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Net primary productivity and nutrient cycling across a mesic to wet precipitation gradient in Hawaiian montane forest

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Abstract Variation in rainfall in humid tropical forests has the potential to alter patterns of primary productivity andnutrient cycling. Net primary productivity (NPP) and nutrient cycling were measured at six sites similar in temperature regime, parent material, ecosystem age, vegetation and topographical relief, while mean annual precipitation (MAP) varied from 2,200 toover 5,000 mm/year. Aboveground NPP declined by a factor of 2.2 with increased MAP across the precipitation gradient. Increased water availability in excess of plant demand is likely to have decreased the other resources for plant growth. Patterns of nutrient cycling and other factors that affect plant growth suggest that increased nutrient limitation in wetter sites could be the direct cause of the decline in NPP. Foliar nitrogen (N) and soil N availability decreased with increased precipitation, corresponding with the decrease in forest growth. In contrast, patterns of foliar and soil phosphorus (P) did not correspond with the decrease in growth; P availability was highest at either end of the precipitation gradient and lowest across the middle. Natural abundance of δ^{15}N in foliage and soils decreased with increased precipitation, further supporting the idea that N availability declined. Decreased N availability was associated with a decrease in soil reduction-oxidation potentials. Oxygen limitation in soil microsites was a factor at all sites, but became increasingly widespread at higher MAP regimes. There was no strong evidence that soil oxygen availability, expressed in foliar δ^{13}C values, directly limited plant growth. In addition foliar micronutrients either showed no change (Ca, Mg) or declined (Al, Fe) with increased MAP while soil pH was low but constant, suggesting that toxic elements in the soil solution were also not direct factors in decreased plant growth across the gradient. Thus, the decline in NPP with associated MAP appeared to be most directly associated with decreased N availability in these humid forests. Fluctuating anaerobic conditions that increased in intensity and duration with increased rainfall could be a mechanism that slows decomposition and N mineralization while concurrently increasing P solubility from soil mineral-bound pools.

Keywords Tropical forest · Soil oxygen · Carbon isotopes · Nitrogen isotopes · Phosphorus

Introduction

The structure and productivity of montane forests in the humid tropics differs dramatically from lowland forest as a result of moisture and temperature regimes that change with altitude on tropical mountains (Leigh 1975; Grubb 1977). The effect of precipitation alone on forest growth is relatively poorly understood in humid ecosystems because data tend to berelatively scarce for ecosystems where rainfall is abundant (e.g., Lieth and Whittaker 1975; Austin and Vitousek 1998). In such forests, it is likely that moisture supply in excess of plant demand does notact as a resource for biotic processes (Schuur et al. 2001), but instead may suppress forest growth through a variety of mechanisms. For example, high rainfall can increase soil leaching rates (Radulovich and Sollins 1991), leading to low nutrient and low pH conditions. Water also restricts gas diffusion in soil and can limit resupply of oxygen from the atmosphere to the soil (Smith and Tiedje 1979; Richards 1987). In fact, fluctuating anaerobic conditions are widely observed in upland soils that receive high rainfall or have restricted drainage (Nisbet et al. 1989; Magnusson 1992; Silver et al. 1999;

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Hobbie et al. 2000). Anaerobic conditions can restrict root metabolism (Crawford 1982), alter concentrations of toxic elements in soil solution (Ponnamperuma 1972),or slow the mineralization of nutrients from decomposing soil organic matter (Gale and Gilmour 1988; Updegraff et al. 1995). In addition to changes in soil resources, decreased light availability as a result of increased cloudiness is another potential consequence of higher rainfall environments (Bruijnzeel and Veneklaas 1998). Differences in rainfall could increase the intensity of any or all of these limiting factors and thereby control patterns of forest growth in humid areas.

We measured biomass, net primary productivity (NPP), and foliar and soil nutrients to understand how changes in rainfall and nutrient cycling interact to control patterns of growth in mesic to wet montaneforests. We isolated the effect of precipitation by selecting sites on the island of Maui, Hawaii across a gradient of precipitation while minimizing variation in parent material, ecosystem age, temperature regime, and local topography. This natural gradient encompasses both short term consequences of variation in rainfall such as moisture, light, and soil oxygen availability, and long term consequences such as differences in soil weathering that control soil nutrient and element pools. Using this gradient, we asked: (1) does increased precipitation alter rates of NPP in mesic to wet forests when all other state factors remain constant, and (2) what is the effect of variation in rainfall on nutrient availability and other factors that may limit forest growth?

Materials and methods

Site description

In the Hawaiian Islands, state factors controlling ecosystem processes [climate, organisms, relief, parent material, and time (Jenny 1941)] range widelyyet systematically. We selected six montane forest sites on the island of Maui across a gradient of precipitation where the other state factors were relatively constant (Table 1, Fig. 1). The rain shadow created by the 3,055 m Haleakala volcano allowed us to select similar sites over a large range of precipitation while changes in temperature associated

Table 1 Site characteristics across the mesic to wet precipitation gradient. Mean annual precipitation values were interpolated from Giambelluca et al. (1986), and mean annual temperatures were estimated from the Atlas of Hawaii (1983). Substrate age and parent material are from Stearns and MacDonald (1942) and MacDonald et al. (1983)

Site	Elevation (m)	Mean annual precipitation (mm year^{-1})	Mean annual temperature (°C)	Parent material	Substrate Age (years)
1	1,370	2,200	16	Lava and ash	410,000
2	1,370	2,450	16	Lava and ash	410,000
3	1,370	2,750	16	Lava and ash	410,000
4	1,320	3,350	16	Lava and ash	410,000
5	1,300	4,050	16	Lava and ash	410,000
6	1,270	5,050	16	Lava and ash	410,000

