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The Effect of Water on Decomposition Dynamics in Mesic to Wet Hawaiian Montane Forests

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Abstract

I used a mesic to wet precipitation gradient on Maui, Hawaii, to test whether variation in rainfall regulates decomposition in tropical wet forest. Decomposition rates of leaves and roots from the dominant tree species, *Metrosideros polymorpha*, were measured at six sites similar in temperature regime, parent material, ecosystem age, vegetation, and topographical relief, whereas mean annual precipitation (MAP) at these six sites varied from 2200 to over 5000 mm/y. In situ decomposition rates of leaves placed on the soil surface declined by a factor of 6.4 with increased precipitation, whereas the decomposition rate of roots placed below ground declined by a factor of 2.3 across the gradient. Leaves collected from the 2200-mm site and placed at all sites on the gradient decomposed faster on the soil surface than they did below ground, whereas both above- and belowground decomposition rates of the common leaves decreased by a factor of 2.5 with increased precipitation. Of the environmental variables that changed with MAP, soil oxygen availability appeared to be the proximal factor that limited decomposition rates across the gradient, both above and below ground. When plant tissue collected from all sites across the gradient was decomposed at a common site, leaves from the wettest sites decomposed almost three times more slowly than leaves from the mesic sites. In contrast, roots from across the gradient all decomposed at a similar rate in a common site. Of tissue chemistry variables, high lignin concentration was correlated consistently with slow decomposition for roots and leaves. These results suggest that soil oxygen limitation combined with poorly decomposable leaves caused slower rates of decomposition and nutrient release with increased rainfall in these upland forests.

Key words: Hawaii; tropical forest; precipitation; litter chemistry; foliar nutrients; reduction–oxidation potential; nitrogen; phosphorus; gradient; lignin.

Introduction

Leaf and root decomposition comprises more than half of the global annual carbon flux from the soil to the atmosphere and mediates in part the effect of climate change on ecosystem carbon storage (Swift and others 1979; Raich and Schlesinger 1992; Couteaux and others 1995). The effect of climate on decomposition rates has often been summarized using an index variable, actual evapotranspiration (AET), which predicts faster decomposition in warmer, wetter conditions (Meentemyer 1978a, 1978b; Berg and others 1993; Aerts 1997). However, in moist tropical areas and other regions with abundant rainfall, AET does not predict decay rates well (Tanner 1981; Aerts 1997). This has led to suggestions that plant tissue chemistry plays a more important role in decomposition dynamics than either moisture or temperature regimes in these systems (Couteaux and others 1995). Nevertheless,

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there is evidence that carbon storage can be strongly affected by climate in ecosystems where the water supply is in excess of plant demand. Soil organic carbon (SOC) storage increases with increased mean annual precipitation (MAP) in mesic to wet upland (non wetland) ecosystems, both at a global scale when temperature regime is held constant (Post and others 1982) and across a local precipitation gradient in tropical montane forest where other state factors (elevation, parent material, vegetation, topography, and ecosystem age) are held constant as well (Schuur and others forthcoming). One factor that may be an important determinant of this increase in the SOC pool is reduced decomposition rates and slower turnover of the soil C pool, which is the focus of this study.

Decomposition and carbon turnover can be influenced by precipitation in mesic to wet ecosystems if water alters the environment for decomposers or alters the chemistry of the tissue that is produced by plants in those environments. Higher rainfall can increase soil leaching rates (Radulovich and Sollins 1991), over time leading to low nutrient and low pH conditions (Hedin and others 1995). Water also restricts gas diffusion in soil and can limit the resupply of oxygen from the atmosphere to the soil (Smith and Tiedje 1979; Richards 1987). Anaerobic processes such as denitrification occur commonly in upland soils as a result of oxygen limitation, varying spatially within soil aggregates or with depth in the soil profile, or temporally following rainfall events (Currie 1961; Robertson and Tiedje 1987; Leffelaar 1993). In fact, fluctuating anaerobic conditions have been observed to be common in upland soils that receive high rainfall or have restricted drainage (Silver and others 1999; Hobbie and others forthcoming). Changes in any of these factors caused by variation in precipitation have the potential alone or in combination to affect the activity of decomposers and alter rates of decomposition (Swift and others 1979). Furthermore, changes in environmental factors such as oxygen availability are not necessarily similar at the soil surface and within the soil; therefore, leaf and root decomposition may respond independently to differences in rainfall regime.

Changes in the environment caused by rainfall may also affect the decomposability of tissue produced by plants in that precipitation regime. Low soil nutrient availability can lead to plant tissue with low nutrient content and concomitant changes in leaf chemistry (such as increased lignin) that are related to low-resource environments (Chapin 1980; Austin and Vitousek 1998). In addition, high rainfall can leach nutrients and labile carbon (C) from senescing plant tissue, further reducing the quality of the litter (Miller and others 1976; Bruijnzeel and Veneklaas 1998). In humid ecosystems, precipitation could control decomposition rates by modulating the supply of other resources and altering tissue chemistry.

I isolated the effect of precipitation on decomposition dynamics in mesic to wet forests by selecting sites on the island of Maui, Hawaii, across a gradient of precipitation where variation in parent material, ecosystem age, temperature regime, and local topography was minimal. These sites were similar in all respects except that each had developed under a different mean annual precipitation regime. I used this natural rainfall gradient to address three main questions:

1. Does increased precipitation alter rates of leaf and root decomposition in mesic to wet forests when all other state factors remain constant?
2. Does the effect of precipitation on decomposition differ between plant tissue decomposed on the soil surface and belowground?
3. Are changes in tissue quality or changes in the environment for decomposition more important in explaining variation in leaf and root decomposition along this gradient?

