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Amy T. Austin · P.M. Vitousek

Nutrient dynamics on a precipitation gradient in Hawai'i

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Abstract We evaluated soil and foliar nutrients in five native forests in Hawai'i with annual rainfall ranging from 500 mm to 5500 mm. All of the sites were at the same elevation and of the same substrate age; all were native-dominated forests containing *Metrosideros polymorpha* Gaud. Soil concentrations of extractable NO_3-N and PO_4-P, as well as major cations (Ca, Mg, and K), decreased with increasing annual precipitation, and $\delta^{15}N$ values became more depleted in both soils and vegetation. For *M. polymorpha* leaves, leaf mass per area (LMA) and lignin concentrations increased significantly, while $\delta^{13}C$ values became more depleted with increasing precipitation. Foliar phosphorus, and major cation (Ca, Mg, and K) concentrations for *M. polymorpha* all decreased significantly with increasing precipitation. For other native forest species, patterns of LMA, $\delta^{13}C$, and $\delta^{15}N$ generally mirrored the pattern observed for *M. polymorpha*. Decreasing concentrations of available rock-derived nutrients in soil suggest that the effect of increased rainfall on leaching outweighs the effect of increasing precipitation on weathering. The pattern of decreased foliar nutrient concentrations per unit leaf area and of increased lignin indicates a shift from relatively high nutrient availability to relatively high carbon gain by producers as annual precipitation increases. For nitrogen cycling, the pattern of higher inorganic soil nitrogen concentrations in the drier sites, together with the progressively depleted $\delta^{15}N$ signature in both soils and vegetation, suggests that nitrogen cycling is more open at the drier sites, with smaller losses relative to turnover as annual precipitation increases.

Key words Biogeochemistry · Nitrogen cycle · Carbon cycle · Folior nutrients · *Metrosideros polymorpha*

Introduction

Water availability affects the dynamics of ecosystems through a number of pathways (Jenny 1980). The effects of water availability can be viewed both directly, as the effects of water supply on organisms, and indirectly, as mediated through effects on nutrient availability or other processes. Water availability can control ecosystems by affecting long-term balances between ecosystem inputs and outputs of elements, by affecting the cycling of carbon and nutrients within ecosystems, and by affecting growth of and allocation within individual organisms.

The net effects of water availability on nutrient cycling in ecosystems are therefore inherently complex, and they are complicated further in that the controlling processes occur on widely different time scales. The effects of precipitation on element inputs and outputs, in particular, are too long-term for effective experimentation. Studies along natural gradients of water availability can address these controls, but most moisture gradients themselves are complicated by variation in other potentially controlling factors.

In this study, we evaluated the effects of water availability on ecosystem-level nutrient availability and cycling along a relatively simple rainfall gradient on the island of Hawai'i. We asked:

1. How does the balance between element inputs and losses (as reflected in soil nutrient availability) change with increasing precipitation?
2. How do nutrient availability and rainfall interact to shape tissue chemistry across the gradient, and how could that, in turn, affect nutrient availability?
3. How does precipitation affect the openness of nitrogen cycling?

A.T. Austin (✉)[1] · P.M. Vitousek
Department of Biological Sciences, Stanford University
Stanford, CA 94305-5020, USA

Present address:
[1] Faculty of Agronomy, University of Buenos Aires,
Avenida San Martín 4453, Buenos Aires (1417) Argentina
Fax: (415) 725-1856; e-mail: austin@ifeva.edu.ar

We evaluated changes in nutrient availability with increasing rainfall by measuring available soil concentrations of rock-derived nutrients, as well as nitrogen (question 1). Rates of weathering, leaching, and atmospheric deposition of nutrients all increase with increasing water availability (Stark 1994; Newman 1995; Quilchano et al. 1995a), but it is the balance between these processes of input and loss that ultimately determines nutrient supply. Studies of variation in soil properties in different precipitation regimes generally show that concentrations of extractable/exchangeable nutrients are relatively high in semiarid sites and decrease with increasing precipitation (Högberg 1989; Schulze et al. 1991). Soil organic carbon follows the opposite pattern, increasing with increasing annual rainfall (Amundson et al. 1989; Burke et al. 1991; Quilchano et al. 1995a). While total soil nutrient contents may also increase, C:N and C:P ratios in soils widen with increasing mean annual precipitation (MAP) (Roberts et al. 1989), suggesting that with increasing rainfall, the rate of carbon accretion in soil exceeds that of total nutrient accumulation. Ecosystems with very high precipitation often have low nutrient availability because of slow decomposition and high leaching loss (Berendse et al. 1989; Zak and Grigal 1991; Vitousek et al. 1995). The overall pattern thus suggests an inverse relationship between carbon and nutrient availability with a gradient from systems relatively rich in available nutrients to those relatively rich in carbon (and water availability). This pattern of relative availability could influence carbon/nutrient balance in vegetation (Scholes 1994).

For question 2, we analyzed foliar nutrients, δ^{13}C, and lignin in the widespread tree *Metrosideros polymorpha*, as well as other native woody plants. Foliar nutrients can serve as indicators of the nutrient status of plants and ecosystems (van den Driessche 1974; Grubb 1977; Tanner 1985; Medina and Cuevas 1989). Leaf longevity, seasonality, and herbivore pressure can obscure the connection between availability and foliar concentrations (Chapin et al. 1986; Reich et al. 1992; Medina and Cuevas 1994), but foliar analysis is particularly useful where a single species occupies a broad range of sites. δ^{13}C measurements have been used widely as an integrated measure of intrinsic water-use efficiency (WUE) within C_3 species (Ehleringer 1989; Farquhar et al. 1989a, b; Griffiths 1991). The ubiquitous nature of the single species *M. polymorpha* in Hawaiian ecosystems has encouraged a number of studies of foliar nutrients (Vitousek et al. 1988, 1992, 1995), and δ^{13}C (Vitousek et al. 1990; Meinzer et al. 1992); these studies serve as a useful reference for the relationships among foliar characteristics of *M. polymorpha*, soil nutrient availability, and WUE.