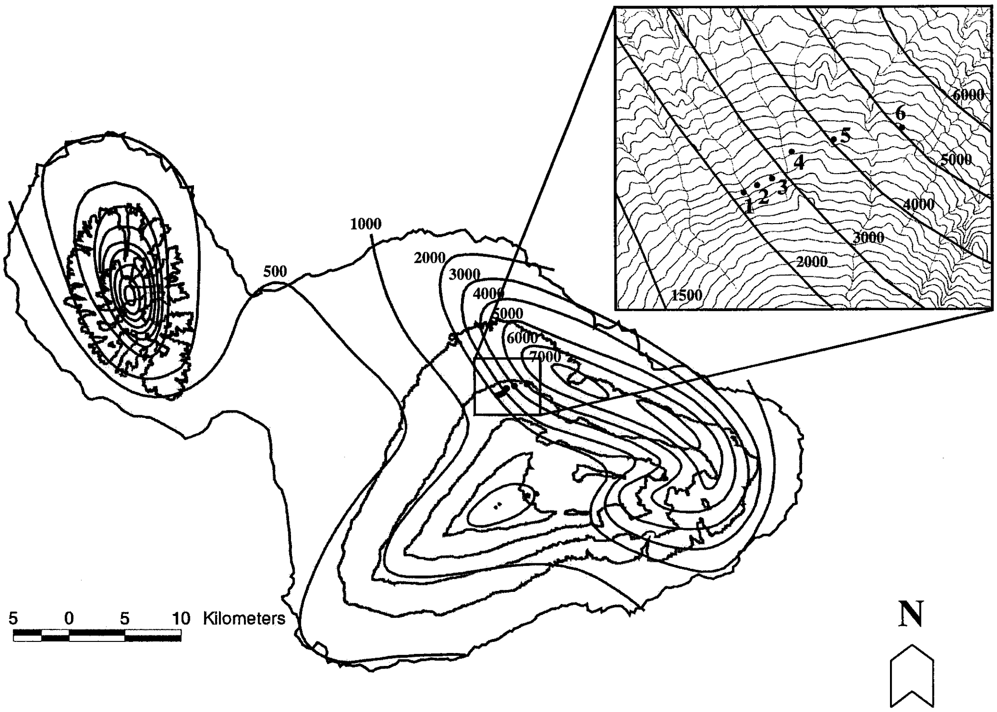

Fig. 1 The location of study sites on the island of Maui, Hawaii showing isohyets (mm) of mean annual precipitation (*black*) and 610 m elevation contours (*grey*). The inset magnifies the study area showing 12.2 m elevation contours and site locations. (GIS database courtesy of S. Joe, Hawaiian ecosystems at risk project, Hawaii Volcanoes National Park, Haleakala, Maui)

with most other altitudinal/climatic gradients were minimized. All sites were located within a geographic distance of less than 5 km in the Makawao and Koolau Forest Reserves on the north flank of Haleakala volcano. Temperature regimes were similar at the constant altitude of the sites (1,300 m) while mean annual precipitation ranged systematically from 2,200 mm/year (mesic) to over 5,000 mm/year (wet) as a function of aspect relative to the prevailing trade winds (Giambelluca et al. 1986). Soil temperature follows air temperature closely in this area due to high soil moisture content (Nullet et al. 1990), and rainfall is aseasonal with sites receiving at least 100 mm rainfall per month, on average and during the study period (Giambelluca et al. 1986). Rainfall during this study period was well correlated with long-term average rainfall estimated for the sites (Pearson r=0.986). Climate characteristics of the sites were monitored during the 1996–1997 study period and are discussed in more detail by Schuur et al. (2001).

The sites were located on lava flows from the Kula volcanic series (mean age 410,000 years) which was part of the shield-building phase of Haleakala volcano (Stearns and MacDonald 1942; MacDonald et al. 1983). The original shield surface has been dissected by steep-sided stream channels, so all study sites were located on shield volcano remnant surfaces on broad, flat (<5% slope) interfluve areas to minimize variation in local topography. The soils are classified as Inceptisolsand Andisols developed from lava with surface ash deposits.

The Hawaiian Islands flora is relatively species-poor; thus a few species and genera occupy a broad range of environmental conditions (Carlquist 1983; Wagner et al. 1990). As a result, the forest canopy at all sites on this gradient was consistently dominated by the native evergreen tree *Metrosideros polymorpha* (Myrtaceae) which can comprise more than 80% of basal area in Hawaiian montane forests (Crews et al. 1995). The understory vegetation was dominated by a variety of ferns and other herbaceous species at all sites, but the dominance of particular understory species shifted among sites. This watershed area has never been cleared by humans and all six sites were located in mature forests stands.

Live and dead biomass

Tree biomass

Aboveground tree biomass was calculated using forest inventory and regression techniques. We established a single 25×25 m productivity plot at each site and measured the diameter at breast height (dbh) of all woody vegetation greater than 5 cm diameter. These measurements were converted to aboveground biomass using species-specific allometric equations derived from other studies in the Hawaiian Islands (Aplet and Vitousek 1994; Raich et al. 1997). For species other than *M. polymorpha*, allometries included tree height measured with an extension pole. Because heights were not available for all *M. polymorpha* trees, we used an allometric equation that relied on dbh alone (J. Raich, unpublished data). Finally, there were several large *Acacia koa* trees at sites 2 and 3. For these, a generalized wet forest allometric equation was used to estimate biomass for those individual trees (Brown and Iverson 1992) because no species-specific allometric equation that includes *A. koa* trees of that size exists.

Understory and litter biomass

The understory biomass (all woody stems <5 cm dbh plus herbaceous vegetation) and the litter layer was harvested from three randomly placed 1×2 m quadrats at each site. We separated harvested biomass into understory components (shrubs, ferns, herbs, bryophytes, litter, and woody litter) and subsampled each homogenized component to determine total dry mass at 70°C. The detrital compartment is the sum of litter, woody litter, and forest floor (Oa horizon, sampled separately in Schuur et al. 2001).

Root biomass

We estimated fine root biomass in cores collected with a 5 cm diameter soil corer (Vogt and Persson 1991). At three randomly located spots at each site, three contiguous 17 cm soil cores were collected to quantify roots to 51 cm depth in the mineral soil. At sites 5 and 6, where there was a significant organic horizon, roots were collected from this horizon in addition to the 51 cm of mineral soil. Roots were sieved, washed, and sorted by size into a <2 mm diameter size class and a 2–5 mm size class, but all size classes were subsequentlycombined because 2–5 mm roots were scarce. Due to the small core diameter, larger coarse woody roots were not sampled by this technique. Roots were separated into live and dead fractions based on visual identification of roots. Site 6 understory had a large component of the sedge *Carex alligata* whose fine roots could not be readily identified as live or dead; hence only total root biomass is presented for that site.

Aboveground net primary productivity

We estimated ANPP as the sum of increases in the aboveground biomass plus the litter production in the 25×25 m production plots established at each site. All litter was dried at 70°C to obtain a consistent dry weight measurement. We collected litterfall in 15 trays (0.156 m^2) per site randomly placed on the forest floor and emptied at monthly intervals. Three sites (sites 3, 5, 6) contained understory species whose litter production could not be collected with littertraps because senesced leaves did not fall to the forest floor. In sites 3 and 5, production of the fern *Dicranopteris linearis* (N.L. Burm.) Underw. (Gleicheniaceae) was measured by tagging 30 individual fronds, tagging new segments as they grew, and collecting and weighing the tagged frond segments that senesced during the study period. At 10 random points in each production plot we counted frond density in 1×1 m quadrats. Total litter production by *D. linearis* was calculated by multiplying the density of fronds by the annual litter produced by each frond. At site 6, we measured the litter production of *Carex alligata*, an understory sedge, in a similar fashion. Leaves from 30 individual tillers were tagged as they grew, collected and weighed after they senesced, and multiplied by an estimate of tiller density.