I conducted a series of litterbag experiments using leaf litter and roots to address these questions and to determine whether variation in rainfall controls decomposition in ecosystems where water supply exceeds plant demand. These manipulative experiments were combined with measurements of environmental variables (nutrient availability, soil reduction–oxidation potentials, and pH), and plant tissue chemistry that have the potential to control patterns of decomposition.

Methods

Site Description

In the Hawaiian Islands, state factors controlling ecosystem processes (climate, organisms, relief, parent material, and time) (Jenny 1941) range widely yet systematically. I selected six montane forest sites on the island of Maui across a gradient of precipitation where the other state factors were held relatively constant (Figure 1 and Table 1). The rain shadow created by 3055-m Haleakala volcano allowed the selection of similar sites over a wide range of precipitation; changes in temperature associated with most other altitudinal/climatic gradients were minimized. All sites were located within

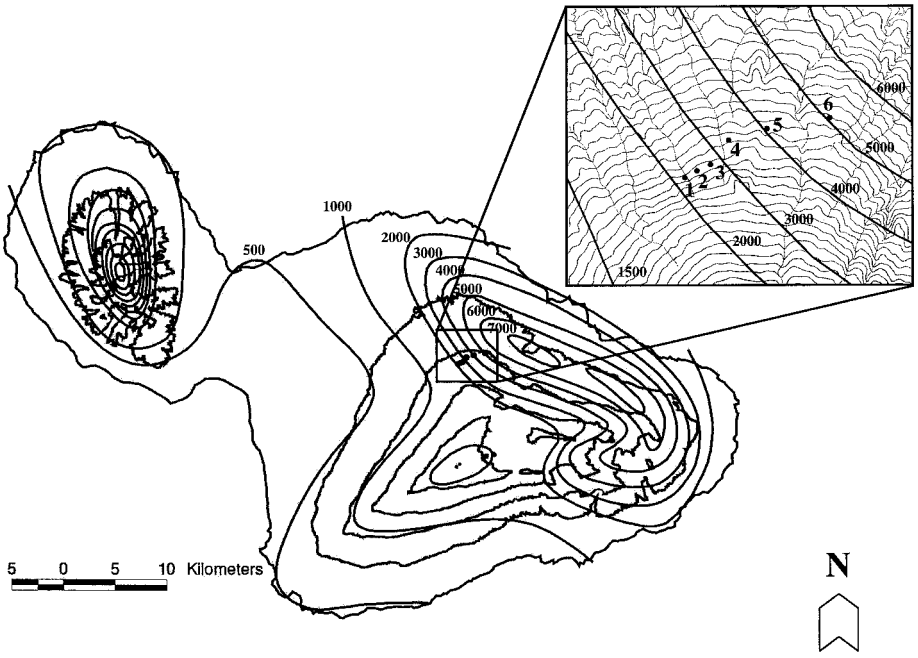

Figure 1. Location of the study sites on the island of Maui, Hawaii, showing isohyets (mm) of mean annual precipitation (MAP) (black) and 610-m elevation contours (gray). The inset magnifies the study area, showing 12.2-m elevation contours and site locations. (GIS database courtesy of S. Joe, Hawaiian Ecosystems At Risk Project, Hawaii Volcanoes National Park, Haleakala, Maui, Hawaii).

Table 1. Site Characteristics across the Mesic to Wet Precipitation Gradient

Site	Coordinates (Latitude [deg min sec]) (Longitude [deg min sec])	Elevation (m)	Mean-Annual Precipitation[a] (mm/y)
1	20°48′21.0″ 156°15′19″	1370	2200
2	20°48′26.5″ 156°15′10.5″	1370	2450
3	20°48′30.0″ 156°15′0.0″	1370	2750
4	20°48′47.5″ 156°14′49.5″	1320	3350
5	20°48′47.5″ 156°14′25″	1300	4050
6	20°48′54.5″ 156°13′47″	1270	5050

All sites were located on Kula volcanic series lava flows (mean age, 410,000 years). The parent material was lava with surface ash deposits (Stearns and MacDonald 1942; MacDonald and others 1983). The mean annual temperature was 16°C at all sites, and the forests were dominated by a single evergreen tree species, Metrosideros polymorpha *(Anonymous 1983).*
[a]*Interpolated from Giambelluca and others (1986).*

a geographic distance of less than 5 km in the Makawao and Koolau Forest Reserves on the north flank of Haleakala volcano. Although temperature regimes did not differ at the constant altitude of the sites (about 1300 m), mean annual precipitation ranged systematically from 2200 mm/y (mesic) to over 5000 mm/y (wet) as a function of aspect relative to the prevailing trade winds (Giambelluca and others 1986). Soil temperature follows air temperature closely in this area due to high soil moisture content (Nullet and others 1990). Rainfall is aseasonal, with sites receiving at least 100 mm rainfall per month on average and during the study period (Giambelluca and others 1986). Climate characteristics of the sites were monitored during the 1996–97 study period and are discussed in more detail elsewhere (Schuur and others forthcoming). Rainfall during this study period was well correlated with long-term average rainfall estimated for the sites (Pearson $r = 0.986$).

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 and others 1983). The original shield surface has been dissected by stream channels, so all of the study sites were located on shield volcano remnant surfaces on broad, flat ($< 5\%$ slope) interfluve areas to minimize variation in local topography. The soils on this precipitation gradient are classified as Inceptisols (sites 1, 2, 3, and 6) and Andisols (sites 4 and 5) developed from lava with surface ash deposits.

