher WUE compared to Geonomoid seedlings ($F_{1,60} = 4.00$, $P < 0.05$). There was a significant N addition treatment by genus interaction, with *Chamaedorea* seedlings increasing $A_{\max(\text{mass})}$ by 27% and Geonomoid seedlings increasing $A_{\max(\text{mass})}$ by 39% ($F_{1,60} = 4.30$, $P < 0.05$). Similarly, there was a significant interaction between N treatment and genus for PNUE, with *Chamaedorea* increasing PNUE with N addition by only 6% compared to the 24% increase for Geonomoid seedlings ($F_{1,60} = 5.14$, $P < 0.05$). *Chamaedorea* seedlings had significantly higher levels of herbivory with an average of 28% leaf area missing compared to 16% leaf area missing for Geonomoid species ($F_{1,61} = 4.78$, $P < 0.005$). However, the effect of N addition was relatively mild for *Chamaedorea* species (12% increase in leaf damage), compared to Geonomoid species (76% increase in leaf damage) ($F_{1,60} = 5.15$, $P < 0.05$). *Chamaedorea* species also had greater leaf toughness than Geonomoid species ($F_{1,57} = 32.22$, $P < 0.0001$) across both treatments. There were no genus level differences in respiration, conductance or photosynthetic rates on an area-basis.

Discussion

The extent to which soil N limits productivity in tropical montane forests remains unclear, in part because few studies have experimentally manipulated nutrient concentrations in such ecosystems (Vitousek & Farrington 1997; Tanner, Vitousek & Cuevas 1998; Adamek, Corre & Holscher 2009). Here, N addition had no direct effect on growth of palm seedlings in the shaded understory after 21 months. Rather, strong increases in foliar N increased photosynthetic rates, but higher quality leaves were more susceptible to herbivory, masking any potential growth response of the seedlings. Thus, the lack of growth response to N addition may be mediated by herbivores or limitation by additional resources. For example, low light availability and soil P concentrations may have restricted the response of the seedlings to added N, as has been shown in other studies (Walters & Reich 2000; Palmiotto *et al.* 2004; Baltzer *et al.* 2005). Ratios of foliar N : P were higher for plants in the N addition treatment compared to the control, suggesting that P became increasingly limiting. Further experimental manipulations of light and soil P availability would be necessary to show limitation from other resources. Nonetheless, our results suggest that soil N affects physiological traits and herbivore pressure of understory plants and, thus, may influence species distributions along soil N gradients in this montane forest.

MECHANISMS FOR SOIL-BASED HABITAT ASSOCIATIONS

Field experiments have provided evidence for several mechanisms in generating soil-based habitat partitioning in tropical forests, including trade-offs between growth and biomass allocation patterns, resource-use efficiency, and herbivore defense can influence species–soil associations (Fine, Mesones & Coley 2004; Palmiotto *et al.* 2004; Baltzer *et al.* 2005). Our results provide support for both physiologically based and herbivore-mediated responses to soil N addition among closely related groups of understory palms.

Biomass allocation

We found no responses in biomass allocation patterns to soil N addition, yet many growth experiments have found shifts in RMR with soil N availability (Tilman & Wedin 1991; Aerts & Chapin 2000; Walters & Reich 2000). Phenotypic shifts in RMR with soil N were particularly common in fast-growing species (Aerts & Chapin 2000), which may explain why the slow-growing understory palms in the current study showed no shift in biomass allocation patterns with N addition. Alternatively, consistent RMR among control and N addition plots may indicate that plants were foraging for additional soil resources, such as P or water.

Biomass allocation patterns differed among contrasting species–soil associations. Economic theory suggests that faster-growing species from fertile sites should allocate relatively more biomass to leaves compared to slower-growing species from infertile sites (Chapin 1980; Bloom, Chapin & Mooney 1985; Aerts & Chapin 2000). There was a strong positive correlation between LMR and RGR across species and N treatments in the current experiment. However, species from nutrient-rich dacitic soils had higher RMR and lower LMR and RGR compared to species from nutrient-poor rhyolitic soils. It is important to note that the rhyolitic species naturally occur at the site of the experiment. Therefore, the locally adapted rhyolitic species may have employed alternative mechanisms, such as symbiosis with native soil biota, allowing them to maintain a high LMR and, thus, RGR. The dacitic species, on the other hand, may have been nutrient-stressed across both treatments and increased their investment in the acquisition of belowground resources at the expense of LMR and RGR.

Physiological responses

We found significant increases in foliar N concentration and photosynthetic capacity with N addition. However, there were no differences in potential PNUE among any of the treatments or species groups. Increased photosynthetic capacity with foliar N content suggests that at least some of the additional N was invested in N-rich photosynthetic structures (Field & Mooney 1986; Lambers, Chapin & Pons 1998). Reich, Walters & Ellsworth (1997) showed a strong correlation between foliar N content and maximum photosynthetic

rates across a wide spectrum of ecosystems. The increased photosynthetic rate following N addition suggests that soil N limited physiological function of seedlings in the control gardens at this low N site. However, higher potential photosynthetic rates did not translate to increased growth rates, possibly due to low understory light levels, increasing P limitation and/or increases in herbivory.

