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Nutrient cycling and plant–soil feedbacks along a precipitation gradient in lowland Panama

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Abstract: This study addresses patterns of nutrient dynamics on a precipitation gradient (1800–3500 mm y^{-1}) in lowland tropical forest with heterogeneous soil parent material, high plant species diversity and large changes in species composition. Mean foliar concentrations of phosphorus, potassium, calcium and magnesium decreased with increasing precipitation, whereas foliar carbon:nitrogen increased with increasing precipitation. Mean foliar nitrogen:phosphorus varied from 16.4–23.8 suggesting that plant productivity at these sites is limited by phosphorus. Total soil nitrogen increased as a function of foliar litter lignin:nitrogen, whereas net nitrogen mineralization rates decreased with increasing lignin:N indicating that as litter quality decreases, more soil nitrogen is held in soil organic matter and the mineralization of that nitrogen is slower. Extractable phosphorus in soil was negatively correlated with foliar litter lignin:phosphorus, illustrating effects of litter quality on soil phosphorus availability. Overall, the results suggest that variation in plant community composition along this precipitation gradient is tightly coupled with soil nutrient cycling. Much of our understanding of effects of precipitation on nutrient cycling in tropical forest is based on precipitation gradients across montane forest in Hawaii, where species composition and soil parent material are constant. Our results suggest that variation in parent material or species composition may confound predictions developed in model island systems.

Resumen: Este estudio trata sobre los patrones de dinámica de nutrientes en un gradiente de precipitación (1800–3500 mm y^{-1}) en un bosque tropical de tierras bajas con material parental heterogéneo, alta diversidad de especies de plantas, y un gran cambio en la composición de especies. Las concentraciones promedio de fósforo, potasio, calcio y magnesio disminuyen con un aumento en la precipitación, mientras que la proporción carbono:nitrógeno aumenta con un aumento en la precipitación. La proporción promedio de nitrógeno foliar:fósforo varía de 16.4 a 23.8, lo cual sugiere que estos sitios tienen limitaciones de fósforo. El nitrógeno total del suelo aumenta como una función de la proporción de lignina foliar de la hojarasca:nitrógeno, mientras que la tasa de mineralización del nitrógeno neto disminuye con un aumento de la proporción de lignina:nitrógeno, lo cual indica que mientras la calidad de la hojarasca disminuye, más nitrógeno del suelo es retenido en la materia orgánica y la mineralización de ese nitrógeno es más lenta. El fósforo extraíble está correlacionado negativamente con la proporción de lignina foliar de la hojarasca:fósforo, lo cual ilustra el efecto de la calidad de hojarasca en la disponibilidad de fósforo del suelo. En resumen, estos resultados sugieren que la variación en la composición de plantas de una comunidad a lo largo de este gradiente de precipitación tiene un efecto considerable en la retroalimentación de los ciclos nutricionales del suelo. Gran parte de nuestros conocimientos sobre el efecto de los gradientes de lluvia en ciclos nutricionales del suelo han sido basados en estudios de gradientes de precipitación de bosques de montaña en Hawaii, en donde tanto la composición de especies y el material parental del suelo son constantes. Nuestros resultados sugieren que la variación del material parental del suelo y la composición de especies pueden confundir las predicciones desarrolladas en sistemas modelos de islas.

Key Words: calcium, foliar nutrients, litterfall productivity, magnesium, nitrogen, Panama canal, phosphorus, potassium, soil carbon, tropical forest

INTRODUCTION

Precipitation has the potential to affect nutrient cycling in tropical forest through a variety of direct and indirect processes. Direct effects of precipitation on nutrient

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cycling include removal of highly mobile nutrients in the soil solution via leaching (Radulovich & Sollins 1991, Schuur & Matson 2001), reduced mineralization of nitrogen (N) and phosphorus (P) in poorly drained soils or anaerobic microsites (Schuur & Matson 2001), and more intense weathering to produce secondary minerals with higher surface area and thus higher capacity to adsorb organic matter (Torn *et al.* 1997). Studies of nutrient cycling in humid montane tropical forest (precipitation $> 2000\,\mathrm{mm\,y^{-1}}$) show that soil carbon (C) pool sizes increase whereas N availability decreases with increasing precipitation (Schuur & Matson 2001, Schuur *et al.* 2001), and 5 y of experimental irrigation in lowland Panama increased permanent charge and cation retention, leading to less sorption of phosphate and thus increased P mobility (Yavitt & Wright 2002) demonstrating strong direct effects of water availability on nutrient cycling. However, it is important to note that effects of water on nutrient cycling are nonlinear and response trajectories to water manipulation depend on initial water status (Schuur 2003, Yavitt & Wright 2002). Indirect effects of precipitation on nutrient cycling in tropical forest include variation in vegetation that can influence nutrient cycling through effects on litter quality and decomposition. For example, across precipitation gradients in Hawaiian montane forest, leaves from wetter sites ($> 2500\,\mathrm{mm\,y^{-1}}$) decomposed more slowly than leaves from the same tree species from drier sites when decomposed at a common site (Austin & Vitousek 2000, Schuur 2001), illustrating how precipitation may affect mass loss and nutrient release from litter through leaf traits and litter quality. Much of our understanding of precipitation effects on nutrient cycling in tropical forest is based on montane systems in Hawaii, where species composition and soil parent material are constant. The purpose of the current study is to observe patterns of plant and soil nutrient cycling along a precipitation gradient in lowland Panama with large variation in species composition and soil parent material and discuss possible mechanisms for observed patterns.