The flora and fauna of the Hawaiian Islands are relatively species-poor; thus, a few species and genera occupy a broad range of environmental conditions (Carlquist 1983; Wagner and others 1990). As

a result, the forest canopy at all sites was consistently dominated by the native evergreen tree *Metrosideros polymorpha* (Myrtaceae), which can make up more than 80% of basal area in Hawaiian montane forests (Crews and others 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 between sites. This watershed area has never been cleared by humans, and all six sites were located in mature forests stands.

Decomposition Experiments

I estimated the decomposition rates of *M. polymorpha* leaf litter and roots as a function of MAP along the precipitation gradient (Bocock and Gilbert 1957; Swift and others 1979). Senescent leaves were collected in litter traps on the forest floor at each of the six sites. Traps (n = 15/site) were emptied biweekly to ensure that collected leaves had fallen from the canopy recently. Leaves collected from a site were composited, and sorted to remove green or insect-damaged leaves; subsamples (1.0–1.5 g dry weight) of this homogeneous mixture were then sewn into 10 × 10 cm fiberglass mesh bags (1 mm mesh size). All leaves were dried at 50°C for 48 h to standardize the initial weights but minimize potential changes in tissue chemistry (Gartlan and others 1980; Makkar and Singh 1991); 50–70°C weight conversions were used to standardize all mass and nutrient concentrations to 70°C dry weight. Litterbags were placed back in the field either on the soil surface (above ground) or below the soil surface (below ground). I cut a slit in the forest floor with a wide-bladed machete and inserted belowground litterbags vertically so that the top of the bag was 5 cm below the soil surface; disturbance to the soil was minimized.

Roots from the top 15 cm of the soil were collected from each site and *M. polymorpha* roots < 2 mm in diameter were separated for use in the experiment. Because there was no way to determine reliably whether roots were newly senescent, I used live roots to ensure that the decomposition process was not already underway before the initiation of the experiment. All root tissue was dried as described above for leaves. For the root decomposition experiments, I used nylon mesh (0.3 mm mesh size) to retain fine roots (0.5–1.0 g dry weight) inside the 10 × 10 cm litterbag. A previous study comparing the effect of differences in mesh size (1 mm vs 0.3 mm) in a range of montane forests across the Hawaiian Islands showed that there was no effect of mesh size on the decomposition rate (S. E. Hobbie unpublished).

I used five replicate sets with five identical bags per set to represent a series of time points in the litter decay process (25 bags/site per experiment). Bags in a single set were adjacent to one another within a 50 × 50 cm area; replicate sets were distributed randomly within a 25 × 25 m plot at each site such that the sets were more than 5 m apart. One bag per replicate set was collected approximately 1, 3, 6, 9, and 15 months after they had been placed in the field. After collection, remaining plant material in the litterbag was gently rinsed with DI water to remove any soil particles; it was then dried and weighed to determine percent of initial mass remaining. The decomposition rate constants (k) reported here were derived from exponential decay curves fit to plots of fraction mass remaining as a function of time, including the initial time point (mass = 1, t = 0) (Olson 1963; Wieder and Lang 1982). The median R^2 = 0.93 for exponential curve fits from all experiments (n = 235 curve fits); 72% of curve fits had $R^2 \geq 0.90$, and 90 % of curve fits had $R^2 \geq 0.83$.

This litterbag method was used in all of the following experiments. Leaves (25 bags/site) and roots (25 bags/site) were decomposed above ground and below ground respectively in the site where they were collected as an estimate of the in situ decomposition rate at each MAP regime. To isolate the effect of changes in environment on the decomposition rate, I decomposed a common substrate (leaves collected from site 1) above ground (25 bags/site) and below ground (25 bags/site) at all sites. To isolate the effect of changes in tissue quality on the decomposition rate, leaves collected from all the sites (25 bags from each site) were decomposed above ground at a common site (site 1), and roots from all sites (25 bags from each site) were decomposed below ground at the same site. Finally, to determine whether the effect of tissue chemistry on the decomposition rate of leaves was similar in different environments, I used *M. polymorpha* leaves collected from sites on another Hawaiian island that were known a priori to differ in their tissue quality, primarily in lignin concentration (Hobbie and Vitousek 2000). I decomposed these high-lignin leaves (25 bags/site) (Table 2, Thurston) and low-lignin leaves (25 bags/site) (Table 2, Kaniku) below ground at all sites on the precipitation gradient. This final experiment was designed to test whether there was an interaction between tissue quality and the environment for decomposition since the common site experiment was not repeated at all sites. Thus, I chose the substrate (high vs low lignin) and the environment (belowground) that were most likely to have such an interaction since low oxygen avail-

Table 2. Initial Tissue Chemistry of Roots and Leaves from *Metrosideros polymorpha*