Physiological traits were consistent with species–soil preferences whereby species associated with relatively nutrient-rich, dacitic soil exhibited higher foliar N content and potential photosynthetic rates than species with preferences for low nutrient soils, suggesting that physiological traits are important in determining species–soil associations (Chapin, Autumn & Pugnaire 1993; Aerts & Chapin 2000). Previous soil nutrient augmentation experiments with tropical woody species have not detected responses in leaf level physiology with increases in nutrient availability (Tanner, Vitousek & Cuevas 1998; Baltzer *et al.* 2005). In contrast, the accumulation of foliar N in response to increased N supply may be a key mechanism for understory palms to persist in low light environments. Increased uptake of N may be advantageous to slow-growing palms, allowing them to store N for later use when ephemeral supplies are exhausted (Chapin 1980; Lawrence 2001). However, the herbivory costs associated with high foliar N content suggests that N-rich leaves may be particularly disadvantageous for palms at low soil N sites and may influence species–soil associations.

Plant–herbivore interactions

Palms are generally slow growing plants that invest heavily in structural defenses (lignin, fibre, spines) rather than secondary chemical defenses (Braker & Chazdon 1993; Coley & Barone 1996). Structural defenses limit the suite of herbivores capable of accessing leaf tissue, and low nutritional quality may also serve as an anti-herbivore defense mechanism, as well as a means of optimizing metabolism and growth rate in low resource environments (Moran & Hamilton 1980; Coley & Barone 1996; Campo & Dirzo 2003; Fine *et al.* 2006). Both the present study, and a study comparing herbivory among three Geonomoid species at the La Selva Biological Station, Costa Rica (Braker & Chazdon 1993), showed large differences among species in the proportion of leaf area damaged, indicating herbivore preferences for species with particular leaf traits. Leaf quality traits, such as cuticular waxes, high leaf water content, high leaf area per unit mass, and low lignin content, were suggested as preferred leaf traits for herbivores at La Selva (Braker & Chazdon 1993). In the present study, herbivore damage was higher in the N addition treatment, in which plants had higher foliar N concentrations at a given leaf toughness, indicating foliar N content was an important trait determining herbivore preference.

Growth rates of palm seedlings were indirectly affected by N addition due to increased herbivory in the N addition treatment. The main response to N addition was increased foliar

N concentration and potential photosynthetic capacity. However, the cost of increased foliar N, or leaf quality, was a corresponding increase in the amount of leaf area consumed by herbivores. Thus, generalist species and species associated with low N soils maintained higher realized growth rates than species with andesitic or dacitic soil associations. Realized growth is the growth potential minus the tissue losses (Kitajima 1996). The similar realized growth rates in control and N addition treatments, despite higher herbivory in the N addition treatment, suggests that potential growth rates of species associated with dacitic and andesitic soils were higher in the N addition treatment. Thus, leaf quality may influence species distribution patterns indirectly through susceptibility to herbivore attack.

PHYLOGENETIC CONSTRAINTS

Phylogenetic constraints may also influence species distribution along soil N gradients. Physiological and herbivore-mediated responses to N addition revealed a phylogenetic signature regardless of species–soil association. After controlling for differences in species–soil group, *Chamaedorea* species consistently had higher foliar N concentrations, gas exchange rates, and consequently, herbivory, whereas *Geonoma* species, with lower quality leaves, maintained higher RGR. Furthermore, *Chamaedorea* species had greater leaf toughness than *Geonoma* species, indicating the two groups differ in nutrient use and defense strategies. This suggests that *Geonoma* species, with their more conservative nutrient strategy, should be able to occupy more nutrient-poor sites compared to *Chamaedorea* species within a given soil-based habitat. This pattern may account for the regional distribution of *Geonoma* and *Chamaedorea* species in Panama. *Geonoma* reaches its highest species diversity in eastern Panama where soils are generally more weathered and nutrient poor (reflecting a longer time since volcanic activity), whereas *Chamaedorea* reaches its highest species diversity in western Panama where soils are generally younger and more nutrient rich (reflecting more recent volcanic activity) (Henderson, Galeano & Bernal 1995; Hodel 1992).

In conclusion, we found that the main response of understory palm seedlings to increased soil N supply was increased foliar N concentration resulting in higher potential photosynthetic capacity and increased leaf area damage by herbivores. We found no growth response or biomass allocation shifts with N addition, although growth responses of the seedlings may have been offset by increased herbivory with N addition. Alternatively, other soil nutrients, such as P, may have limited the growth response to added N. Palm species associated with low nutrient, rhyolitic soils maintained relatively high growth rates in control and N addition treatments compared to species from nutrient-rich sites. Our results suggest that leaf quality and susceptibility to herbivore attack may influence the distribution of palm species, and likely additional plant species, along soil gradients in this lower montane forest.

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