Because the annual increment of growth is relatively small, we placed aluminum, spring-loaded dendrometer bands on a subset of ten trees randomly selected from all trees in the production plot. Growth increments were recorded at 6-month intervals over 18 months, starting after the bands had been allowed to settle on the trees for 6 months. The average growth of trees with dendrometer bands was applied to the total basal area (>5 cm dbh) of the study plot to estimate the biomass increment added on an annual basis, using the regression equations previously described.

Soil respiration

We measured carbon dioxide flux from the soil surface at monthly intervals over the period of a year. Soil carbon dioxide fluxes from all measurement points were averaged to estimatean average daily efflux of carbon dioxide that incorporates seasonal fluctuations. The surface flux of carbon dioxide consists of autotrophic root respiration plus heterotrophic decomposition of organic matter and has been used in ecosystems approaching equilibrium as a measure of C inputs (Raich and Nadelhoffer 1989). The sites on this precipitation gradient cover a broad climatic range of unmanipulated, mature forests, meeting the general assumptions of this method. Therefore weassume that carbon released from the soil from heterotrophic respiration is approximately equivalent to the annual input of carbon entering the soil and, by subtracting measured litterfall, can be used as an index for belowground NPP (Raich and Nadelhoffer 1989; Gower et al. 1996).

To measure carbon dioxide flux, we used static chambers placed over tins containing soda lime for a 24 h period, following established methods (Edwards 1982; Raich and Schlesinger 1992;

Zibilske 1994). Initially, ten randomly placed rings per site were pressed 1 cm into the surface of the soil and remained in the field during the course of this study so that fine roots would not be disturbed during measurements. During the 24-h measurement periods, rings were removed and replaced with chambers of the same diameter such that a seal formed between the chamber and the soil. Tins of soda lime were dried at 105°C and weighed before and after the field measurements, and blanks were used to correct for the drying process. We calculated grams of CO_2 adsorbed using a revised correction factor of 1.69 to account for weight differences between H_2O and CO_2 (Edwards 1982; Grogan 1998). Soda lime has been shown in laboratory studies to overestimate very low (zero) fluxes and underestimate high fluxes but it is linear within a range of moderate fluxes where most of our measurements occurred (Nay et al. 1994). Furthermore, field studies have shown that it can be reliable compared to more sophisticated techniques over the range of carbon dioxide fluxes from soil, given the natural variability of soilfluxes (Raich et al. 1990).

We estimated total belowground carbon allocation (root respiration plus root turnover) as the amount of carbon in soil respiration minus the amount of carbon in litterfall, with the assumption that litterfall is 48% C (Raich and Nadelhoffer 1989).

Foliar analysis

Live leaves from *M. polymorpha* were collected to determine nutrient and trace element patterns in foliage produced in different sites. To compare leaves between sites, we used a slingshot or shotgun to collect the fully developed leaf cohort closest to the developing bud at the branch apex from branches in full sunlight (Reich et al. 1992; Vitousek et al. 1995). Each sample was the composite of 3–10 mature leaves from an individual plant, and there were five individual trees sampled at every site. Leaf area was measured on freshly collected leaves with a LiCor 3100 Area Meter (LiCor, Lincoln, Neb., USA)and then leaves were dried at 70°C and weighed to determine leaf mass per area (LMA). We measured N and P content on the leaf samples using Kjeldahl sulfuric acid/cupric sulfate digests followed by colorimetric analysis on a Lachat autoanalyzer (Lachat Instruments, Wisconsin, USA). All other elements were measured by inductively coupled plasma emission on a nitric acid digest of the ground foliage. We measured natural abundance $^{13}C/^{12}C$ ratio in foliage as an index of plant stress and $^{15}N/^{14}N$ ratio to assess changes in ecosystem N cycling. Natural abundances of the stable isotope of carbon ($^{13}C/^{12}C$ ratio) and nitrogen ($^{15}N/^{14}N$ ratio) were measured on ground foliage of *M. polymorpha* and three other taxa common to all sites with a Europa 20/20 continuous flow mass spectrometer with a C/N attachment. Foliage from 11 other taxa common to all sites on the gradient was collected in the same manner as described above in the light environment most typical for each species, and analyzed for N and P concentration. To compare among species, actual N and P concentrations were divided by the mean for each species across the gradient as a relative index of N and P content. An acid-insoluble fraction (mainly lignin) was determined on a single composite sample per site of senescent *M. polymorpha* leaves at the Center for Water and the Environment (Natural Resources Research Institute, University of Minnesota, Duluth, Minnesota). The C fraction was determined using forest-products techniques (Ryan et al. 1989), and is presented as percent ash-free total dry mass.

Soils

Resin bags

We assessed soil nutrient availability using buried resin bags in the field (in situ) as a relative measure of nutrient availability (Lajtha and Klein 1988; Giblin 1994). Three grams of anion exchange resin (Biorad, AG 1-X8, 20–50 mesh, Cl^- form) and cation exchange resin (Biorad, AG 50W-X8, 20–50 mesh, H^+ form) were weighed into separate 6×5 cm monopolyester bags (approx. 190 µm mesh size). In the field, resin bags were placed vertically 5 cm below the soil surface by slicing the forest floor with a machete and inserting the resin bag to minimize soil disturbance. Resin bags were attached to a PVC stake with monofilament fishing line to facilitate recovery of the bags. Each site on the precipitation gradient had five PVC stakes randomly located within a 25×25 m plot, while each PVC stake had one cation and one anion resin bag attached. All resin bags werechanged at monthly intervals over the period of a year by recovering bags from the field and replacing them with recharged resin bags. As resin bags were changed, new sets of resin bags were inserted in a different spot in the soil each month within a 30 cm radius of each PVC stake.

Resin bags retrieved from the field were rinsed with DI water to remove adhered soil particles and ions were extracted with either 50 ml of 0.5 M NaCl for anion resin bags, or 50 ml of 0.5 M HCl for cation resin bags for 6 h on a shaker table. We measured phosphate and nitrate on the anion extracts and ammonium on the cation extracts colorimetrically using a Lachat autoanalyzer (Lachat Instruments, Wisconsin, USA) to determine nutrient content per bag. Finally, used bags were recharged with 2 M HCl or 2 M NaCl and rinsed with DI water before returning them to the field. Used bags were recharged no more than three times before they were replaced (Crews et al. 1995).