Lowland tropical forests often exhibit changes in species composition in the range of precipitation from approximately 1500–3000 $\mathrm{mm\,y^{-1}}$, with seasonally dry forest dominated by deciduous tree species and aseasonal wet forest dominated by evergreen species (Eamus 1999). Changes in canopy tree species composition and phenology along precipitation gradients in lowland Panama are associated with coordinated changes in leaf functional traits that have the potential to affect nutrient cycling (Santiago & Mulkey 2005). Short leaf life spans of deciduous species are associated with higher photosynthetic capacity and leaf N concentration resulting in a pattern of decreasing leaf N concentration of dominant canopy tree species with increasing precipitation (Santiago *et al.* 2004). In addition, increasing leaf life span of dominant canopy tree species with increasing precipitation is correlated with increasing leaf lignin:N and structural toughness (Santiago *et al.* 2004), which have the potential to influence decomposition and nutrient release from decaying litter (Cornelissen & Thompson 1997, Melillo *et al.* 1982), illustrating the potential for effects of precipitation-induced shifts in species composition to feed back into nutrient cycling processes in lowland Panamanian forest. Although consistency of species composition and soil parent material of montane forests in Hawaii have allowed natural experiments that test how precipitation affects nutrient cycling, continental tropical forests are characterized by heterogeneity of species composition and soil parent material. Therefore, we examined patterns of nutrient dynamics in lowland continental tropical forest for a greater understanding of how patterns from model island ecosystems extend to other forest types.

METHODS

Study site

This study was conducted in lowland tropical forest along a rainfall gradient in Central Panama. Mean annual precipitation (MAP) across these sites varied from 1800 $\mathrm{mm\,y^{-1}}$ at the driest site to approximately 3500 $\mathrm{mm\,y^{-1}}$ at the wettest site (ACP 2002). Four 1-ha lowland forest study plots established by the Center for Tropical Forest Science (CTFS) over a range of precipitation with minimal changes in altitude and temperature were used as study sites (Santiago *et al.* 2004) (Table 1). All sites have a mean monthly precipitation >100 mm during the wet season between May and December, but dry season length (mean number of 30-d periods with <100 mm precipitation) varies between 129 d at the 1800-mm site and 67 d near the 3500-mm site (Condit 1998). Variation in rainfall during the study period (2000–2002) was within 15% of MAP at all sites.

The soils in the Panama Canal forests are generally well-drained and rich in clay, calcium (Ca), magnesium (Mg) and nitrogen (N), but poor in phosphorus (P) and potassium (K) relative to other tropical soils (Dietrich *et al.* 1982, Kursar *et al.* 1995, Yavitt *et al.* 1993). All of the study sites lie on volcanic substrate except the 3100-mm site, which lies on sedimentary substrate (Table 1). The 1800-mm site is derived from the early to late Oligocene (25–30 million y ago; MYA), principally agglomerate, generally andesitic in fine-grained tuff and includes stream-deposited conglomerate (Woodring *et al.* 1980). Soils of the 2300-mm and 3500-mm sites are derived from altered basaltic and andesitic lavas and tuff, including dioritic and dacitic intrusive rocks (36–66 MYA). The 3100-mm site is derived from the late

Table 1. Characteristics of sites along a precipitation gradient across the Isthmus of Panama.

Site	Mean annual precipitation (mm)	Parent material[a]	Order	Suborder
Parque Metropolitano	1800	Panama formation	Ultisol	Ustult
Pipeline Road	2300	Pre-Tertiary basalt	Ultisol	Humult
Fort Sherman	3100	Chagres Sandstone	Histosol	Saprist
Santa Rita	3500	Pre-Tertiary basalt	Ultisol	Humult

[a] After Woodring *et al.* (1980).

Table 2. Study species from four sites along a precipitation gradient in Panamanian lowland tropical forest, including phenological classification into deciduous (losing leaves for more than a few weeks), brevi-deciduous (losing leaves once per year and immediately flushing a new set) and evergreen. Modified from Santiago *et al.* (2004).