Site and Tissue Type	Ash (%)	Litter Forest-Products Carbon Fractions (%)									
		NPE	WS	AS	AIS	TE	WS GE	AS GE	%N	%P	Lignin:N
Site 1 Leaf	3.38	23.76	24.89	30.63	20.71	11.86	5.33	16.58	0.92	0.048	22.45
Site 2 Leaf	3.83	18.76	28.56	30.59	22.09	13.52	6.16	17.07	0.71	0.029	31.15
Site 3 Leaf	3.45	14.09	34.19	28.65	23.06	16.54	8.39	16.36	0.81	0.034	28.42
Site 4 Leaf	3.08	14.38	32.30	28.99	24.33	15.25	7.17	16.32	0.90	0.044	26.90
Site 5 Leaf	2.80	15.38	18.48	31.51	34.63	8.62	5.08	18.16	0.55	0.030	63.12
Site 6 Leaf	3.29	23.19	16.14	30.58	30.10	7.79	4.03	16.36	0.62	0.045	48.38
Site 1 Root	3.26	10.78	13.98	44.83	30.41	4.65	3.38	33.92	0.95	0.053	31.87
Site 2 Root	4.71	15.42	9.83	45.96	28.79	1.43	2.31	32.85	1.54	0.057	18.68
Site 3 Root	3.81	13.71	8.56	45.80	31.93	1.82	1.80	32.27	1.31	0.049	24.40
Site 4 Root	3.23	15.56	12.27	43.00	29.17	5.01	2.60	31.03	0.61	0.040	47.63
Site 5 Root	3.19	14.02	12.84	42.81	30.33	5.03	3.02	28.56	0.73	0.042	41.37
Site 6 Root	2.69	11.58	11.92	46.30	30.20	4.47	2.88	36.15	0.75	0.039	40.12
Thurston Leaf	3.36	12.62	15.00	44.56	27.82	6.78	4.09	32.01	0.40	0.024	69.41
Kaniku Leaf	8.05	28.65	24.15	36.83	10.38	9.10	6.99	21.49	0.48	0.029	21.76

Carbon fractions: nonpolar extractives (NPE), water-solubles (WS), acid-solubles (AS), acid-insolubles (AIS), glucose equivalent (GE), and tannin equivalent (TE) for leaves and roots from the precipitation gradient, and leaves from Thurston and Kaniku. All C fractions are presented as percent ash-free total dry mass.

ability is thought to limit the decomposition of macromolecules (Paul and Clark 1996).

Tissue Chemistry. I measured carbon (C) fractions, nitrogen (N), and phosphorus (P) concentration of leaves and roots from all sites on the precipitation gradient and on leaves from Thurston and Kaniku. Carbon fractions were determined on ground subsamples of the original plant tissue at the Center for Water and the Environment (Natural Resources Research Institute, University of Minnesota, Duluth, Minnesota). The C fractions, which were determined using forest-products techniques (Ryan and others 1989), included nonpolar extractives (NPE: fats, oils, and waxes), water-solubles (WS: amino acids, simple sugars, soluble phenolics), acid-solubles (AS: cellulose, hemicellulose, starch, polypeptides, nucleic acids), and acid-insolubles (AIS: mainly lignin). Two glucose equivalent (GE) fractions and a tannin equivalent (TE) fraction were also separated, representing subsets of the WS and AS fractions (WS GE: simple sugars; AS GE: cellulose, hemicellulose, starch; WS TE: tannins). All C fractions are presented as percent ash-free total dry mass. I measured N and P concentration on the initial decomposition samples using Kjeldahl sulfuric acid/cupric sulfate digests followed by colorimetric analysis on a Lachat autoanalyzer (Lachat Instruments, Wisconsin, USA). Because litter was homogenized within a site at the initiation of the experiment, five subsamples of the homogenized litter from each site were composited for initial tissue chemistry measurements.

In experiments where common leaves were decomposed at all sites on the gradient and where leaves were decomposed in situ, I analyzed N and P concentrations in remaining plant tissue at each time point for all replicate litterbags to determine patterns of nutrient immobilization and mineralization. The percent of initial nutrient remaining is calculated as the nutrient concentration at each time point multiplied by mass fraction remaining at that time point, divided by the initial nutrient concentration, multiplied by 100.

Foliar Analysis. Live leaves were collected from 12 taxa that were present in all six of the sites to determine N and P patterns in foliage produced in different MAP regimes. Nutrient concentration in live leaves is presented here as an index of soil nutrient availability at each site (Vitousek and others 1995). To compare canopy tree leaves between sites, I 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 and others 1992; Vitousek and others 1995). The youngest cohort of fully developed leaves from understory taxa were collected in the light environment typical of their growth patterns. Each sample was the composite of three to 10 mature leaves from an individual plant; a minimum of three replicate samples of each taxon were collected from every site. All leaves were collected during a single week, dried at 70°C, and ground; N and P concentrations were then determined by the procedure described above.

Soils

Resin Bags. I also directly assessed soil nutrient availability using buried resin bags in the field as a relative measure of nutrient availability (Lajtha and Klein 1988; Giblin and others 1994). Three grams of anion exchange resin (Biorad, AG 1-X8, 20–50 mesh, $C1^-$ form) and cation exchange resin (Biorad, AG 50W-X8, 20–50 mesh, H^+ form) were weighed into separate 6 × 5 cm monopolyester bags (approximately 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 located randomly within a 25 × 25 m plot; each PVC stake had one cation and one anion resin bag attached. All resin bags were changed at monthly intervals over the period of 1 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 extracted with either 50 mL 0.5 M NaCl for anion resin bags or 50 mL 0.5 M HCl for cation resin bags for 6 h on a shaker table. I measured phosphate and nitrate concentrations on the anion extracts and ammonium concentration on the cation extracts colorimetrically using a Lachat autoanalyzer to determine nutrient concentration 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 and others 1995).

Reduction–Oxidation Potentials and pH. Reduction–oxidation (redox) potential measurements were made with an Orion 290A portable pH/mV meter (Orion Research, Beverly, MA, USA) using platinum-tipped copper probes and a calomel reference electrode (Faulkner and others 1989). I inserted probes in the field at a depth of 15 cm in the soil profile, using 10 replicates per site. Probes were 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). These redox measurements were repeated at monthly intervals over the course of 1 year and combined to obtain an annual estimate of soil redox potentials. Because redox potentials represent microsite measurements, I 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). Finally, I mixed soil and 0.01M $CaCl_2$ in a 1:2 ratio and measured soil pH of the top 15 cm of soil using an Orion pH meter (n = 4/site).