Extractable cations

We dug soil pits, described soil profiles (Schuur et al. 2001), and collected soil samples by horizon for extractable cations. Soil samples were sent to the USDA Natural Resources Conservation Service Laboratory in Lincoln, Nebraska where a single soil profile per site was analyzed for extractable base cations. Subsamples of soils were kept field-moist and analyzed for pH in a 1:2 mixture with 0.01 M $CaCl_2$, with 4 replicates per site. All extractable cations and pH measurements represent the average of the top 30 cm of soil. Natural abundance of the stable isotope of nitrogen ($^{15}N/^{14}N$ ratio) was measured on ground soil with a Europa 20/20 continuous flow mass spectrometer with a C/N attachment.

Reduction-oxidation potentials

Reduction-oxidation (redox) potential measurements were made with an Orion 290A portable pH/mV meter (Orion Research, Beverly, Mass., USA) using platinum-tipped copper probes and a calomel reference electrode (Faulkner et al. 1989). In the field, ten replicate platinum probes per site were inserted to three depths in the soil profile (15 cm, 35 cm, and 50 cm) and allowed to stabilize for 45 min prior to recording measurements. Final redox values were standardized relative to a hydrogen reference electrode at pH 7 (+244 mV at 17°C, –59 mV for each pH unit below pH 7) (Urquhart and Gore 1973). We made redox potential measurements at monthly timepoints over the course of 1 year and combined all measurements to obtain an annual estimate of the soil redox potential. Because redox potentials represent microsite measurements, we report medians and quartiles of all measurements made over the period of 1 year. In laboratory conditions, +330 mV is the threshold below which molecular oxygen is no longer present (Laanbroek 1990).

Statistical analyses

We used linear regression analysis to statistically quantify the relationship between ecosystem properties and the state variable mean annual precipitation because both are continuous variables (SYSTAT 1992). In this study, the purpose of the regression analysis was not to find the best fit line since the number of replicates is relatively low (n=6). Instead, we used linear regression to test whether increased mean annual precipitation had a positive, negative, or neutral effect on patterns of productivity and nutrient cycling. The use of linear regression for all analyses also provides a common metric that can be compared between processes. All graphs reported here show means and standard error bars for subreplicate samples obtained at each site. The error bars illustrate the within-site variability; we used the mean of each site as a single point for the regression analysis thus avoiding the problem of psuedoreplication that affects use of ANOVA (Hurlburt 1984). Statistics presented in text and figures refer to regression lines with *n*=6 sites. In some cases where there were no linear trends across the gradient, ANOVA was used to determine differences among sites. On graphs, sites that share letters in common do not differ significantly (Tukey's HSD).

Results

Biomass

All sites on this gradient were dominated by *Metrosideros polymorpha* which comprised 81% of the tree biomass, on average, across the gradient (Table 2). A single large *Acacia koa* tree contributed 14% of the tree biomass in site 2, while four *A. koa* trees contributed 29% of the biomass in site 3. Large *Acacias* were sparsely scattered throughout the entire watershed but were not present in the other study plots. In combination with *Cheirodendron trigynum*, these three tree species comprised 98–100% of tree biomassat all sites. Basal area and total tree biomass were similar in all sites with the exception of the wettest site which had approximately half as much tree biomass as the other five sites.

Ferns were a dominant component of the understory biomass at the mesic end of the gradient and reached a maximum density at by site 4, which had a high proportion of *Cibotium* spp., a tree fern with relatively high biomass (Table 2). Site 3 also had high fern biomass which was composed of a climbing fern, *Dicronopteris linearis*, to the exclusion of most other understory species. Fern biomass dropped at the wet end of the gradient (sites 5 and 6) while bryophyte, shrub, and herb (largely *Carex alligata*) biomass increased. Understory biomass as a proportion of total biomass increased from 2.8% at the mesic end of the gradient to 8% at the wet end of the gradient.

Total root biomass and live root biomass were similar in all sites with the exception of site 6, which contained at least twice as much total root biomass as the other sites (Table 2) probably because dead roots decomposed most slowly at this site (Schuur 2001). The distribution of roots in the soil profile did not differ across the gradient, with more than 80% of live roots concentrated in the upper 17 cm of the soil profile. Detrital mass (litter plus organic horizon) increased dramatically with increased precipitation across the gradient largely as a result of the development of an organic horizon in the wetter sites (Table 2). The thickness of the organic horizon (Oa) increased from 3 cm in site 4 up to 17 cm in site 6 and was 6–20 times the mass of the surface litter in those sites.

Aboveground net primary productivity

Total ANPP was negatively related to increased MAP on this precipitation gradient (Fig. 2a; R^2=0.89, P=0.005, n=6). Aboveground NPP dropped on average by a factor

Table 2 Biomass of aboveground vegetation, roots, and detritus for sites across a mesic to wet precipitation gradient, Maui Hawaii. All values are mean (SE), units of g/m^2, and *n*=3, except for the overstory which was measured in a single 25×25 m plot

MAP (mm)	Site 1 2,200	Site 2 2,450	Site 3 2,750	Site 4 3,350	Site 5 4,050	Site 6 5,050
Overstory						
Tree density (no./ha)	1,136	1,264	1,648	1,104	2,352	1,440
Basal area (m^2/ha)	36.6	34.8	39.4	35.4	35.6	16.6
Tree biomass (g/m^2)	24,306	20,997	23,091	23,596	23,413	11,631
Understory (g/m^2)						
Ferns	597 (88)	415 (47)	811 (198)	1,427 (863)	219 (103)	193 (131)
Shrubs	94 (71)	331 (121)	6 (6)	1 (1)	1,018 (640)	446 (213)
Bryophytes	1 (1)	3 (2)	1 (1)	2 (1)	330 (154)	167 (59)
Herbs	0	1 (1)	0	1 (1)	11 (6)	192 (14)
Total	692 (58)	749 (95)	818 (196)	1431 (861)	1579 (679)	999 (179)
Total aboveground biomass (g/m^2)						
	24,998	21,746	23,909	25,027	24,992	12,630
Fine roots (g/m^2)						
Live	128 (14)	425 (193)	349 (83)	202 (98)	175 (62)	–
Dead	465 (73)	809 (66)	774 (152)	377 (63)	361 (43)	–
Percent Live	23 (4)	31 (11)	31 (3)	30 (9)	31 (9)	–
Total Detritus (g/m^2)	594 (67)	1,234 (139)	1,123 (217)	579 (135)	536 (77)	2,386 (235)
Litter	541 (6)	443 (84)	2,397 (401)	658 (137)	1236 (165)	688 (119)
Woody Litter	466 (174)	244 (42)	222 (68)	89 (21)	137 (90)	70 (12)
Soil O Horizon	0	0	0	3,380 (337)	13,871 (1,261)	14,340 (831)
Total	1,007 (170)	687 (121)	2,638 (288)	4,137 (370)	15,262 (1,221)	15,086 (836)