Species	Family	Phenology
1800 mm		
Anacardium excelsum (Bertero & Balb. ex Kunth) Skeels	Anacardiaceae	Brevi-deciduous
Astronium graveolens Jacq.	Anacardiaceae	Deciduous
Calycophyllum candidissimum (Vahl) DC.	Rubiaceae	Evergreen
Chrysophyllum cainito L.	Sapotaceae	Evergreen
Enterolobium cyclocarpum (Jacq.) Griseb.	Fabaceae	Deciduous
Luehea seemannii Triana & Planch.	Tiliaceae	Brevi-deciduous
Pseudobombax septenatum (Jacq.) Dugand	Bombacaeae	Deciduous
Spondias mombin L.	Anacardiaceae	Deciduous
2300 mm		
Poulsenia armata (Miq.) Standl.	Moraceae	Brevi-deciduous
Pourouma bicolor Mart.	Moraceae	Evergreen
Sterculia apetala (Jacq.) H. Karst.	Sterculiaceae	Deciduous
Tabebuia guayacan (Seem.) Hemsl.	Bignoniaceae	Deciduous
Tapirira guianensis Aubl.	Anacardiaceae	Evergreen
Terminalia amazonica (J. F. Gmel) Exell	Combretaceae	Brevi-deciduous
Trattinickia aspera (Standl.) Swartz	Burseraceae	Deciduous
Virola sebifera Aubl.	Myristicaceae	Evergreen
3100 mm		
Aspidosperma cruenta Woodson	Apocynaceae	Evergreen
Brosimum utile (Kunth) Pittier	Moraceae	Evergreen
Calophyllum longifolium Willd.	Clusiaceae	Evergreen
Dussia munda C. H. Stirt.	Fabaceae	Evergreen
Manilkara bidentata (A. DC.) A. Chev.	Sapotaceae	Evergreen
Marila laxiflora Rusby.	Clusiaceae	Evergreen
Poulsenia armata (Miq.) Standl.	Moraceae	Brevi-deciduous
Tapirira guianensis Aubl.	Anacardiaceae	Evergreen
3500 mm		
Aspidosperma cruenta Woodson	Apocynaceae	Evergreen
Carapa guianensis Aubl.	Meliaceae	Evergreen
Cassipourea elliptica (Sw.) Poir	Rhizophoraceae	Evergreen
Erisma blancoa Marc.-Berti	Vochysiaceae	Evergreen
Sacoglottis trygynum Mart.	Hernandiaceae	Evergreen
Sterculia costaricana Pittier	Sterculiaceae	Brevi-deciduous
Virola koschnyi Warb.	Myrsticaceae	Evergreen
Zygia ramiflora (Benth.) Barneby & J. W. Grimes	Fabaceae	Evergreen

Miocene or early Pliocene (3.5–10 MYA) with massive, generally fine-grained sandstone (Woodring *et al.* 1980).

Species composition and phenological habit of the most common canopy trees change rapidly across this gradient as species richness increases steeply with mean annual precipitation (Pyke *et al.* 2001) (Table 2). All study plots are located in mature forest (> 200 y), except the 1800-mm site, which is a forest of mixed age (70–100 y) because of more recent disturbance. Foliar measurements on the largest canopy trees at the 1800-mm site are comparable to other sites even though this forest is younger, because canopy composition was representative of mature seasonally dry forest (Croat 1978).

Foliar chemistry

As part of a larger study on photosynthetic leaf traits of canopy tree species along this precipitation gradient (Santiago *et al.* 2004), the eight canopy tree species at each site with the largest relative proportion of basal area were studied. These eight species were not the same among sites (Table 2). Fully expanded mature sun leaves or leaflets in the case of compound leaves were cut from the petiole or rachis and collected from 2–4 individuals for a total of 15 leaves per species from a site. Leaves were collected using canopy cranes maintained by the Smithsonian Tropical Research Institute at the 1800-mm and 3100-mm sites. At the 2300-mm and 3500-mm sites, leaves were collected from the upper canopy using a shotgun. Leaf material was dried for 48 h at 65 °C. Leaf samples from the same tree were pooled for chemical analysis. One composite subsample from each tree was analysed for C and N using an elemental analyser (Model NCS 2500, Carlo Erba, Milano, Italy). A separate subsample was analysed for P, K, Ca and Mg using inductively coupled plasma (ICP) atomic emission spectroscopy at the University of Florida Institute of Food and Agricultural Sciences (IFAS).

Litterfall collection and processing

Litter was collected in ten 0.25-m^2 traps randomly located at 20 ×2 0-m grid points in each 1-ha plot. Large items, such as palm fronds often fell across traps and only material that fell in the area above the trap was collected. Litter was collected 11 times at intervals ranging from 1 to 12 wk for the period between February 2001 and February 2002. Litter used in chemical analysis was collected at intervals of 7–10 d in February–June 2001, October 2001 and February 2002. Litter collected at intervals > 2 wk was adjusted for mass loss within traps using mean decomposition rates from 36 species at the 3100-mm site (Santiago 2003). This adjustment was 32% for the longest time interval. Litter was sorted into four classes: (1) fine woody debris ≤ 1 cm in diameter; (2) leaves; (3) reproductive structures including fruits, flowers and seeds; and (4) other components of litterfall including insects, frass, canopy soil and items too decomposed to identify. Litter was dried for 48 h at 65 °C and the separate classes were weighed. Entire samples of foliar litter from each site and pickup date were ground in a Wiley mill (mesh size 40) and homogenized. A 120-ml subsample was then retained for further chemical analyses.

Foliar litter chemistry

Foliar litter lignin analysis was performed using a series of increasingly aggressive extractants culminating with digestion in 72% H_2SO_4 (Ryan *et al.* 1989). Digests were then ashed at 500 °C to determine ash-free lignin concentration. Litter C and N concentrations were determined with an elemental analyser (Model ECS 4010, Costech, Valencia, CA). Foliar litter P, K, Ca and Mg were analysed using ICP at IFAS.