For the third question, we propose a definition of the "openness" of the nitrogen cycle in terms of the relative importance of within-system cycling versus inputs/outputs. In drier sites, reduced plant demand as a result of water stress coupled with a less pronounced effect of low water availability on decomposition and nutrient release result in large, standing soil pools of inorganic nitrogen (particularly nitrate). These relatively labile pools could be subject to loss through leaching because of infrequent large storms or lost in gaseous form through ammonia volatilization. While the magnitude of loss may be smaller, the loss relative to nitrogen cycled between plants and soil could be large, resulting in an open nitrogen cycle at the drier sites. With increasing rainfall, increased production should lead to increased plant uptake and a larger organic carbon pool in soil and litter. Higher soil carbon availability would favor nutrient immobilization, and together with increased plant demand results in decreasing inorganic soil nitrogen and an increasing organic nitrogen pool. The retention of nitrogen in these wetter sites could increase, leading to smaller losses from the system relative to turnover between soils and vegetation. We assessed openness of nitrogen cycling by examining the patterns in soil and foliar concentrations of nitrogen and δ^{15}N. δ^{15}N represents an integrated measure of nitrogen dynamics over time; δ^{15}N has been used in several studies to interpret nitrogen transformations at the ecosystem level (Schulze et al. 1991; Abbadie et al. 1992; Evans and Ehleringer 1993; Högberg and Johannisson 1993; Shearer and Kohl 1993). Nearly all nitrogen transformation processes fractionate preferentially for ^{14}N (Handley and Raven 1992), generally resulting in more positive signatures in soil due to losses of ^{15}N-depleted nitrogen. Vegetation values are generally less positive than soil values (Lajtha and Marshall 1994), reflecting the uptake by plants of relatively ^{15}N-depleted, inorganic nitrogen (Nadelhoffer and Fry 1994). The patterns of δ^{15}N in soils and vegetation represented the integrated dynamics of nitrogen cycling along this rainfall gradient.

Materials and methods

Sites

The occurrence of broad climatic variation in a relatively small geographic area and a relatively simple geology and flora (Carlquist 1980; Wagner et al. 1990; Vitousek and Benning 1995) make Hawai'i a good location to test hypotheses about carbon/nutrient interactions with changing water availability. We identified a natural precipitation gradient consisting of five sites ranging from 500 mm to 5500 mm mean annual precipitation.

The five study sites were located near 700 m elevation on the island of Hawai'i (Fig. 1). The dominant wind pattern is the northeast trade wind, which brings year-round precipitation to most of the northeast part of the island (Giambelluca et al. 1986). However, the masses of Mauna Loa and Mauna Kea Volcanoes (elevation 4169 m and 4205 m respectively) prevent precipitation from reaching the west and northwest sides of the island, resulting in much drier conditions on the leeward slopes (Carlquist 1980). These parts of the island receive precipitation through the action of daytime, sea-to-land breezes resulting from the differential heating of land and ocean, which are maximum during the summer months (Price 1983). As a result, Hawai'i supports a wide gradient of precipitation at a single elevation in a small area.

Three of the sites were on lava flows from Mauna Loa Volcano, while two sites were located on Hualalai Volcano. The geology of both Hualalai and Mauna Loa have been well mapped, and the age of many of the flows is known with precision. The substrate age at each of the sites was between 2300 and 2800 years (Lockwood et al. 1988; Moore and Clague 1991). We conducted sampling in areas with relatively gentle slopes at all sites to minimize possible complications from run-on and upslope effects. Community composition varied from an open-canopied, savanna-type forest, dominated by *Metrosideros polymorpha* Gaud. (Myrtaceae) and *Diospyros sandwicensis* (A. DC.) Fosb (Ebenaceae) at the driest extreme to a close-canopied multistoried forest dominated by *M. polymorpha* and *Acacia koa* Gray (Fabaceae) at the wettest site (Wagner et al. 1990). Many of the plant species were present in two or more sites, while other species were restricted to a single site. *M. polymorpha* was present at all sites and was the dominant species at four of the five sites. Only a pubescent variety (var. *incana*) of *M. polymorpha* was found at the drier sites and only a glabrous variety (var. *glaberrima*) was found at the wetter sites (Stemmerman 1983). General site characteristics are described in Table 1.

Soil analysis

Surface soil samples were taken at each site in a stratified design in June 1995. In general, the nature of ‘a’a lava flows does not allow