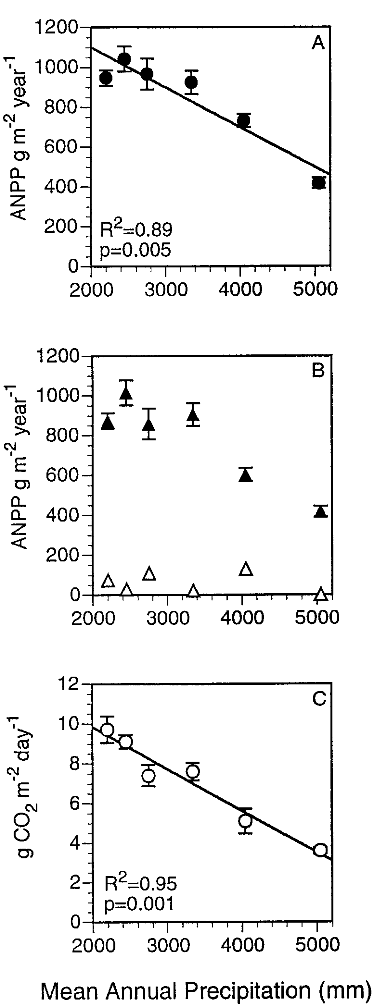

Fig. 2 Aboveground net primary productivity. **(A),** Components of ANPP **(B),** litterfall (*dark triangles*) and biomass increment (*open triangles*), and average daily soil carbon dioxide flux **(C),** for sites across the precipitation gradient. Values are means (± 1SE)

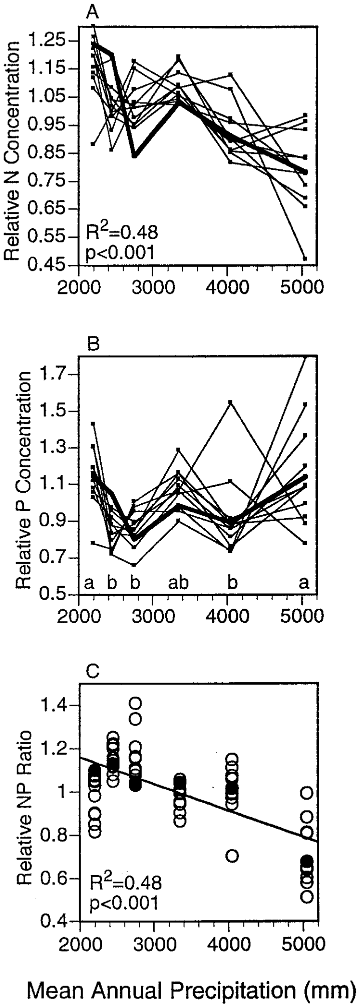

Fig. 3 Relative concentration of nitrogen (**A**), phosphorus (**B**), and N: P ratio (**C**) in live leaves from 12 taxa common to all sites on the precipitation gradient. Actual N and P concentrations were divided by the mean for that species across the gradient. *Heavy solid lines* in **A** and **B**, and *solid black circles* in **C** represent *Metrosideros polymorpha* leaves. Each point is the mean of 3–5 individuals

of 2.2 with increased MAP across the gradient, ranging from over 1,000 g/m^2 at the mesic end of the gradient to almost 500 g/m^2 at the wet end of the gradient. The litterfall component dominated total ANPP in these mature forests in comparison to the relatively small increase in stem increment during the study period (Fig. 2b). Litterfall comprised more than 80% of ANPP at all sites on the gradient and more than 95% of ANPP at half the sites on the gradient.

Soil respiration

The average soil surface carbon dioxide flux ranged from 9.7±0.67 g CO$_2$/m^2 per day at the mesic end of the gradient to 3.6±0.17 g CO$_2$/m^2 per day at the wettest site. Carbon dioxide efflux decreased monotonically across the gradient by a factor of 2.75 (Fig. 2c; R^2=0.95, P=0.001, n=6). The calculated percent total belowground allocation (soil respiration-C minus litterfall-C, divided by soil respiration-C) averaged over all sites was 45±2% and there was no significant trend over the precipitation gradient. While this is an indirect method, it does constrain values of belowground NPP and allow for comparison with ANPP.

Foliar analyses

Nitrogen concentration in live leaves decreased with increased MAP across the gradient in an analysis of the relative nutrient concentration of 12 taxa common to all sites on the gradient (Fig. 3a; R^2=0.48, P<0.0001, n=72). In contrast, P concentration in foliage was highest at the

Table 3 Concentration of elements in foliage from *Metrosideros polymorpha* across a mesic to wet precipitation gradient, Maui Hawaii. Values are means (SE)

MAP (mm)	Site 1 2,200	Site 2 2,450	Site 3 2,750	Site 4 3,350	Site 5 4,050	Site 6 5,050
LMA (g m^{-2})	172 (8)	172 (14)	196 (9)	190 (4)	179 (8)	174 (8)
Lignin (%)	20.71	22.09	23.06	24.33	34.63	30.10
N (%)	1.33 (0.03)	1.29 (0.07)	0.90 (0.08)	1.11 (0.06)	0.98 (0.04)	0.84 (0.05)
P (%)	0.066 (0.004)	0.056 (0.004)	0.049 (0.05)	0.057 (0.002)	0.056 (0.005)	0.073 (0.006)
K (%)	0.39 (0.02)	0.41 (0.03)	0.42 (0.03)	0.40 (0.05)	0.45 (0.03)	0.60 (0.02)
Ca (%)	0.51 (0.14)	0.69 (0.14)	0.65 (0.07)	0.49 (0.03)	0.44 (0.07)	0.50 (0.07)
Mg (%)	0.11 (0.02)	0.11 (0.01)	0.10 (0.01)	0.10 (0.01)	0.12 (0.01)	0.11 (0.02)
Na (%)	0.031 (0.02)	0.032 (0.002)	0.027 (0.005)	0.030 (0.002)	0.027 (0.005)	0.024 (0.003)
S (ppm)	1,515 (30)	1,417 (113)	1,294 (115)	1,280 (54)	1,036 (65)	1,154 (55)
Mn (ppm)	429 (93)	464 (146)	514 (54)	409 (15)	245 (33)	260 (28)
Fe (ppm)	205 (37)	172 (47)	109 (13)	122 (29)	106 (12)	94 (11)
Zn (ppm)	13.2 (0.73)	9.3 (0.4)	9.0 (0.9)	8.4 (0.5)	7.6 (0.9)	7.3 (0.9)
Cu (ppm)	30.8 (8.1)	19.4 (1.8)	12.4 (1.5)	14.5 (2.9)	11.1 (1.0)	11.3 (1.2)
B (ppm)	83 (5)	91 (6)	71 (7)	71 (15)	71 (11)	80 (12)
Al (ppm)	138 (22)	106 (8)	90 (15)	77 (18)	70 (11)	76 (10)

ends of the gradient and dropped to a minimum across the middle of the gradient (Fig. 3b, ANOVA; $F=7.40$, $P<0.001$). The ratio of N to P decreased with increased MAP in the 12 common taxa (Fig. 3c; $R^2=0.48$, $P<0.0001$, $n=72$).