Soil nutrient availability

Soil cores were taken at each of the four sites in July 2002, approximately 2 mo after the beginning of the 8-mo wet season. Six 10-cm-deep soil samples were taken with a slide hammer corer at random locations in each 1-ha plot. Samples were returned to the laboratory and hand-sorted to remove roots and rocks, and three subsamples were taken. Weakly sorbed P was extracted from the first 10-g subsample in 50 ml 0.5 M $NaHCO_3$ (Miller *et al.* 2001). Extracts were shaken for 1 min and after 24 h a 10-ml sample of the supernatant was removed and frozen until transported to IFAS for analysis. We extracted NH_4 and NO_3 from the second 10-g subsample for 24 h in 50 ml 2 M KCl. The third 10-g subsample of each core was weighed into a 100-ml sample cup, covered, and allowed to incubate aerobically for 10 d in a dark cabinet at 24 °C. After 10 d, incubated samples were extracted in 2 M KCl as described above and net N mineralization was calculated as changes in the NO_3 and NH_4 pools (Riley & Vitousek 1995). Net nitrification was calculated as the change in NO_3 concentration per gram dry soil mass divided by the time period of incubation.

The remaining sample of each soil core was dried at 50 °C for 48 h, and sifted to pass through a 2-mm sieve. Total soil C and N were analysed on an elemental analyser (Model ECS 4010, Costech). We measured soil pH in a 2:1 mixture of water to soil by weight. Bulk density of surface 10 cm was estimated using 5-cm-diameter volumetric cores dried at 105 °C. Soil moisture was determined gravimetrically on bulk density samples and expressed as grams of water per unit mass of dry soil.

We determined *in situ* soil nutrient availability with ion exchange resins (Binkley & Matson 1983). Three grams of anion exchange resin (Biorad, AG 1-X8, 20–50 mesh, Cl^- form) and the same amount of cation exchange resin (Biorad, AG 50W-X8 20–50 mesh, H^+ form) were weighed into separate 5 × 6-cm undyed monopolyester bags (*c*. 190 μm mesh size). At each of the four sites, resin bags were placed vertically 4–7 cm deep. One anion and one cation resin bag were secured to a plastic stake with monofilament line at six random locations in each 1-ha plot. Resin bags were collected from the field after 21 d

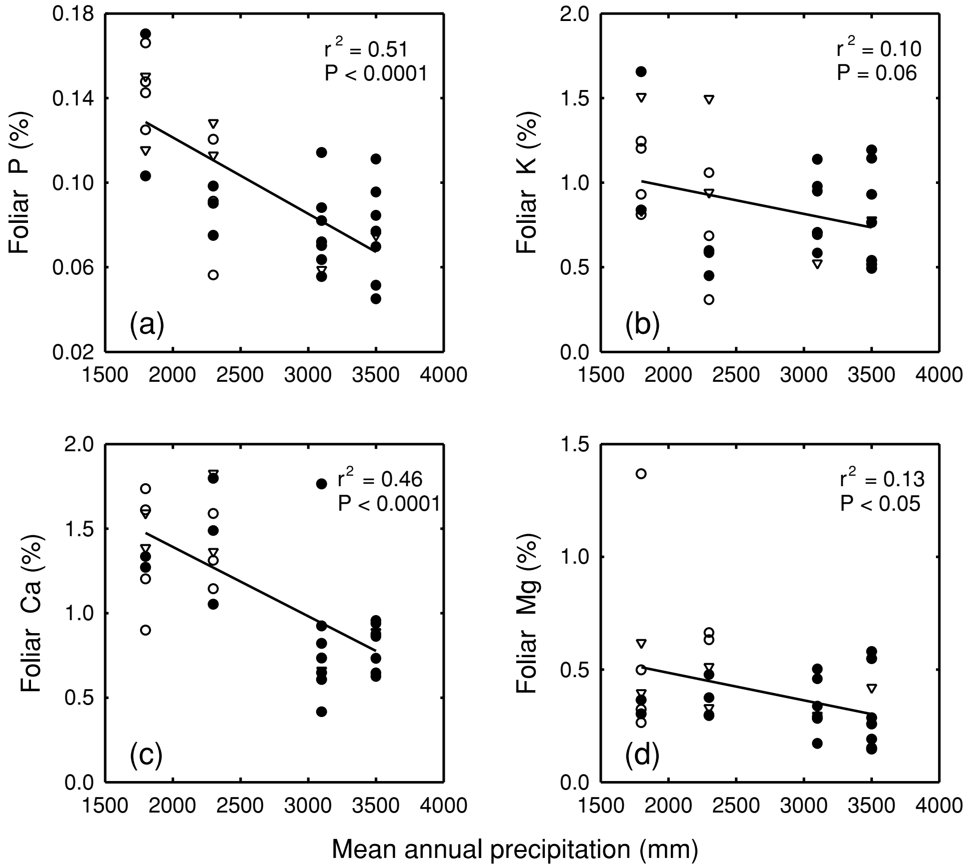

Figure 1. Foliar nutrient concentrations of sun leaves of the eight most common canopy species at each site as a function of mean annual precipitation (MAP) along a precipitation gradient in lowland Panamanian forest. (a) phosphorus ($P = -3.6 \cdot 10^{-5}$ MAP + 0.19); (b) potassium ($K = -1.6 \cdot 10^{-4}$ MAP + 1.3); (c) calcium ($Ca = -4.1 \cdot 10^{-4}$ MAP + 2.1); (d) magnesium ($Mg = -1.2 \cdot 10^{-4}$ MAP + 0.72). Symbols: deciduous (○), brevi-deciduous (▽), and evergreen (●).

and rinsed with deionized water to remove soil particles. Ions were extracted with 20 ml of 0.5 M HCl and then neutralized with 20 ml of 0.5 M NaOH. PO_4 and NO_3 from anion extracts and NH_4, K, Ca and Mg from cation extracts were measured at IFAS to determine nutrient content per unit mass of resin.