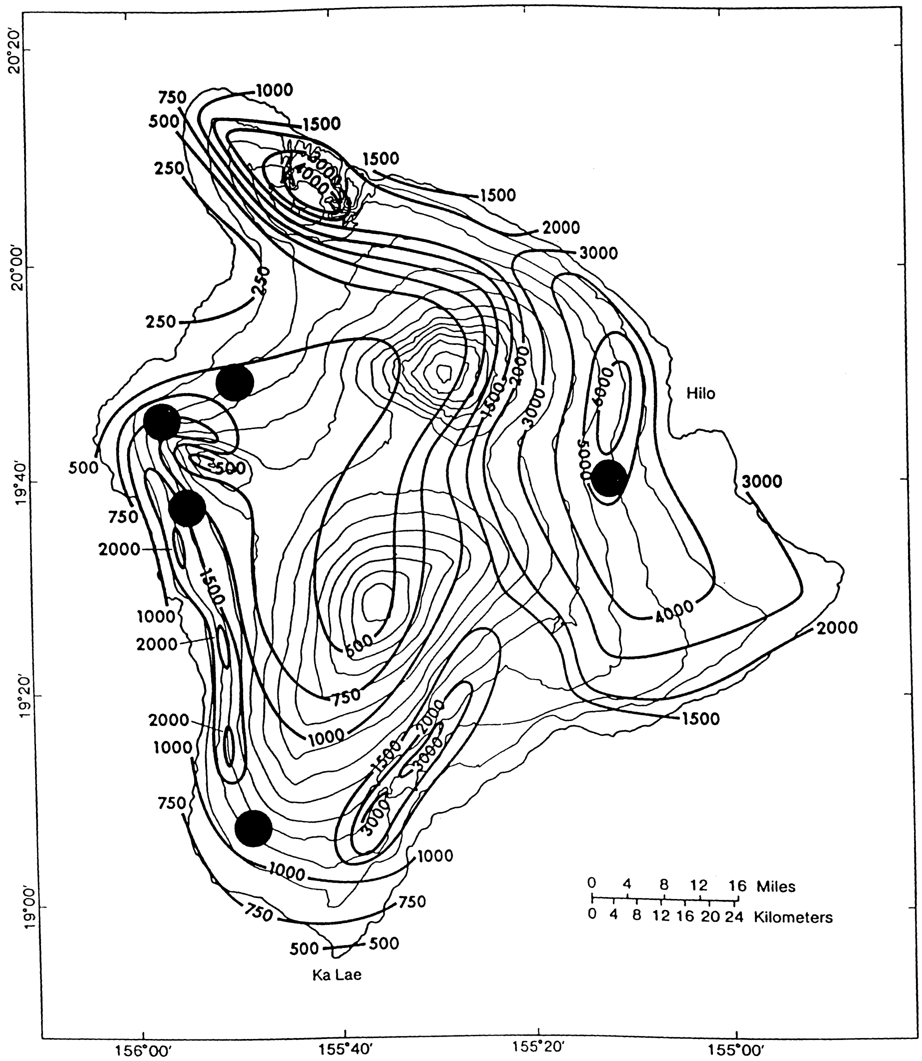

Fig. 1 Location of study sites along precipitation gradient on the island of Hawai’i. All sites are located at 700 m elevation, on ‘a’a flows aged 2500 ± 300 years. Isohyets are mean annual precipitation (MAP) in mm, elevation in 300 m intervals. Taken from Giambelluca et al. (1986)

Table 1 Climate and age characteristics for sites sampled along precipitation gradient in Hawai’i. Mean annual precipitation values were determined from Giambelluca et al. (1986). Flow ages, elevation and origin were determined from maps for Mauna Loa (Lockwood et al. 1988) and Hualalai (Moore and Clague 1991) and personal communication with J. Lockwood. Dominant vegetation type from Wagner et al. 1991

Site	Name	Precipitation (mm)	Flow age	Elevation (m)	Volcano	Dominant vegetation
1	Kaniku	500	2800	700	Mauna Loa	*Metrosideros-Diospyros* forest
2	Kaupulehu	900	2800	680	Hualalai	*Diospyros* forest
3	Manuka	1500	2330	710	Mauna Loa	*Metrosideros-Nestigis* forest
4	Kaloko	2000	2300	705	Hualalai	*Metrosideros-Psychotria* forest
5	Waiakea	5500	2300	710	Mauna Loa	*Metrosideros-Acacia* forest

for the development of a true soil profile. Organic matter and weathered parent material collect in the interstices of the rocks, and the result is a patchy distribution of fine material among the original ‘a’a rocks. Whenever possible, we sampled the top 10 cm of soil, but at the two driest sites (Kaniku and Kaupulehu), we collected soil in crevices of the ‘a’a flows. At all sites, we located five 50-m transects, spaced 20 m apart. Samples were taken at 10-m intervals along each transect, and then all samples from the transect were composited and treated as a sample. Within 48 h, we determined soil moisture for each composite sample by drying a subsample in a 105°C oven for 48 h, and we extracted a 10-g soil sample (5 g for the Kaniku site) in 75 ml (50 ml for the Kaniku site) 2 M KCl to determine concentrations of inorganic ammonium and nitrate. A second sample from each transect was incubated at ambient soil moisture for 14 days and then extracted in 2 M KCl for determination of net mineralization. A subsample of each composite was analyzed in a soil slurry of 1:1 with distilled water for pH; another subsample was acid-digested for total nitrogen and phosphorus using a standard Kjehdahl acid-digestion procedure. Concentrations of magnesium, potassium, and calcium were determined by extraction of 10 g of soil in 50 ml of 2 M NaCl and analysis of extracts with an atomic absorption spectrophotometer. We determined inorganic phosphate concentrations in soils by extraction in water with anion-exchange-resin bags and subsequent extraction of resin bags in 0.5 M HCl. All extracts for nitrogen and phosphorus were analyzed colorimetrically on an Alpkem autoanalyzer.

Foliar analysis

We collected small branches of *M. polymorpha* and other overstory species in full sunlight in all of the sites and collected fully developed, mature leaves closest to the developing bud. While leaf-age differences could be important (Reich et al. 1992), we used this consistent method of collection in order to minimize possible developmental differences in leaf growth among the sites. Leaves taken from each individual tree were placed in plastic bags on ice within hours of collection and were treated collectively as a single sample. We measured leaf areas within 48 h of collection using a Delta-T leaf-area meter. Samples were oven-dried at 70°C for at least 48 h and then weighed to determine leaf mass per area. We ground the dried leaves in a 20-mesh Wiley mill, and subsamples were analyzed for foliar nitrogen and phosphorus using a standard Kjehldahl acid-digestion procedure. Extracts were analyzed with an Alpkem autoanalyzer. We combusted a second subsample in a 500°C muffle furnace, extracted the ash in nitric acid, and determined concentrations of magnesium, calcium, and potassium of the extracts using an atomic absorption spectrophotometer. Finally, lignin concentrations in *M. polymorpha* were determined using a modified acetyl bromide procedure, with extracts analyzed with a Hitachi U-2000 spectrophotometer (Morrison 1972; Iiyama and Wallis 1990).

Isotopic analysis

Five samples of *M. polymorpha* from each site, a composite sample of each of the other native trees, and five composite soil samples from each site were ground to a fine powder in a ball mill grinder and sent for analysis to the University of Utah Stable Isotope Facility for Environmental Research in Salt Lake City. Foliar samples were analyzed for δ^{13}C and δ^{15}N (expressed in parts per mil, ‰), while soils were analyzed for δ^{15}N only, following methods described in Evans and Ehleringer (1993) and Ehleringer and Cooper (1988). Values are expressed relative to the PDB standard for δ^{13}C and relative to atmospheric nitrogen for δ^{15}N, according to the following equation:

$$\partial Z = \left[(R_{\text{sample}})/(R_{\text{standard}}) - 1\right] \times 1000$$

where Z = the heavy isotope of either nitrogen or carbon, and R = ratio of heavier to lighter isotope for the sample and standard (^{13}C/^{12}C or ^{15}N/^{14}N).

Statistical analysis for soils and *M. polymorpha* leaves involved a series of one-way ANOVA with mean annual precipitation as the treatment effect. *Post hoc* mean comparisons were completed using the Tukey-Kramer honestly significant difference (HSD) test. Soil values were log-transformed in order to correct for non-normality, while the analysis for *M. polymorpha* used untransformed data, with a significance level of 5% in all cases.