Statistical Analysis. I 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). Linear regression tests whether increased MAP had a positive, negative, or neutral effect on decomposition rates and allows calculation of ratios that can be compared between experiments. All graphs show means and standard error bars for subreplicate samples obtained at each site (n = 5 *sets*/*site* per experiment). The error bars illustrate the within-site variability; in each experiment, the mean of each site was treated as a single point for the regression analysis. Thus, the problem of pseudoreplication, which limits the use of analysis of variance (ANOVA), was avoided (Hurlburt 1984). Statistics presented in text refer to regression lines with n = 6 sites in most cases. Analysis of covariance (ANCOVA) was used to test whether decomposition rates differed between litter types (main effect) and whether slopes between litter types were different (interaction). Although this experiment was not designed for ANOVA, site differences were determined in some cases when there was no linear trend across the gradient. On graphs, sites that share letters in common do not differ significantly (Tukey's HSD).

Results

In Situ Experiment

Decomposition rates decreased as MAP increased for leaves decomposed on the soil surface (Figure 2A) and for roots decomposed below the soil surface (Figure 2B). The decomposition rate was faster for leaves than for roots (ANCOVA main effect; F = 14.3, P = 0.007), and the slope of this relationship differed (ANCOVA interaction; F = 7.36, P = 0.03). Leaf decomposition rates were almost twice as high on average as root decomposition rates at the mesic end of the gradient, but they were similar at the wet end of the gradient. The decomposition rate of leaves decreased by a factor of 6.4 across the precipitation gradient, whereas root decomposition

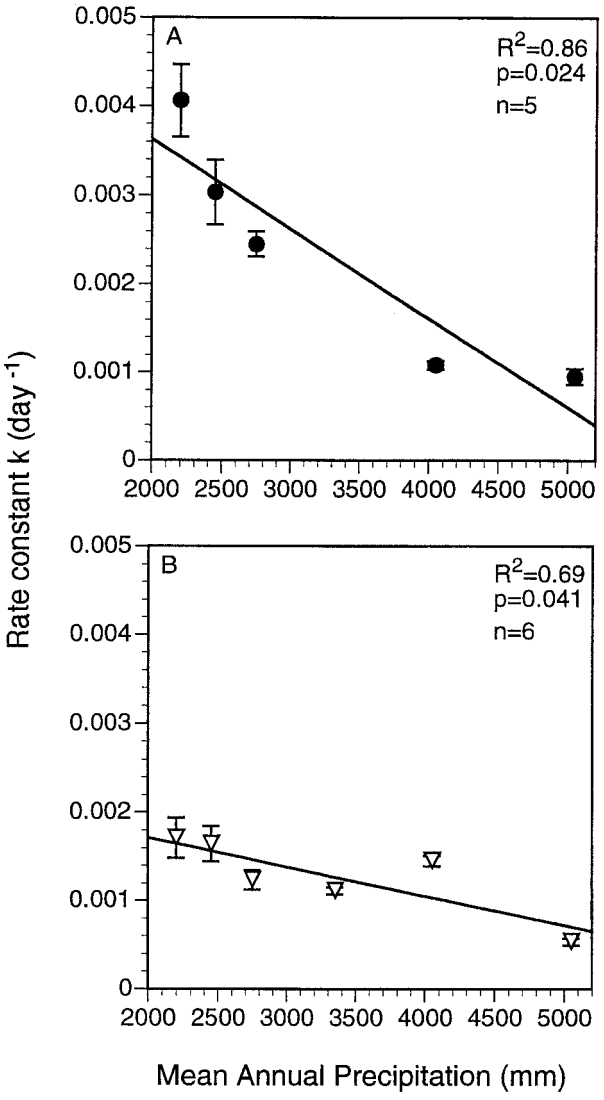

Figure 2. Decomposition rate constants for leaf litter (**A**) on the soil surface and roots (**B**) below ground across the precipitation gradient. Values are means (±1 SE). Site 4 (3350 mm) surface samples are missing due to vandalism. A linear relationship was used because the relationship between the rate constant and mean annual precipitation (MAP) in the root experiment was linear. The sign of the slope of the relationship does not change with or without transformation.