Data analysis

Analyses of the statistical effect of mean annual precipitation on foliar nutrient concentrations were conducted with one-way general linear models using annual precipitation as an independent continuous variable. Comparisons of litter chemistry and soil nutrients were performed with 1-way analysis of variance (ANOVA). Differences within the factor (site) were analysed with a post-hoc Duncan's multiple range test. The effect of litter quality on soil N, net N mineralization and extractable P, were analysed with one-way general linear models using litter quality as an independent continuous variable. All analyses were performed using SAS version 8.02.

RESULTS

Foliar chemistry

Foliar nutrient concentrations of the eight most common canopy tree species tended to decrease with increasing precipitation across this precipitation gradient. Mean foliar P (± 1 SE) ranged from 0.076 ± 0.007% at the 3100-mm site to 0.140 ± 0.009% at the 1800-mm site and decreased significantly with increasing precipitation (Figure 1a). Mean foliar K ranged from 0.76 ± 0.14% at the 2300-mm site to 1.13 ± 0.12% at the 1800-mm site and showed a weak decreasing trend with increasing precipitation (Figure 1b). Mean foliar Ca decreased significantly with increasing precipitation and ranged from 0.82 ± 0.05% at the 3500-mm site to 1.45 ± 0.11% at the 2300-mm site (Figure 1c). Mean foliar Mg varied between 0.32 ± 0.07% at the 3500-mm site and 0.52 ± 0.14% at the 1800-mm site and also decreased significantly with increasing precipitation (Figure 1d). Mean foliar C:N ranged from 23.0 ± 2.1 at the 1800-mm site to 37.2 ± 2.7 at the 3100-mm site and increased with

Table 3. Litterfall rates separated by component for the year between February 2001–February 2002 and litter chemistry of leaf litterfall from four sites along a precipitation gradient in lowland Panamanian forest. Values for foliar litter chemistry are means ± 1 SE ($n = 4$). Values with a different letter are significantly different at a P-value of 0.05.

	Site			
	1800 mm	2300 mm	3100 mm	3500 mm
Litterfall (Mg ha^{-1} y^{-1})				
Fine woody debris	1.37	1.37	1.65	1.58
Leaf	9.47	6.33	6.45	6.74
Reproductive structures	0.94	1.40	1.79	0.64
Other	0.69	0.93	0.62	0.83
Total	12.47	10.03	10.51	9.79
Leaf litter chemistry				
N (%)	$0.96^{a} \pm 0.04$	$1.34^{b} \pm 0.06$	$1.13^{ab} \pm 0.06$	$1.28^{b} \pm 0.09$
C (%)	$39.7^{a} \pm 0.6$	$44.3^{b} \pm 0.5$	$47.1^{c} \pm 0.3$	$45.5^{bc} \pm 0.5$
P (%)	$0.081^{a} \pm .008$	$0.047^{b} \pm .002$	$0.034^{b} \pm .006$	$0.037^{b} \pm .004$
K (%)	$0.74^{a} \pm 0.13$	$0.36^{bc} \pm 0.36$	$0.27^{c} \pm 0.03$	$0.57^{ab} \pm 0.07$
Ca (%)	$2.23^{a} \pm 0.48$	$1.45^{b} \pm 0.11$	$1.15^{b} \pm 0.10$	$1.46^{b} \pm 0.14$
Mg (%)	$0.55^{a} \pm 0.04$	$0.40^{b} \pm 0.03$	$0.33^{c} \pm 0.01$	$0.26^{d} \pm 0.01$
Lignin (%)	$15.4^{a} \pm 1.9$	$20.9^{b} \pm 1.6$	$23.8^{b} \pm 1.6$	$23.7^{b} \pm 1.2$
Lignin:N	$16.0^{a} \pm 1.5$	$15.6^{a} \pm 1.0$	$21.1^{b} \pm 2.0$	$18.5^{ab} \pm 1.7$
Lignin:P	$194.9^{a} \pm 31.4$	$448.8^{b} \pm 21.9$	$752.1^{c} \pm 154.5$	$655.6^{bc} \pm 59.2$

increasing precipitation ($r^2 = 0.34$; $P < 0.001$), consistent with previously reported decreasing foliar N with increasing precipitation across these sites ($r^2 = 0.21$; $P < 0.01$) (Santiago *et al.* 2004). Mean foliar N:P ranged from 16.4 ± 1.8 at the 1800-mm site to 21.7 ± 2.4 at the 2300-mm site.

Litterfall production

Total litter production was largest at the 1800-mm site (12.47 Mg ha^{-1} y^{-1}) and smallest at the 3500-mm site (9.79 Mg ha^{-1} y^{-1}) (Table 3). Fine woody litterfall represented 11–17% of total litter and was about 20% larger at the two wetter sites (Table 3). Leaf litter represented 60–75% of total litter and was 45% larger at the 1800-mm site than the other three sites (Table 3). Reproductive structures comprised 7–15% of total litterfall, whereas other litter components were 5–9% of total litterfall. Litterfall rates were seasonal with more litter falling during the dry season at all sites, but seasonal differences between maximum and minimum litterfall rates were greatest at the driest site (21.44 Mg ha^{-1} y^{-1}) and decreased with increasing precipitation to the wettest site (6.84 Mg ha^{-1} y^{-1}), showing a shift away from deciduous species toward evergreen species in wetter forest.