Results

Soils

Concentrations of inorganic NO_3-N, NH_4-N, and PO_4-P varied significantly across the gradient ($P < 0.001$, 0.01, and 0.001, respectively). For NO_3-N, PO_4-P, and total inorganic nitrogen (NO_3-N + NH_4-N), concentrations were highest at the driest site, and they declined monotonically with increasing precipitation (Fig. 2). Major cations (Ca, Mg, and K) in soils generally decreased with increasing precipitation (Fig. 3). Other changes in soil characteristics included a decrease in soil pH (6.3–5.0) with increasing precipitation (Table 2). Nitrogen mineralization from laboratory incubations did not differ significantly from zero at any of the sites (Table 2). δ^{15}N values in soil were consistently positive with mean values ranging from +4.10‰ to +0.76‰. They became significantly less enriched ($P < 0.001$) with increasing rainfall.

Vegetation

Because *M. polymorpha* is present at all sites, results for this species are considered separately from the other native-forest species. For *M. polymorpha*, LMA decreased among sites with increasing rainfall ($P < 0.001$) from 220 g/m^2 at the driest site to 145 g/m^2 at the wettest site (Fig. 4). Foliar phosphorus and cation concentrations varied significantly with increasing precipitation ($P < 0.01$, and $P < 0.005$ respectively), while nitrogen did not (Figs. 2 and 3). Because of the dramatic decrease in LMA across the gradient, however, all nutrients decreased significantly with increasing precipitation on a per unit leaf area basis (Table 3). Lignin concentrations increased with increasing precipitation from 11.4% to 19.9% ($P < 0.001$) (Fig. 4), as did lignin:nitrogen concentrations, ranging from 12.1 to 20.8 ($P < 0.05$) with increasing precipitation (Table 3). δ^{13}C values became more depleted ($P < 0.001$), with mean values from −25.6‰ to −29.0‰ (Table 4). Foliar δ^{15}N values for *M. polymorpha* were significantly more depleted with increasing precipitation ($P < 0.001$), with values ranging from +0.45‰ to −3.38‰ (Fig. 5).

The other native forest species showed some trends similar to *M. polymorpha*, although the results were not analyzed statistically due to small sample sizes and the discontinuous occurrence of many of the species. Interspecific variation within a site was greater than the intraspecific differences observed for *M. polymorpha* among sites (Table 4). The unweighted average for all

Fig. 2A–D Nitrogen and phosphorus concentrations for soil and foliar *Metrosideros polymorpha* for five sites across precipitation gradient. Each *bar* represents mean (+SE). For soils, $n = 5$ composited transect samples, for *M. polymorpha*, $n = 8$. **A** Extractable inorganic soil nitrogen concentrations. SE bars are for total nitrogen (NO_3-N + NH_4-N). **B** Resin-extractable soil phosphorus (PO_4-P). **C** Foliar nitrogen concentrations of *M. polymorpha*. **D** Foliar phosphorus concentrations of *M. polymorpha*

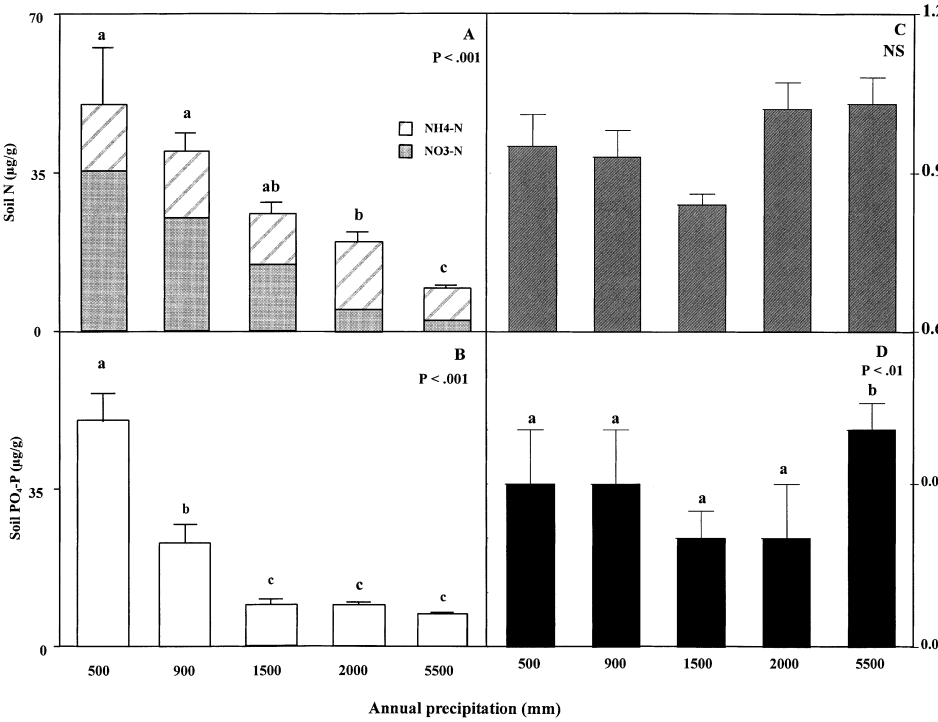

Fig. 3A–F Cation concentrations (Ca, Mg, K) in soil and *Metrosideros polymorpha*, for five sites across precipitation gradient. Each *bar* represents mean (+SE). For soils, $n = 5$ composited transect samples; for *M. polymorpha*, $n = 8$. **A** Extractable soil calcium. **B** Extractable soil magnesium. **C** Extractable soil potassium. **D** Foliar calcium concentrations of *M. polymorpha*. **E** Foliar magnesium concentrations of *M. polymorpha*. **F** Foliar potassium concentrations of *M. polymorpha*