In *M. polymorpha* foliage, K was the only element that increased in concentration with increased precipitation (Table 3; $R^2=0.77$, $P=0.02$, $n=6$), but this increase was driven by higher concentrations in site 6 alone. Foliar Ca and Mg concentrations did not vary significantly with MAP, while all other foliar elements decreased with increased precipitation. Of particular interest because of its potential for plant toxicity, foliar aluminum concentration also decreased with increased MAP. Changes in element concentration in *M. polymorpha* foliage were not driven by changes in leaf mass per unit area (LMA), because LMA did not vary significantly with MAP across the gradient. Even though LMA stayed constant with increased precipitation, there were changes in allocation to different C compounds within theleaves. Most notably, the acid insoluble fraction (mainly lignin) measured in senescent *M. polymorpha* foliage increased significantly with increased MAP across the gradient (Table 3; $R^2=0.69$, $P=0.04$, $n=6$).

There was no significant trend in δ^{13}C in the foliage of *M. polymorpha* or three other common taxa with increased precipitation, although there were differences between species that remained consistent among sites (Fig. 4). In contrast, natural abundance δ^{15}N in the same foliage showed a striking decline with increased precipitation (Fig. 5a; $R^2>0.85$, $P<0.01$, $n=6$ for each taxon), ranging from +2‰ at the mesic end of the gradient to –6‰ at the wet end of the gradient. Soil δ^{15}N from all horizons also declined with increased precipitation (Fig. 5b; $R^2=0.27$, $P<0.001$, $n=204$), but the difference between the foliar and soil δ^{15}N followed the opposite trend and increased across the gradient (Fig. 5c; $R^2=0.78$, $P=0.02$, $n=6$). Foliar δ^{15}N was more negative than soil at all sites, and the increasing difference between foliage and soils was consistent no matter what soil depth interval was used in this calculation.

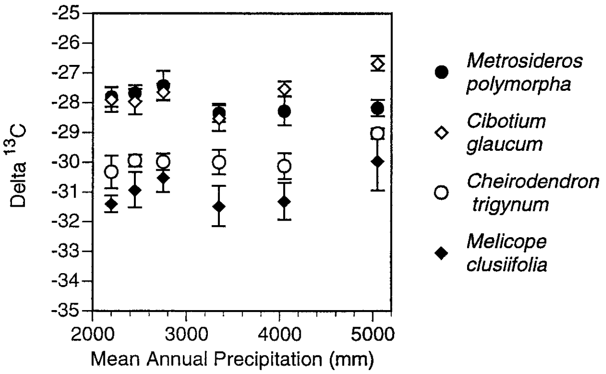

Fig. 4 Natural abundance of δ^{13}C in live foliage of four common taxa across the precipitation gradient. There are no significant relationships between MAP and δ^{13}C for any of the four taxa. Values are means (± 1SE)

Soil resources

The availability of N and P in soil generally followed patterns of foliar nutrients across the gradient (Fig. 6). In situ resin bag nitrate ranged from 39.2±8.5 to 2.8±0.33 μgN bag^{-1} day^{-1} and declined across the gradient ($R^2=0.69$, $P=0.04$, $n=6$) while resin bag ammonium was generally much lower, averaging 5.0±0.7 μgN bag^{-1} day^{-1} and was constant across the gradient. Resin phosphate ranged from 4.1±0.47 to 0.24±0.04 μgP bag^{-1} day^{-1} (Fig. 6b). In contrast to N, resinP availability was highest at both ends of the gradient and dropped to a minimum across the middle of the precipitation gradient (ANOVA; $F=9.97$, $P<0.001$). Across the gradient, soil N and P availability determined with resin bags generally corresponded to N

Table 4 Soil cation availability and chemical characteristics for sites across a mesic to wet precipitation gradient, Maui Hawaii. All values are means (SE)

MAP (mm)	Site 1 2,200	Site 2 2,450	Site 3 2,750	Site 4 3,350	Site 5 4,050	Site 6 5,050
Extractable cations (Meq·100 g^{-1} soil)						
Ca	0.41	0.55	1.47	0.47	0.42	0.39
Mg	0.30	0.39	0.42	0.27	0.12	0.24
K	0.19	0.22	0.20	0.23	0.10	0.27
Na	0.19	0.22	0.20	0.20	0.13	0.27
Al	3.54	0.73	0.93	2.76	3.58	7.31
CEC	23.1	22.8	17.6	28.1	32.2	41.7
BS (%)	3.9	5.5	11.8	4.1	2.6	4.1
pH	3.4 (0.06)	3.7 (0.12)	3.9 (0.13)	3.9 (0.02)	3.8 (0.07)	3.3 (0.04)

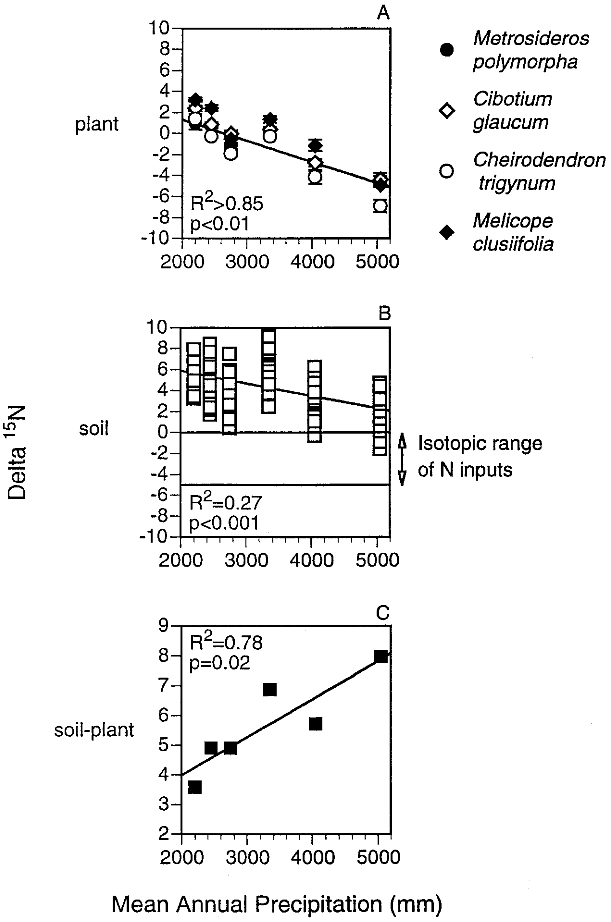

Fig. 5 Natural abundance of $\delta^{15}N$ in live foliage of four common taxa (**A**), soils (**B**), and the absolute difference between plant and soil (**C**) across the precipitation gradient. Values for foliage are means (± 1SE). Regression statistics in **B** shown for all taxa; there were no significant differences in slopes between taxa. Each soil value in **B** represents a measurement from a single soil horizon. Soil horizons were sampled to 1 m depth in four replicate soil pits per site. **C** is the absolute difference between the average for the four plant species and the average soil isotope value for the top 30 cm soil, weighted by % N and bulk density