Foliar litter chemistry

Foliar litter chemistry showed substantial variation among sites (Table 3). Mean litter N ranged from 0.96% at the 1800-mm site to 1.34% at the 2300-mm site. Mean litter C ranged from 39.7% at the 1800-mm site to 47.1% at the 3100-mm site. Mean litter P, Ca and Mg were largest at the 1800-mm site relative to the three other sites. Mean litter K ranged from a minimum of 0.27% at the 3100-mm site to a maximum of 0.74% at the 1800-mm site. Litter lignin concentration was significantly lower at the 1800-mm site than the other three sites. Litter lignin:N peaked at the 3100-mm site, and litter lignin:P was smallest at the 1800-mm site and largest at the 3100-mm site. Nutrient retranslocation efficiency, calculated on a mass basis from leaves of the eight most common canopy species per site and total ecosystem foliar litterfall, ranged from 21–58% for N, 42–54% for P and 32–66% for K.

Soil nutrient availability

Total soil N and C concentrations of the top 10 cm were greatest at the 3100-mm site, followed by the 3500-mm site and the two drier sites (Table 4). Soil N showed a strong linear increase in relation to litter lignin:N (Figure 2a). Net N mineralization, nitrification and extractable NH_4 were not different among sites (Table 4), but N mineralization decreased linearly with increasing litter lignin:N (Figure 2b). Nitrification was large at all sites and varied from 73–99% of total net N mineralization. Extractable NO_3 was significantly greater at the wettest site than at the three drier sites ($F = 4.80$; $P < 0.05$; Table 4). Soil extractable P was significantly greater at the 1800-mm site than at the three wetter sites ($F = 3.50$; $P < 0.05$; Table 4). Extractable P also decreased with increasing litter lignin:P (Figure 3).

Resin extractable NO_3 was significantly larger at the 2300-mm and 3500-mm sites compared with the other

Table 4. Soil chemical and physical properties to a depth of 10 cm from four sites along a precipitation gradient in lowland Panamanian forest. Values are means (± 1 SE) of averages measured using six samples per site during the early wet season of 2002. Values with a different letter are significantly different at a P-value of 0.05.

	Site			
	1800 mm	2300 mm	3100 mm	3500 mm
Bulk soil chemistry				
Total C (%)	$2.52^{a} \pm 0.28$	$2.86^{ab} \pm 0.31$	$7.07^{c} \pm 0.54$	$3.96^{b} \pm 0.48$
Total N (%)	$0.29^{a} \pm 0.08$	$0.27^{a} \pm 0.02$	$0.53^{b} \pm 0.05$	$0.39^{ab} \pm 0.04$
Nitrogen transformations				
Net N mineralization (mg kg^{-1} d^{-1})	$0.98^{a} \pm 0.19$	$1.13^{a} \pm 0.26$	$0.57^{a} \pm 0.20$	$0.94^{a} \pm 0.43$
Net N nitrification (mg kg^{-1} d^{-1})	$0.71^{a} \pm 0.20$	$1.13^{a} \pm 0.21$	$0.57^{a} \pm 0.20$	$0.94^{a} \pm 0.43$
Extractable nutrients (mg kg^{-1})				
NO_3	$0.07^{a} \pm 0.08$	$0.73^{a} \pm 0.61$	$0.23^{a} \pm 0.25$	$3.73^{b} \pm 1.59$
NH_4	$2.73^{a} \pm 1.19$	$2.95^{a} \pm 0.28$	$3.91^{a} \pm 0.40$	$4.73^{a} \pm 0.85$
P	$5.26^{a} \pm 0.78$	$3.21^{b} \pm 0.53$	$2.85^{b} \pm 0.77$	$3.33^{b} \pm 0.36$
Resin extractable nutrients (mg d^{-1} per kg resin)				
NO_3	$0.111^{a} \pm 0.070$	$0.776^{b} \pm 0.095$	$0.174^{a} \pm 0.096$	$0.829^{b} \pm 0.248$
NH_4	$0.022^{a} \pm 0.004$	$0.029^{a} \pm 0.006$	$0.023^{a} \pm 0.004$	$0.026^{a} \pm 0.004$
PO_4	$0.381^{a} \pm 0.096$	$0.016^{b} \pm 0.005$	$0.015^{b} \pm 0.002$	$0.005^{b} \pm 0.002$
K	$32.0^{a} \pm 3.2$	$25.9^{b} \pm 0.7$	$21.4^{b} \pm 0.6$	$27.2^{ab} \pm 1.6$
Ca	$1.96^{a} \pm 0.40$	$1.16^{b} \pm 0.29$	$0.15^{c} \pm 0.04$	$0.47^{bc} \pm 0.02$
Mg	$0.17^{a} \pm 0.08$	$< 0.01^{b}$	$< 0.01^{b}$	$< 0.01^{b}$
Soil bulk density (g cm^{-3})	$0.92^{a} \pm 0.02$	$0.73^{b} \pm 0.03$	$0.51^{c} \pm 0.02$	$0.60^{d} \pm 0.02$
Water content (g g^{-1})	$0.53^{a} \pm 0.02$	$0.58^{a} \pm .001$	$0.82^{b} \pm 0.02$	$0.98^{c} \pm .006$
Soil pH	$6.49^{a} \pm 0.10$	$5.27^{b} \pm 0.19$	$4.15^{c} \pm 0.07$	$5.07^{b} \pm 0.12$