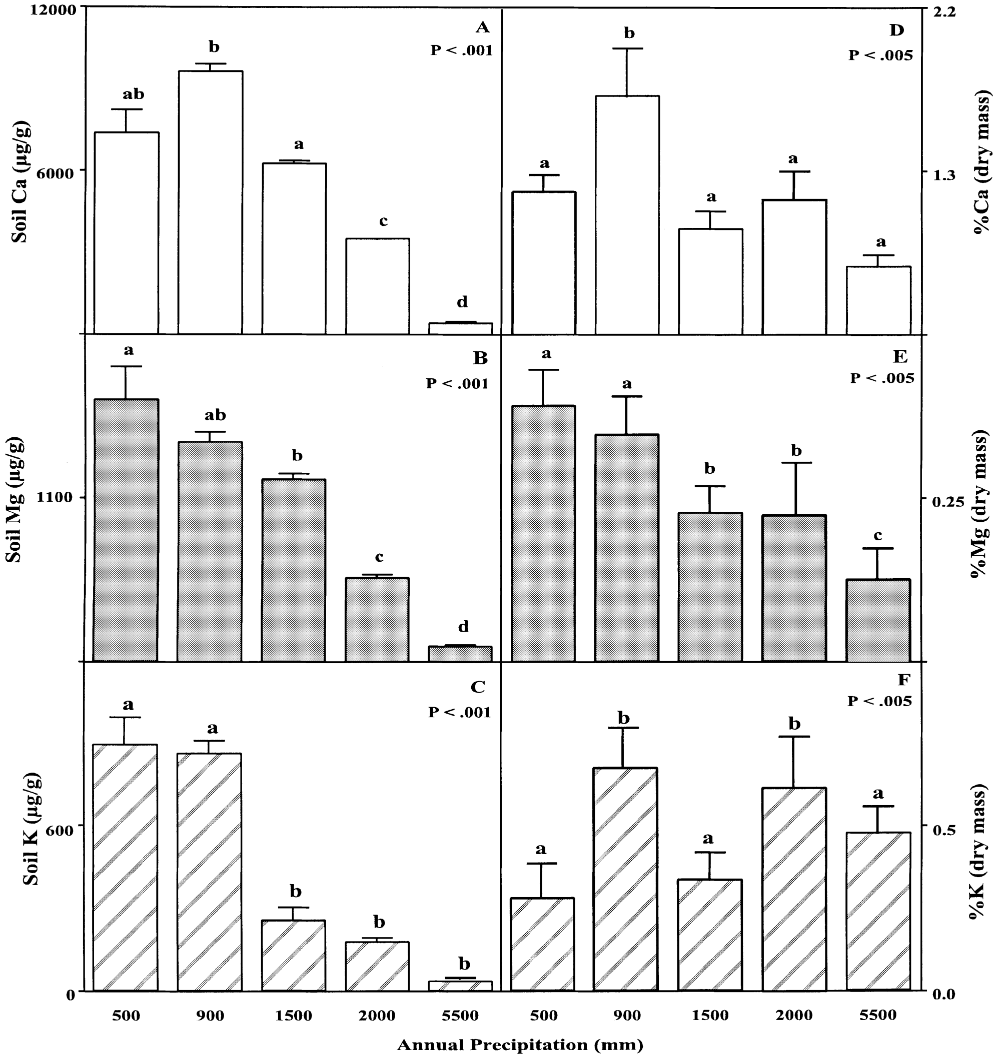

Table 2 Soil characteristics and nitrogen mineralization for transects from sites along precipitation gradient in Hawai'i. Soils were sampled at 0–10 cm, and were composited by transect. Values are mean (± SE) of five transects (*MAP* mean annual precipitation)

Site	Name	MAP (mm)	Soil pH	Total N (µg/g soil)	Total P (µg/g soil)	N min (µg/g/day)
1	Kaniku	500	6.34 ± .04	19412 ± 546	2848 ± 65	−0.085 ± .19
2	Kaupulehu	900	6.82 ± .04	26449 ± 331	2771 ± 39	−0.393 ± .49
3	Manuka	1500	6.62 ± .03	19323 ± 214	2104 ± 35	0.018 ± .16
4	Kaloko	2000	5.94 ± .04	20891 ± 222	2754 ± 76	−0.132 ± .08
5	Waiakea	5500	5.00 ± .06	11844 ± 272	1762 ± 25	−0.035 ± .19

Table 3 Foliar nutrients per unit leaf area and lignin:nitrogen ratios for *Metrosideros polymorpha* along precipitation gradient. Values are mean of 8 samples ± SE. Tests for one-way ANOVA were significant at $P < 0.001$ for all nutrients except potassium, for potassium and lignin:nitrogen, $P < 0.05$

Site	Name	MAP (mm)	Foliar N (g/m²)	Foliar P (g/m²)	Foliar Ca (g/m²)	Foliar Mg (g/m²)	Foliar K (g/m²)	Lignin:N ratio
1	Kaniku	500	2.05 ± .08	0.142 ± .005	2.74 ± .34	0.824 ± .090	0.598 ± .078	12.07 ± 2.04
2	Kaupulehu	900	1.88 ± .11	0.143 ± .007	3.65 ± .73	0.664 ± .079	1.34 ± .438	13.76 ± 3.52
3	Manuka	1500	1.46 ± .11	0.097 ± .006	1.59 ± .29	0.387 ± .040	0.562 ± .067	18.18 ± 0.22
4	Kaloko	2000	1.44 ± .11	0.090 ± .005	1.63 ± .33	0.340 ± .096	0.865 ± .084	17.30 ± 4.15
5	Waiakea	5500	1.47 ± .09	0.118 ± .007	1.04 ± .18	0.231 ± .034	0.668 ± .059	20.72 ± 6.05

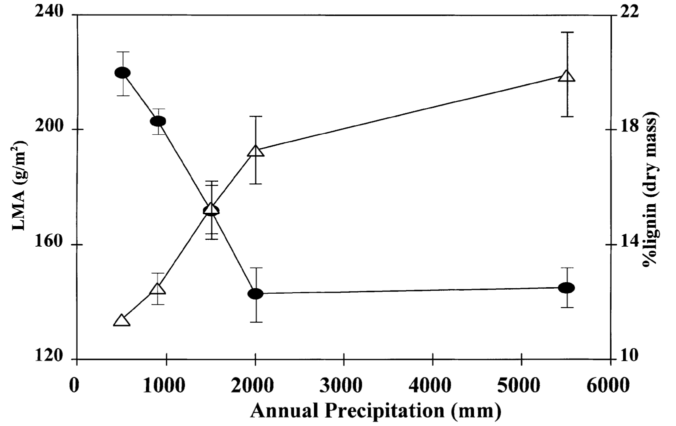

Fig. 4 Variation in leaf mass per area (LMA) and lignin concentrations of *M. polymorpha*. Symbols represent mean values ($n = 8$), (±SE) (● LMA (g/m²); △ % lignin, dry mass)