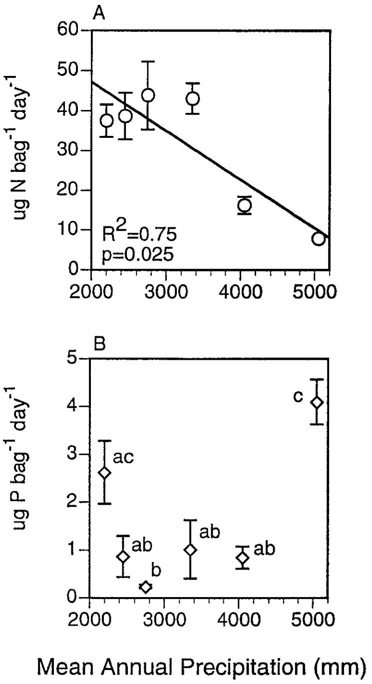

Fig. 6 In situ resin bag N availability (**A**), and in situ resin bag P availability (**B**) across the precipitation gradient. To incorporate seasonal fluctuations, all measurements taken over an annual period were averaged as a daily rate estimate. Values are means (±1SE)

(Pearson *r*=0.760, *P*=0.08) and P (Pearson *r*=0.844, *P*=0.03) in foliage.

There was no consistent variation in soil extractable Ca, Mg, and K with changes in MAP, and concentrations of all cations were low (Table 4). In contrast to patterns observed for foliar Al, extractable Al in soil was high at site 1, but then dropped by site 2 and generally increased with increased MAP thereafter (Table 4). Low pH values at all sites corresponded with very low base saturation indicative of highly leached soils, but there was no linear trend with increased MAP (Table 4). Sites at either end had small, but significantly lower pH than sites across the middle of the gradient (ANOVA; *F*=9.17, *P*=0.001).

Soil redox potential declined dramatically with increased precipitation at all depths (Fig. 7; $R^2>0.88$, $P<0.05$, and $n=6$ for all regressions). All sites had at least 25% of all values below +330 mV, while sites with higher MAP had a greater proportion of low redox values.

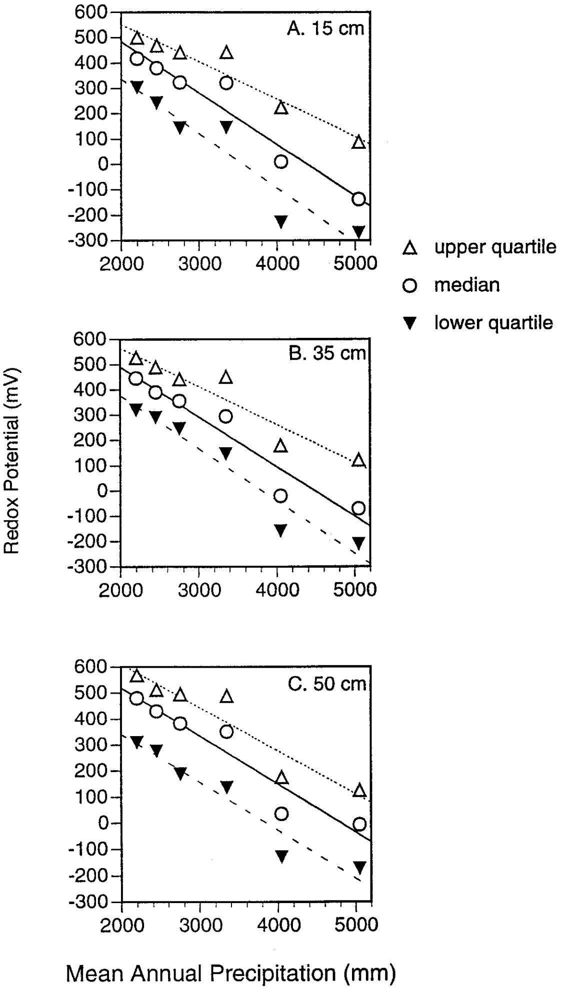

Fig. 7 Soil redox potentials at three depths in the soil profile across the precipitation gradient. Medians and quartiles shown for each site and each depth on the gradient for the combined annual dataset, collected at monthly intervals over the 1996–1997 study period (n=120/site). All regression lines were significant at $P<0.05$ and $R^2>0.88$

Discussion

Aboveground net primary productivity decreased dramatically with increased MAP in montane rainforest when other state factors of ecosystem development were held constant (Fig. 2). In addition, the proportion of carbon allocated below ground stayed constant across the gradient suggesting that belowground NPP also decreased at a similar rate. This is consistent with measurements of NPP in other Hawaiian forests that did not show shifts in allocation either in response to changes in natural soil fertility or to experimental fertilizer additions; this may be characteristic of *M. polymorpha* (R. Ostertag et al., unpublished data). Brown and Lugo (1982) observed that humid tropical forests worldwide tend to decrease in stature and biomass with increased precipitation. This corresponds with a recent, comprehensive review of tropical NPP data that showed that the highest NPP was found in mesic ecosystems while wet ecosystems tended to have lower NPP (Clark et al. 2001). In these humid ecosystems where rainfall exceeds plant demand for water, it is clear that variation in water supply still plays an important role in determining ecosystem structure and function.