two sites ($F = 5.81$, $P < 0.01$; Table 4). Resin extractable Ca was greatest at the driest site and smallest at the 3100-mm site ($F = 11.75$; $P < 0.0005$) and measurable quantities of resin extractable Mg were only detected at the driest site (Table 4). Soil bulk density varied among sites and was lowest at the 3100-mm site (Table 4). Gravimetric water content mirrored precipitation inputs with the smallest values at the driest site and largest values at the wettest site. Soil pH varied from 4.15–6.49 and was most acidic at the 3100-mm site and least acidic at the driest site.

DISCUSSION

Components of ecosystem nutrient cycling varied among four sites along a precipitation gradient in lowland Panama providing evidence that changes in plant species litter chemistry associated with water availability have the potential to influence soil processes. The patterns we observed suggest that precipitation affected nutrient cycling most clearly through effects on plant community composition and litter quality. Foliar nutrient concentrations decreased with increasing precipitation and poor litter quality was associated with relatively low rates of soil N mineralization and low P availability. This demonstrates how shifts in plant community composition from dry-season-deciduous canopy species in seasonally dry forest to evergreen species in wet, aseasonal forest were accompanied by variation in litter quality that appear to feed back into soil processes. Our data are consistent with reports of negative correlation between net N mineralization and litter lignin:N across a range of temperate forest sites (Scott & Binkley 1997). Our data are also in line with precipitation gradients in Hawaiian montane forest, where foliar N, P and major cation (Ca, Mg and K) concentrations decreased with increasing precipitation (Austin & Vitousek 1998, Schuur & Matson 2001). However, unlike precipitation gradients in Hawaiian montane forest, we did not observe decreasing soil N availability with increasing precipitation. This could have been a result of other factors among sites having a stronger effect than precipitation alone, coupled with a relatively low number of sites on this gradient.

Decreasing foliar element concentrations of dominant canopy tree species across the Isthmus of Panama are consistent with patterns of decreasing foliar N reported for the same group of species across this precipitation gradient (Santiago *et al.* 2004), and reflect the predictable shifts in phenology of canopy tree communities observed throughout the lowland tropics (Eamus 1999). Significantly greater soil extractable and resin extractable P at the driest site (Table 4) appears to contribute to the pattern of decreasing foliar P with increasing precipitation. Decreasing foliar Ca and Mg with increasing precipitation also reflect relatively high availability of these elements at the driest site. Decreasing foliar N and increasing

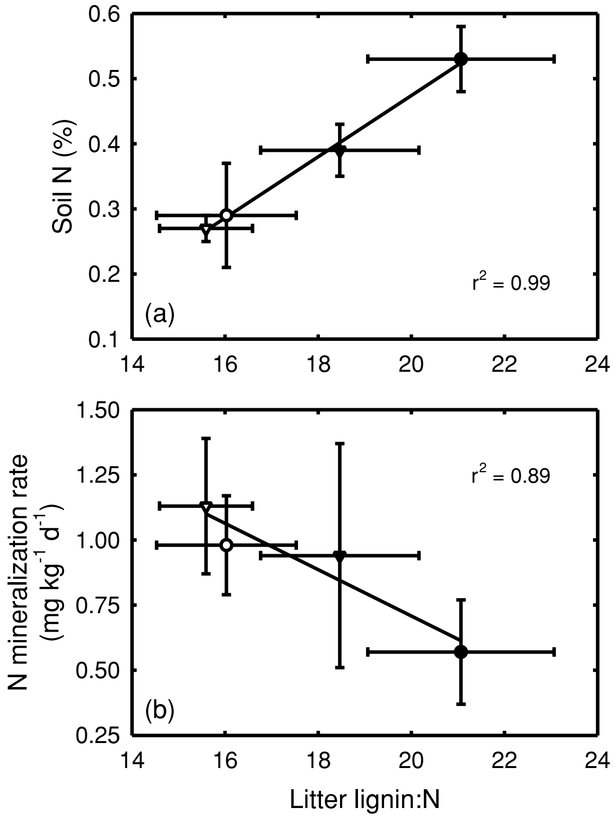

Figure 2. The relationship between mean site leaf litter lignin to nitrogen ratio ($n = 4$) and (a) soil nitrogen concentration for the top 10 cm ($n = 6$) and (b) nitrogen mineralization rate for the top 10 cm ($n = 6$) for four 1-ha forest sites in lowland Panama that vary in mean annual precipitation: 1800 mm (○); 2300 mm (▽); 3100 mm (●); 3500 mm (▼).