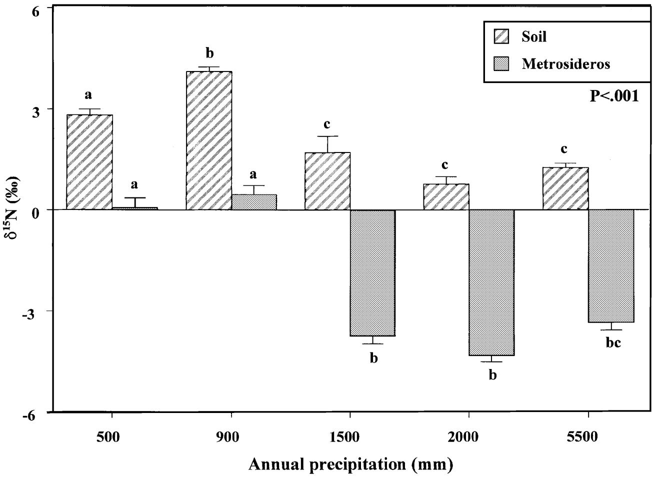

Fig. 5 Variation in $\delta^{15}N$ values (‰) for soil and foliar *M. polymorpha* from all sites across precipitation gradient. Data are mean values ($n = 5$) ± SE

species sampled (including *M. polymorpha*) generally had lower LMA and depleted $\delta^{15}N$ and $\delta^{13}C$ signatures with increasing precipitation (Table 4). The foliar nutrients were similar among sites for nitrogen, calcium, and magnesium, while phosphorus and potassium decreased between the two driest sites and the three wetter sites.

Discussion

Available soil nutrients

The decreasing concentrations of rock-derived nutrients in soils (PO_4-P, Ca, Mg, and K) as precipitation increases suggest that the effect of the increase in precipitation on leaching exceeds its effect on weathering and deposition in the wetter sites (Figs. 2 and 3). This decline in soil nutrient concentrations is seen in the foliar nutrients phosphorus, magnesium, and calcium, suggesting that these soil concentrations could represent relative availability for plant uptake for these nutrients (Figs. 2 and 3). A similar pattern was observed in oak woodlands in Spain, where soil cation concentrations were inversely correlated with precipitation along an arid rainfall gradient (Quilchano et al. 1993). In addition, rates of weathering and leaching on an independent precipitation gradient in the Kohala region of Hawai'i demonstrated a fourfold increase in cation leaching with increasing rainfall (Chadwick et al. 1993). Our results do not address overall nutrient supplying power of soil; greater volume of soil and perhaps faster turnover (not observed here) could mean higher nutrient availability at wetter sites. This pattern of declining inorganic nutrients with increasing precipitation, however, clearly shows that the balance between inputs and loss results in a large pool of available rock-derived nutrients in the drier sites.

Table 4 Leaf mass per area (LMA), foliar nitrogen, phosphorus, major cations, δ^{15}N, and δ^{13}C for native overstory species from sites along the precipitation gradient in Hawai'i. All concentrations are percent dry weight, and values are means with SE in parentheses. Where no SE is reported, a single or composite sample was analyzed. Species names from Wagner et al. (1990)

	Kaniku	Kaupulehu	Manuka	Kaloko	Waiakea
Species	LMA	LMA	LMA	LMA	LMA
Acacia koa					140 (2)
Antidesma platyphyllum			97 (12)	72	94 (11)
Canthium odoratum	181 (20)	214 (17)	115 (7)		
Diospyros sandwicensis	215 (12)	252 (10)	141 (6)		
Freycinetia arborea				105 (5)	60 (5)
Myrsine spp.	164		99 (10)	69 (14)	83
Metrosideros polymorpha	220 (12)	203 (21)	172 (11)	143 (11)	145 (9)
Nestegis sandwicensis			111 (8)		
Psychotria hawaiiense			101 (8)	120 (13.5)	133
Pouteria sandwicensis	206 (4)	202 (12)			
Santalum ellipticum	175 (10)	159 (25)			
Xylosma hawaiiense	108 (3)	113 (12)			
Average	181 (15)	190 (20)	119 (11)	102 (18)	108 (20)

	Kaniku	Kaupulehu	Manuka	Kaloko	Waiakea
Species	%N	%N	%N	%N	%N
Acacia koa					2.37 (.54)
Antidesma platyphyllum			1.22 (.02)	1.38	1.17 (.11)
Canthium odoratum	1.27 (.11)	1.30 (.15)	1.35 (.15)		
Diospyros sandwicensis	0.86 (.05)	0.87 (.05)	0.93 (.06)		
Freyeinetia arborea				1.05 (.21)	1.58 (.22)
Myrsine spp.	1.27		1.06 (.06)	1.21 (.22)	1.13 (.13)
Metrosideros polymorpha	0.95 (.06)	0.93 (.05)	0.84 (.02)	1.02 (.05)	1.03 (.05)
Nestegis sandwicensis			1.27 (.06)		
Psychotria hawaiiense			1.51 (.05)	1.39 (.08)	1.23
Pouteria sandwicensis	1.67 (.06)	1.70 (.08)			
Santalum ellipticum	1.13 (.08)	0.96 (.07)			
Xylosma hawaiiense	1.49 (.12)	1.40 (.21)			
Average	1.23 (.11)	1.19 (.13)	1.16 (.10)	1.21 (.09)	1.42 (.11)

	Kaniku	Kaupulehu	Manuka	Kaloko	Waiakea
Species	%P	%P	%P	%P	%P
Acacia koa					0.10 (.01)
Antidesma platyphyllum			0.07 (.01)	0.09	0.07 (.01)
Canthium odoratum	0.18 (.05)	0.10 (.02)	0.09 (.02)		
Diospyros sandwicensis	0.11 (.02)	0.07 (.01)	0.07 (.01)		
Myrsine spp.	0.20		0.07 (.01)	0.11 (.02)	0.09 (.01)
Metrosideros polymorpha	0.07 (.01)	0.07 (.01)	0.06 (.00)	0.06 (.01)	0.08 (.00)
Nestegis sandwicensis			0.08 (.01)		
Psychotria hawaiiense			0.09 (.01)	0.08 (.01)	0.09
Pouteria sandwicensis	0.18 (.03)	0.15 (.06)			
Santalum ellipticum	0.08 (.01)	0.24 (.06)			
Xylosma hawaiiense	0.12 (.02)	0.11 (.02)			
Average (SE)	0.13 (.02)	0.12 (.03)	0.07 (.01)	0.09 (.01)	0.09 (.01)

	Kaniku	Kaupulehu	Manuka	Kaloko	Waiakea
Species	%Ca	%Ca	%Ca	%Ca	%Ca
Acacia koa					0.48 (.14)
Antidesma platyphyllum			2.44 (.44)	2.14	1.80 (.47)
Canthium odoratum	1.36 (.23)	1.55 (.34)	1.30 (.15)		
Diospyros sandwicensis	1.43 (.18)	1.65 (.25)	1.97 (.32)		
Freycinetia arborea				2.08 (.19)	2.10 (.56)
Myrsine spp.	1.94		1.99 (.45)	1.18 (.15)	1.33 (.13)
Metrosideros polymorpha	1.21 (.11)	1.81 (.33)	0.88 (.11)	1.08 (.16)	0.73 (.14)
Nestegis sandwicensis			1.87 (.38)		
Psychotria hawaiiense			2.62 (.51)	1.77 (.28)	1.01
Pouteria sandwicensis	1.83 (.18)	1.39 (.19)			
Santalum ellipticum	0.90 (.15)	1.67 (.53)			

Table 4 (Contd.)