The decrease in NPP with increased MAP on this precipitation gradient was associated most strongly with a decrease in N availability and with decreased soil redox potential (Figs. 3a, 6a, 7). However, we could find no strong evidence for direct effects of low soil oxygen availability on plant growth using foliar δ^{13}C values as an integrated measurement of stomatal conductance (Ehleringer and Osmond 1989). Plant stress from a variety of different factors can cause lower stomatal conductance as part of a hormone-induced, integrated plant physiological response (Chapin 1991). While often used as a measure for water stress in systems with low water availability, dwarf *M. polymorpha* growing in permanently waterlogged bogs on Kauai had significantly less negative δ^{13}C values compared to *M. polymorpha* growing nearby on better-drained soils (Meinzer et al. 1992). Those authors hypothesized that the stress of the anaerobic soil environment led to decreased stomatal conductance and less discrimination against δ^{13}C. In contrast, we did not observe any significant changes in foliar δ^{13}C across the gradient (Fig. 4). Our data could be confounded by the fact that foliar N declined with increased MAP. If there were changes in assimilation rates with decreased N, this would have the opposite effect on foliar δ^{13}C and could mask changes in stomatal conductance. However, a study of *M. polymorpha* photosynthesis across an elevational gradient found no change in assimilation rate per unit area even though there was twice as much range in N per unit area compared to our study (Cordell et al. 1999), suggesting that this mechanism is unlikely. In addition, a separate study near site 6 showed no difference in direct measurements of stomatal conductance between *M. polymorpha* growing on flat areas and on slopes, representing waterlogged and well-drained soil patches (Santiago et al. 2000). We speculate that *M. polymorpha* may simply avoid directly experiencing low soil oxygen conditions by growing adventitious roots on or above the soil surface where oxygen is available (Crawford 1982; Santiago et al. 2000).

It has been suggested that light availability could become a factor controlling montane rainforest growth if cloudiness increases with precipitation (Bruijnzeel and Veneklaas 1998). However, midday light measurements recorded at the wettest site on our gradient on the cloudiest days were still above the light saturation point [100–250 μmol m^{-2} s^{-1} photosynthetically active radiation (PAR)] for photosynthesis of *M. polymorpha* measured in a common garden (Kitayama et al. 1997) [out of a period of 39 days, only 10% had average daily (between 0800 hours and 1600 hours) PAR <400 μmol m^{-2} s^{-1} ; average PAR for those days =270 μmol m^{-2} s^{-1} (L. Santiago, unpublished data)]. Thus considering light supply alone there is no strong evidence that light limitation drives the changes in ANPP on the scale observed across the precipitation gradient. Patterns of C and N allocation in foliage also suggest that light limitation is not nearly as important as nutrient limitation in these forests. If light were predominantly limiting to carbon fixation, there should be relatively high N per unit area in foliage to maximize photosynthetic gain (Garnier 1991; Herbert and Fownes 1999). In contrast, we observed relatively low N per unit area and high lignin concentrations in leaves from the wettest sites, which is consistent with low N availability relative to C (Table 3). Carbon allocated to leaves in the form of lignin may increase leaf life span and increase N retention by plants, a pattern widelyobserved in low nutrient systems (Chapin 1980; Austin and Vitousek 1998).

While there was no strong evidence that soil oxygen availability affected NPP directly, patterns of N and P availability in foliage and soils suggest that low redox potentials may affect nutrient cycling, which in turn controls forest growth. At the mesic end of our precipitation gradient, high resin N and P availability and high foliar nutrient concentrations (Figs. 3, 6) were similar in magnitude to a fertile site on a Hawaiian montane forest chronosequence that was demonstrated to be limited by N and P together (Vitousek and Farrington 1997). Decreased foliar andsoil N availability with increased MAP could be result of slower decomposition and concomitant nutrient release. Indeed, in a related study of litter decomposition at these sites, Schuur (2001) showed that litter decomposition rates and nutrient release slowed with increased rainfall, apparently as a result of both decreased soil oxygen availability and the production of low quality litter in wetter sites.

Decreased N availability with increased MAP is supported by patterns of natural abundance $\delta^{15}N$ observed in soils and foliage on the precipitation gradient. The $\delta^{15}N$ signature of ecosystem N inputs is determined by a combination of atmospheric deposition with a $\delta^{15}N$ value of approximately –5‰ in Hawaii (Vitousek et al. 1989) and biological fixation with a $\delta^{15}N$ of 0‰ (Shearer and Kohl 1986). Because the enzymatic processes involved in nitrification strongly discriminate against $\delta^{15}N$, nitrate can be approximately 20 ‰ more negativethan soil organic nitrogen, whereas ammonium is typically only a few parts per thousand more negative (Hogberg 1997). Positive $\delta^{15}N$ values in soils relative to N inputs indicates that isotopic enrichment of remaining soilN is caused by fractionating pathways of ecosystem N loss likely involving nitrate in these sites, most importantly denitrification and nitrate leaching (Hogberg 1997; Amundson and Baisden 2001). The $\delta^{15}N$ signature of soils and foliage on this gradient becomes less enriched with increased MAP and generally approaches the isotopic signature of N inputs (Fig. 5a, b), consistent with global patterns (Handley 1999). Less fractionation is expected by increasingly N limited conditions as increased biological demand can reduce both production and loss of nitrate (Hogberg and Johannisson 1993; Riley and Vitousek 1995; Austin and Vitousek 1998; Vitousek et al. 1999; Martinelli et al. 1999). Decreased resin nitrate observed across the gradient supports the idea that less nitrate is produced in wetter forests; thus less substrate is available to be lost by a fractionating pathway. Increased difference between foliar and soil $\delta^{15}N$ across the gradient (Fig. 5c) is consistent if high nitrification rates at the mesic sites causes the ammonium to nitrate reaction to go further towards completion, which would decrease the fractionation factor associated with this conversion (Hogberg 1997). However, other changes in N cycling such as plant uptake processes, or denitrification rates could also contribute to this pattern of plant-soil differences.

Low soil oxygen availability that appears to decrease N availability by inhibiting decomposition rates (Schuur 2001) can also cause the increase inP availability at the wet end of the gradient. The availability of P is strongly controlled by adsorption to soil mineral surfaces and can become soluble under low redox conditions, offsetting reduced P mineralization from litter (Glentworth 1947; Bartlett 1986). Increased P solubility does increase the potential for loss from the ecosystem, and while there were decreases in total soil P in these soils (Miller et al. 2001), high foliar and resin P, and decreased N:P ratios suggest that net effect of increased P solubility is positive in terms of biotic availability. Thus, fluctuating anaerobiosis is a mechanism that appears to decrease N availability while simultaneously increasing P availability in these forests. The same mechanism which increases P availability also increases the solubility of Al, Fe, and Mn from mineral to soluble forms (Gambrell and Patrick 1978); soluble Al in particular has been implicated in plant toxicity (Marschner 1986). However, analysis of foliage showed the highest concentrations of these elements at the mesic end of the gradient, declining towards the wet end of the gradient (Table 3), and did not appear to directly affect forest growth.

We propose that the decline in primary production is related to soil oxygen availability and its subsequent effect on nutrient cycling. As precipitation increased in these upland systems, restricted soil oxygen availability causes slower rates of decomposition, decreased N availability, and a concurrent increase in P availability. There was no strong evidence for other causes of decline in forest growth with increased precipitation. Differential changes to N versus P cycling caused by low redox is one mechanism that could shift highly weathered soils in some humid ecosystems toward N limitation rather than P limitation as biogeochemical theory might suggest.

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