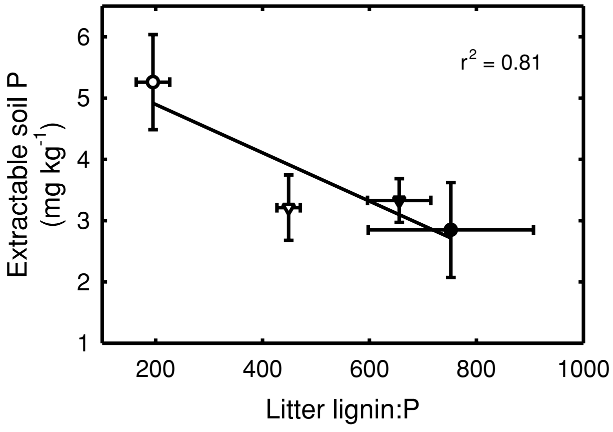

Figure 3. Extractable soil phosphorus ($n = 6$) as a function of mean site leaf litter lignin to phosphorus ratio ($n = 4$) for four 1 ha forest sites in lowland Panama that vary in mean annual precipitation. Symbols as in Figure 2.

C:N with increasing precipitation does not appear to be caused by reduced soil N availability with increasing precipitation as has been observed on rainfall gradients in Hawaii (Austin & Vitousek 1998, Schuur & Matson 2001) because soil N availability did not decrease with increasing precipitation in lowland Panama. Therefore, decreasing foliar N of dominant canopy tree species is likely a result of changes in phenology related to water availability that result in longer-lived, thicker leaves with lower photosynthetic capacity, lower N concentration, and increased allocation to anti-herbivore defence with increasing precipitation (Santiago *et al.* 2004). The apparent independence of foliar N concentrations from soil N availability in these sites also corresponds to foliar N:P which provides evidence that P might be more limiting to plant growth than N, in contrast to the wetter Hawaiian montane forests. This would explain why foliar P mirrors soil nutrient availability while N may be more strongly controlled by leaf traits characteristic of evergreen and deciduous species. Overall, decreasing foliar element concentrations, whether driven by physiological allocation or nutrient availability, appear to provide an important feedback to nutrient cycling via litter quality as demonstrated by the negative relationship between lignin:N and N mineralization (Figure 2b) and between lignin:P and extractable P (Figure 3).

Although we did not perform manipulation experiments to determine which nutrients limit productivity at these sites, N and P are the most widespread limiting nutrients in terrestrial ecosystems (Vitousek & Howarth 1991, Vitousek & Sanford 1986), and therefore N mineralization or extractable P are likely to influence productivity among these sites. Mean foliar N:P above 16 often suggests limitation by P (Aerts & Chapin 2000), and we observed mean foliar N:P values between 16–21 suggesting that productivity is limited by P at these sites. Patterns of litterfall suggest that the driest site may be slightly more productive than wetter forests. However, the highest litterfall site was also the youngest site, so the possibility that the 1800-mm site has yet to achieve quasi-steady state cannot be ignored. Nevertheless, the primary differences in litterfall among sites are greater leaf litter production and stronger seasonality from the 1800-mm site, which has the greatest proportion of dry-season-deciduous tree species. Therefore increased leaf litter production at the driest site may be the result of increased leaf turnover. However, in order to understand the extent to which productivity is regulated by water availability, other components of productivity such as root growth, trunk growth and respiration need to be incorporated even though fine litterfall is one of the largest fractions of productivity (Clark *et al.* 2001). Several recent studies have also revealed that productivity in humid tropical forest declines at high annual precipitation (> 2500-mm) (Nemani *et al.* 2003, Schuur 2003, Schuur & Matson 2001). Further studies of productivity along resource gradients in lowland tropical forest are likely to distinguish among succession, light and nutrient limitation as factors controlling net primary productivity.

Relatively low leaf litter quality appears to result in lower rates of N mineralization and lower availability of P (Figures 2b and 3). Decomposition rates at the 3100-mm site decrease with increases in litter lignin:P ($r^2 = 0.48$; $P < 0.001$) and lignin:N ($r^2 = 0.37$; $P < 0.001$) (Santiago 2003), implicating slow decomposition of poor quality litter as a mechanism for the association between litter quality and nutrient availability. Although, precipitation also affects decomposition (Austin & Vitousek 2000, Schuur 2001, Vitousek *et al.* 1994), we show evidence of a plant-soil feedback through litter quality. In addition, we observed a positive association between litter lignin:N and soil N concentration, suggesting that at the driest site, relatively low leaf litter lignin will result in a lower proportion of litter N entering the slowly decomposing pool of organic matter, thus producing the observed low soil N concentration at this site. We also observed relatively low resin extractable Ca and Mg at wetter sites, suggesting that these elements may experience greater leaching with increased precipitation inputs (Radulovich & Sollins 1991, Schuur & Matson 2001). It is clear that further mechanistic work is needed to confirm the importance of nutrient leaching from soils in tropical forests with high precipitation.

Overall, the results suggest that variation in plant litter chemistry among these study sites has the potential to affect soil nutrient dynamics. Despite variation in soil substrates and plant community composition across short (10 km) distances in Panama, several general patterns, such as decreasing foliar element concentrations of dominant canopy tree species with increasing precipitation are similar to patterns described for montane forest ecosystems in Hawaii, where consistency in community composition and parent material along precipitation gradients have generated empirical predictions. However, other patterns that have been observed in Hawaiian montane forests, such as decreasing soil N availability with increasing precipitation were not observed along this gradient. This suggests that in all tropical forests, soil parent material and vegetation may be used in combination with precipitation to predict nutrient cycling dynamics over large areas. Further studies in lowland continental tropical forest are likely to contribute to our understanding of nutrient cycling in relation to precipitation observed in model island systems.

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