	Kaniku	Kaupulehu	Manuka	Kaloko	Waiakea
Species	%Ca	%Ca	%Ca	%Ca	%Ca
Xylosma hawaiiense	1.62 (.16)	1.59 (.63)			
Average	1.47 (.14)	1.61 (.06)	1.86 (.25)	1.65 (.28)	1.24 (.29)

	Kaniku	Kaupulehu	Manuka	Kaloko	Waiakea
Species	%Mg	%Mg	%Mg	%Mg	%Mg
Acacia koa					0.13 (.02)
Antidesma platyphyllum			0.33 (.01)	0.27	0.37 (.12)
Canthium odoratum	0.36 (.08)	0.20 (.02)	0.32 (.05)		
Diospyros sandwicensis	0.21 (.02)	0.19 (.01)	0.21 (.02)		
Freycinetia arborea				0.39 (.02)	0.43 (.01)
Myrsine spp.	0.32		0.39 (.14)	0.34 (.03)	0.39 (.06)
Metrosideros polymorpha	0.37 (.03)	0.33 (.03)	0.23 (.02)	0.23 (.06)	0.16 (.03)
Nestegis sandwicensis			0.26 (.04)		
Psychotria hawaiiense			0.52 (.09)	0.36 (.03)	0.37
Pouteria sandwicensis	0.37 (.03)	0.28 (.02)			
Santalum ellipticum	0.51 (.09)	0.32 (.05)			
Xylosma hawaiiense	0.47 (.02)	0.38 (.06)			
Average	0.37 (.04)	0.28 (.03)	0.32 (.05)	0.31 (.04)	0.31 (.06)

	Kaniku	Kaupulehu	Manuka	Kaloko	Waiakea
Species	%K	%K	%K	%K	%K
Acacia koa					0.59 (.05)
Antidesma platyphyllum			0.72 (.14)	1.18	0.50 (.08)
Canthium odoratum	0.75 (.12)	0.77 (.12)	1.31 (.31)		
Diospyros sandwicensis	0.96 (.10)	0.93 (.06)	1.10 (.22)		
Freycinetia arborea				1.36 (.25)	1.07 (.29)
Myrsine spp.			1.08 (.29)	0.92 (.15)	1.29 (.14)
Metrosideros polymorpha	0.29 (.05)	0.71 (.01)	0.34 (.04)	0.66 (.12)	0.47 (.06)
Nestegis sandwicensis			0.75 (.08)		
Psychotria hawaiiense			1.08 (.29)	0.92 (.26)	1.29
Pouteria sandwicensis	1.23 (.24)	1.47 (.24)			
Santalum ellipticum	3.58 (.63)	4.35 (.40)			
Xylosma hawaiiense	0.97 (.06)	1.56 (.48)			
Average	1.29 (.44)	1.63 (.56)	0.91 (.14)	1.09 (.20)	0.81 (.17)

	Kaniku	Kaupulehu	Manuka	Kaloko	Waiakea
Species	δ^{15}N	δ^{15}N	δ^{15}N	δ^{15}N	δ^{15}N
Acacia koa					−1.10 (.25)
Antidesma platyphyllyum			−3.30	−3.20	−3.40
Canthium odoratum	−1.30 (.71)	−0.70 (.30)	−3.73 (.78)		
Diospyros sandwicensis	−1.10 (.33)	−0.03 (.48)	−3.18 (.22)		
Freycinetia arborea				−3.60	−3.00
Myrsine spp.	−0.30		−3.56 (.08)	−3.90 (.25)	−3.60 (1.2)
Metrosideros polymorpha	+0.04 (.30)	+0.45 (.29)	−3.78 (.19)	−4.36 (.16)	−3.38 (.18)
Nestegis sandwicensis			−3.90		
Psychotria hawaiiense			−3.20 (.69)	−3.43 (.38)	−2.20
Pouteria sandwicensis	+0.70	−1.80			
Santalum ellipticum	−0.20	−2.00			
Xylosma hawaiiense	+0.80	+1.00			
Average	−0.19 (.30)	−0.51 (.49)	−3.52 (.12)	−3.70 (.23)	−2.89 (.16)

	Kaniku	Kaupulehu	Manuka	Kaloko	Waiakea
Species	δ^{13}C	δ^{13}C	δ^{13}C	δ^{13}C	δ^{13}C
Acacia koa					−28.5 (.71)
Antidesma platyphyllyum			−29.1	−32.4	−31.6
Canthium odoratum	–25.5 (.63)	–25.3 (.53)	–29.9 (.62)		
Diospyros sandwicensis	–25.8 (.18)	–25.6 (.58)	–27.2 (.25)		
Freycinetia arborea				−27.4	−32.0

Table 4 (Contd.)