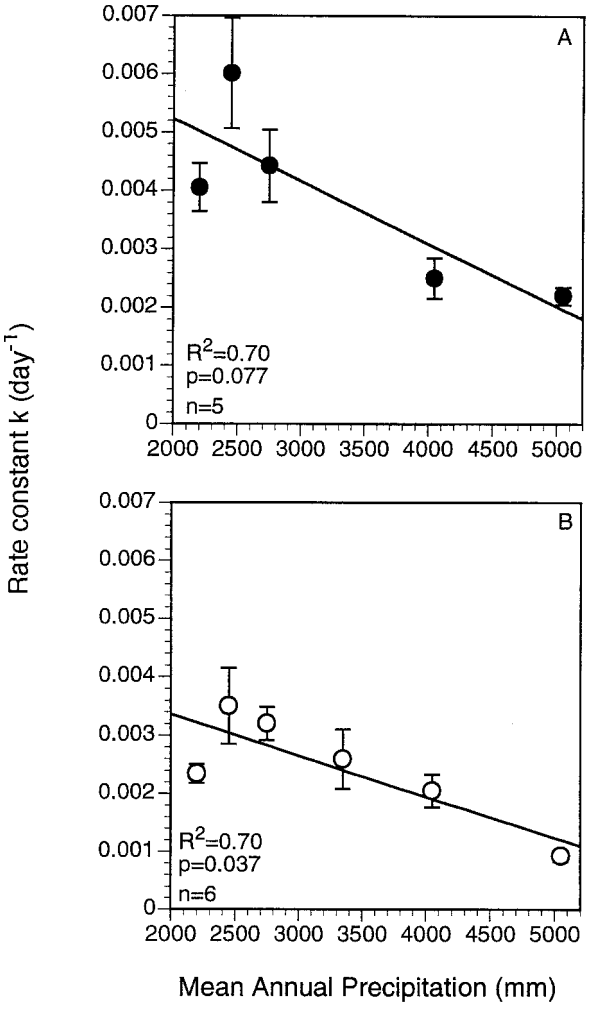

Figure 3. Decomposition rate constants for common leaves (from site 1) decomposed above (**A**) and below ground (**B**) across the precipitation gradient. Values are means (±1 SE).

rates decreased by a factor of 2.3 across the gradient.

Common Litter Experiment

When a common tissue type (site 1 leaves) was decomposed across the precipitation gradient, increased MAP again had a negative effect on the decomposition rate both above ground (Figure 3A) and below ground (Figure 3B). Although the trend in aboveground litter decomposition rates was not significant at $P < 0.05$, this result may be due to the missing sample ($n = 5$) increasing the probability of a type I error. Aboveground leaves decomposed more than 1.5 times faster, on average, than the same type of leaves decomposed below ground (ANCOVA main effect; $F = 9.4$, $P = 0.02$) showing that belowground conditions were less favorable for decomposition. However, above- and belowground litter were affected similarly by the negative impact of MAP on the environment for decomposition, since as the slopes did not differ (ANCOVA interaction; $F = 0.7$, $P = 0.45$). Decomposition rates of common leaves on the soil surface and below ground decreased across the gradient by a factor of about 2.5.

Common Site Experiment

Increased MAP also had a negative effect on decomposition rates via changes in tissue chemistry for leaves (Figure 4A) but not for roots (Figure 4B). Leaves collected from wetter environments decomposed almost three times slower than leaves collected from mesic environments when decomposed in a common site (site 1). In contrast, the decomposition rates of roots collected from all sites and decomposed at a common site did not differ significantly.

Tissue Chemistry

Changes in tissue chemistry associated with increased MAP are related to decomposition rate differences in the common site experiment, since the environment for decomposition is held constant (Table 2). Of all the tissue chemistry indexes, the decomposition rate of aboveground leaves was only highly and negatively correlated with lignin (Table 2, AIS) (Pearson $r = -0.956$) and the lignin:N ratio (Pearson $r = -0.922$) and positively correlated with %N (Pearson $r = 0.845$). In contrast, roots at the common site did not show any significant correlations at all, probably because neither lignin nor decomposition rates varied greatly. When three additional leaf types (site 1, Thurston and Kaniku) that were decomposed below the soil surface along with roots in the common site were included in the root analysis, the decomposition rate of plant tissues below ground was highly and negatively correlated with lignin (Pearson $r = -0.935$) and positively correlated with water-soluble sugar (Pearson $r = 0.831$), but it showed no relationship with %N. The addition of the three leaf types increased the range of lignin by an order of magnitude and the range of sugar threefold compared to the analysis of roots alone (Table 2). However, water-soluble sugar and lignin concentrations were highly and negatively correlated themselves (Pearson $r = -0.948$). The range of %N in roots from different sites across the precipitation gradient (0.61%–1.54%) was slightly larger than the range found in leaves (0.55%–0.92%) (Table 2).

Tissue Chemistry by Environment Experiment

The relative effect of changes in tissue chemistry on decomposition rates was similar for all sites on the gradient. Decomposition rates decreased with increased MAP for both low-and high-lignin leaves (Figure 5A) decomposed below ground. Low-lignin leaves decomposed almost three times faster than high-lignin leaves at all sites across the gradient

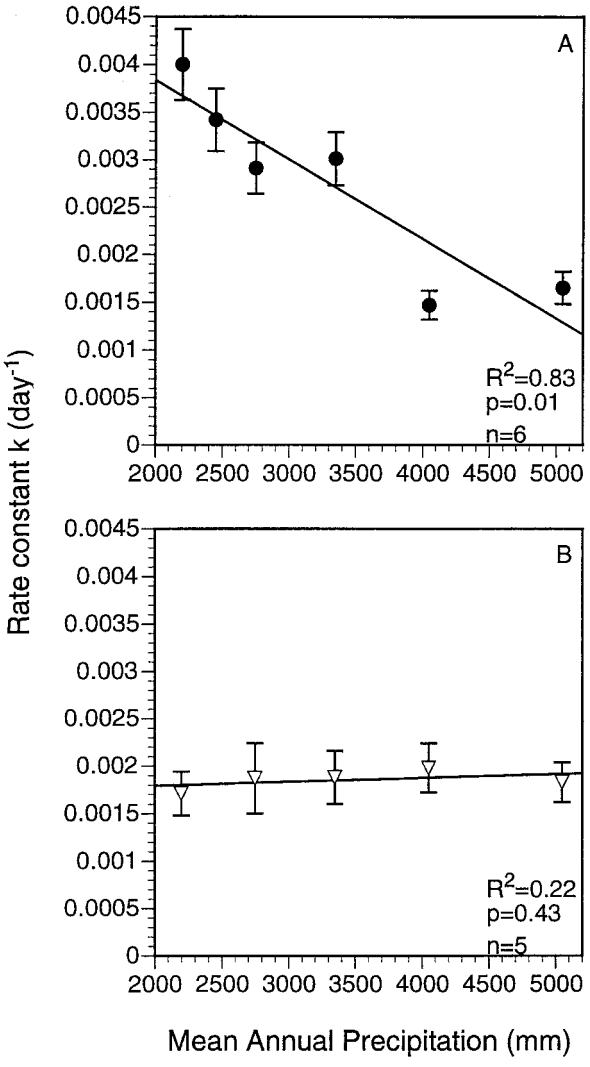

Figure 4. Decomposition rate constants of leaf litter (**A**) and roots (**B**) collected from each site along the precipitation gradient and decomposed at a common site (site 1). The x-axis here is the mean annual precipitation (MAP) from the site of plant tissue origin. Values are means (±1 SE).