	Kaniku	Kaupulehu	Manuka	Kaloko	Waiakea
Species	$\delta^{13}C$	$\delta^{13}C$	$\delta^{13}C$	$\delta^{13}C$	$\delta^{13}C$
Myrsine spp.	–23.6		–29.6 (.24)	–28.8 (1.1)	–29.9 (.26)
Metrosideros polymorpha	–27.7 (1.1)	–26.4 (.98)	–25.8 (.43)	–29.0 (.23)	–28.6 (.50)
Nestegis sandwicensis			–29.6		
Psychotria hawaiiense			–28.2 (.44)	–27.4 (.67)	–29.0
Pouteria sandwicensis	–26.2	–24.6			
Santalum ellipticum	–26.3	–26.2			
Xylosma hawaiiense	–24.1	–24.4			
Average	–25.6 (.52)	–25.4 (.33)	–28.4 (.66)	–29.0 (.50)	–29.9 (.75)

Carbon/nutrient interactions

Changes in the structure and carbon chemistry of *M. polymorpha* leaves (Fig. 4, Tables 3 and 4) along the gradient suggest a shift in the relative importance of carbon versus nutrient resources along this moisture gradient. The patterns of decreased leaf mass per area, increased lignin, more depleted foliar $\delta^{13}C$, and decreasing foliar nutrients per unit leaf area with increasing precipitation collectively support the suggestion that the moisture gradient also represents a gradient from relatively nutrient-rich, water-use efficient (WUE) systems in the drier sites, to relatively carbon-rich, nutrient-use-efficient ecosystems in wetter sites. The significantly depleted $\delta^{13}C$ values in *M. polymorpha* ($P < 0.001$) and the trend for decreased $\delta^{13}C$ in all species (Table 4) suggest that WUE changes systematically across the precipitation gradient. The pattern has been observed elsewhere and interpreted as reflecting plant response to water availability (Ehleringer and Cooper 1988; Garten and Taylor 1992; Stewart et al. 1995). Earlier studies of variation in $\delta^{13}C$ in *M. polymorpha* ascribed variation in $\delta^{13}C$ to both differences in intrinsic WUE and to internal resistance, with intrinsic WUE making the largest contribution in contrasts between dry and wet extremes (Vitousek et al. 1990; Meinzer et al. 1992).

The observed decline in LMA with increasing precipitation (Fig. 4) is consistent with many other studies demonstrating decreased LMA with higher water availability (e.g. Oren et al. 1986; Vitousek et al. 1992; Anderson et al. 1996). While leaf mass per area also varies with nutrient supply (Körner and Diemer 1987; Vitousek et al. 1992; Joel et al. 1995), the effect of low water availability overwhelms the effect of higher nutrient availability in the drier sites in this study. The substantial increase in lignin concentrations in wetter sites (Fig. 4) further supports the suggestion that net carbon gain increases with increasing precipitation; lignin is a carbon-rich, relatively energetically expensive set of compounds (Crawford 1981).

The patterns of foliar and soil nutrients also suggest changes in plant demand for nutrients along the gradient. The fact that soil nutrient concentrations dramatically decrease with increasing precipitation, with a consequent increase in plant cover suggest that water availability is the overriding constraint on production in the drier sites, rather than nutrient availability. As the water constraint on carbon fixation decreases with increasing precipitation, nutrient uptake by vegetation will simultaneously increase. It is not possible to disengage the direct effects of precipitation on the weathering and leaching balance from the indirect effects of precipitation on changes in vegetation on nutrient uptake and turnover, which can contribute substantially to differences in soil nutrient status (Vinton and Burke 1995). It is the interaction of these abiotic and biotic effects of precipitation which ultimately determines patterns of both nutrient supply and demand on this gradient.

Openness of nitrogen cycling

The balance between inputs and outputs of nitrogen can be evaluated using $\delta^{15}N$, which provides an integrated measure of factors affecting nitrogen dynamics over time (Nadelhoffer and Fry 1988; Handley and Raven 1992). The changes in $\delta^{15}N$ values in both soils and vegetation along this natural precipitation gradient can be used to identify the pattern of nitrogen losses relative to turnover among these sites. Two components could shape whole-ecosystem $\delta^{15}N$ signatures. First is the importance of nitrogen fixation compared to deposition, which comprise the inputs of nitrogen. Biological nitrogen fixation adds organic nitrogen with $\delta^{15}N$ near 0‰ (Shearer and Kohl 1986), while deposition in precipitation, although quite variable, in general is strongly depleted in $\delta^{15}N$, particularly in unpolluted areas (Freyer 1978; Wada et al. 1981; Heaton 1987; Garten 1991). Very young soils in Hawai'i whose dominant nitrogen input is atmospheric deposition have negative $\delta^{15}N$ values (Vitousek et al. 1989). While inputs by both pathways could increase with increasing rainfall, and while the ratio of fixation to deposition could change, overall nitrogen inputs should be ^{15}N depleted, or near 0‰.

The second component determining soil $\delta^{15}N$ is the relative importance of nitrogen outputs by fractionating pathways. Nitrification, denitrification, and ammonia volatilization all fractionate nitrogen, so the nitrogen lost through leaching and nitrogen transformations is depleted in ^{15}N relative to the soil. Consequently, the nitrogen remaining in systems is ^{15}N-enriched (Nadelhoffer and Fry 1994). Most soils have positive δ^{15}N values, due to accumulated losses of ^{15}N-depleted nitrogen during soil development (Shearer and Kohl 1989; Handley and Raven 1992). Other studies show clear associations between enriched soil δ^{15}N and loss of nitrogen in both disturbed and fertilized sites (Evans and Ehleringer 1993; Högberg and Johannisson 1993); the degree of enrichment should be greater when accumulated losses are large in comparison to the nitrogen pool in the system.

The consistently positive soil δ^{15}N clearly indicates that fractionation due to nitrogen transformations and leaching loss must constitute part of the δ^{15}N signature (Fig. 5). Conversion of organic nitrogen to ammonium and nitrate through mineralization and nitrification would enrich soil δ^{15}N as ^{15}N-depleted gaseous products are lost, and that with increased turnover, there would be increasing enrichment of the total soil nitrogen pool (Nadelhoffer and Fry 1994). The fact that the pattern of both soils and vegetation is increasingly depleted in wetter sites indicates that in spite of potentially more rapid turnover, accumulated losses of nitrogen relative to pools are greater in the drier sites. That is, nitrogen cycling is more open in drier sites, and becomes less open with increasing precipitation. The fact that the foliar δ^{15}N parallels the soil pattern along the gradient, although depleted relative to the soil signal, indicates that differences in losses among sites are occurring in the actively cycling pools of nitrogen. Moreover, although soil nitrogen declines, foliar nitrogen concentrations in *M. polymorpha* do not (Fig. 2), further suggesting that nitrogen cycling is more closed at these wetter sites. The relative openness of nitrogen cycling in the drier sites indicates that water availability affects ecosystem functioning by other pathways than simply the direct effect of water on ecosystem processes. A moisture gradient in Namibia had a similar pattern of decreasing enrichment of δ^{15}N with increasing annual precipitation, suggesting that the effect of rainfall on the openness of nitrogen cycling could be a general pattern (Schulze et al. 1991).

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