(ANCOVA main effect; $F = 18.3$, $P = 0.003$) while the slopes differed (ANCOVA interaction; $F = 5.0$, $P = 0.055$), suggesting a multiplicative effect of changing litter quality.

The effect of both MAP and litter quality (lignin concentration) was combined in a model using the regression relationships from high- and low-lignin leaves, common leaves decomposed below ground, and in situ root decomposition. These four litter types span a range of lignin concentrations (Table 2) and were decomposed in an identical environment (below ground) at all sites across the gradient. The model was fit by using lignin concentration as

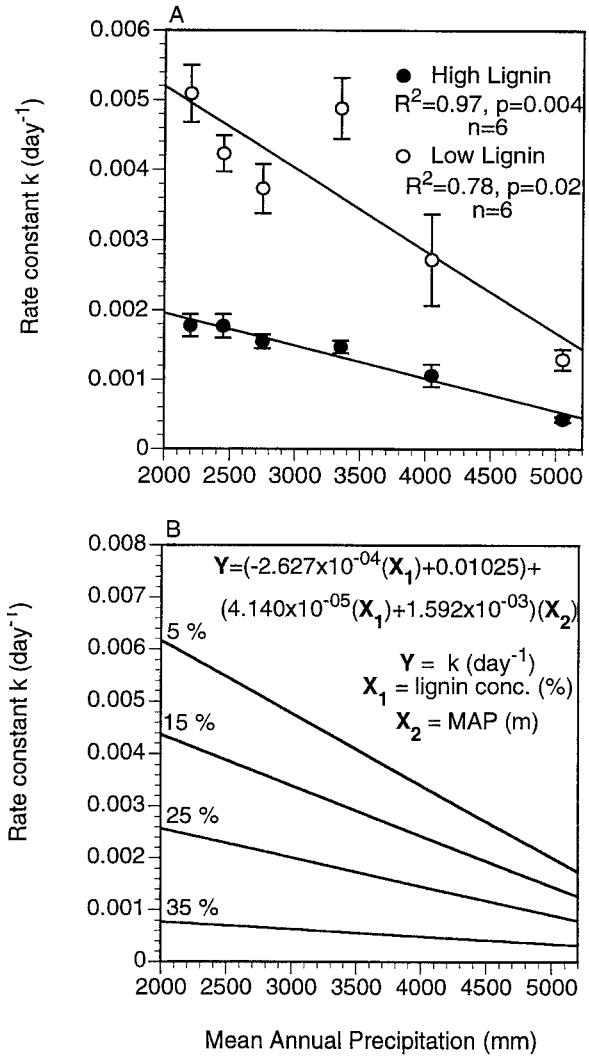

Figure 5. Decomposition rate constants for leaves with high lignin and low lignin (**A**) decomposed below ground across the precipitation gradient. Values are means (±1 SE). General model (**B**) describing the changes in the slope and intercept of the relationship between mean annual precipitation (MAP) and decomposition rates with changes in lignin concentration. Percentages next to regression lines refer to lignin concentration.

an independent variable to predict the slopes and the intercepts of the regression relationships between MAP and decomposition rates for the four litter types. Lignin is a highly significant predictor of slopes ($R^2 = 0.996$, $n = 4$ litter types) and intercepts ($R^2 = 0.999$, $n = 4$), further suggesting that lignin concentration alone is the dominant litter quality factor controlling decomposition rates. The combined model with MAP and litter quality describes a family of linear regressions and is presented in Figure 5B.

The relative (multiplicative) effect of changing litter quality is similar at all points on the rainfall gradient, even though the absolute (additive) effect is different. For example, plant tissue with 20% lignin decomposes 1.5 times faster than plant tissue with 10% lignin at all sites on this gradient, and the CV of this ratio is only 1.2% across all six sites. In contrast, the difference in decomposition rates between 10% and 20% lignin ranges from 0.0017 at the mesic end of the gradient to 0.00054 at the wet end of the gradient, and the CV of this difference is 35.6% across all sites. Within the range of lignin concentrations in these experiments, the linear relationships presented here demonstrate that the relative effect of differences in litter quality is the same at all sites on the gradient.

Litter Nutrient Dynamics

Percent nutrients remaining in leaves decomposed in situ on the soil surface increased with increased MAP for N (Figure 6A) and for P (Figure 6B). The proportion of N and P remaining increased by a factor of 2.2 across the gradient. Common leaves decomposed on the soil surface released both N and P at all stages of decomposition at all sites; there were no site means significantly larger than 1, indicating that no net immobilization of soil nutrients occurred (Figure 7).

Foliar Nutrients

Nutrient concentration in live leaves varied by a factor of two to three among species at a site (Table 3). To compare across species and sites, the mean nutrient concentration for each species at each site was divided by the mean nutrient concentration for that species across all sites as a relative measure of N and P. These data are shown not to differentiate species specific responses but instead to demonstrate that patterns found in *M. polymorpha* across the gradient are, on average, observed in other plant species as well. Relative N concentration in live leaves decreased with increased MAP across the gradient. This decrease was only a trend for *M. polymorpha* alone ($R^2 = 0.59$, $P = 0.07$, $n = 6$), but it was significant in an analysis of 12 taxa common to all sites on the gradient (Figure 8A). In contrast, P concentration in live *M. polymorpha* was highest at the ends of the gradient and dropped to a minimum across the middle of the gradient (Table 3), but there was no linear trend with increased MAP. This pattern was supported by an analysis of P in 12 common taxa (ANOVA, $F = 7.40$, $P < 0.001$) (Figure 8B). Concentrations of N and P in senescent *M. polymorpha* leaves followed the same general pattern as live foliar nutrient concentrations.

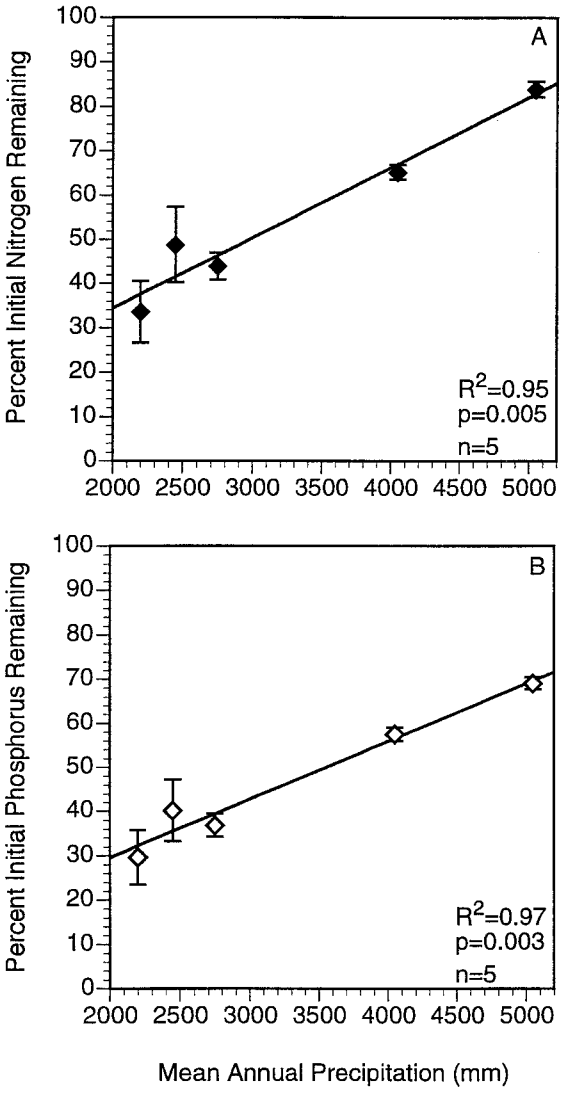

Figure 6. Nitrogen (**A**) and phosphorus (**B**) remaining in leaf tissue after 15 months of decomposition across the precipitation gradient. Leaves were decomposed on the soil surface in the site where they were collected. Percent nutrient remaining is the amount of nutrient remaining divided by the initial amount contained in senescent leaves at the outset of the experiment. Values are means (±1 SE).

Soil Resources

In situ resin bag N availability decreased with increased MAP across the gradient (Table 4). Average resin bag nitrate for all sites declined across the gradient (R^2 = 0.69, P = 0.04, n = 6), whereas while resin bag ammonium was generally much lower and was constant across the gradient. In contrast to N, resin P availability was highest at both ends of the gradient and dropped to a minimum across the middle (ANOVA, F = 9.97, $P<0.001$) (Table 4). In broad terms, patterns of average resin bag nutrient availability mirrored the average foliar nutrients in live leaves across the precipitation gradient for N (Pearson r = 0.760, P = 0.08) and P (Pearson r = 0.844, P = 0.03).

Median soil redox potential declined dramatically with increased MAP across the gradient (R^2 = 0.94, P = 0.002, n = 6) (Table 4). All sites had at least 25% of all values below +330 mV, whereas sites with higher MAP had a greater proportion of low redox values. Soil pH was generally low at all sites, but there was no directional trend across the gradient (R^2 = 0.13, P = 0.49, n = 6) (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).

Discussion

When all other state factors were held constant, forests with higher MAP had slower decomposition rates both above and below ground (Figure 2). This experiment supports the relationship between decomposition rates and precipitation proposed by Esser and Lieth (1989) in a review of decomposition dynamics in tropical rain forests. Although their data were sparse, they suggested that increased precipitation in high rainfall regimes could suppress decomposition rates. This idea is contrary to the conclusions of a study of litter decay in a tropical moist forest in Panama, which found that watering had a positive effect on litter decomposition rates in a water addition experiment (Wieder and Wright 1995). However, water was added only during the dry season, when water was in short supply; thus, the experiment was not really designed to address decomposition dynamics when water was in excess.

The suppression of decomposition by precipitation shown here is also consistent with observations that SOC pools are larger in wet montane forests than in mesic forests (Kira and Shidei 1967; Whitmore and Burnham 1969; Schuur and others forthcoming) and that SOC pools on a global scale increase with increased MAP in humid upland ecosystems (Post and others 1982). All else being equal, larger SOC pools with increased MAP in mesic to wet ecosystems can be explained by a decrease in decomposition rates, although other factors such as litter production and soil mineralogy ultimately play a role in SOC storage as well.

The decrease in the decomposition rates of leaves and roots appeared to be due in part to changes in the environment for decomposition and in part to changes in the substrate that was being decom-

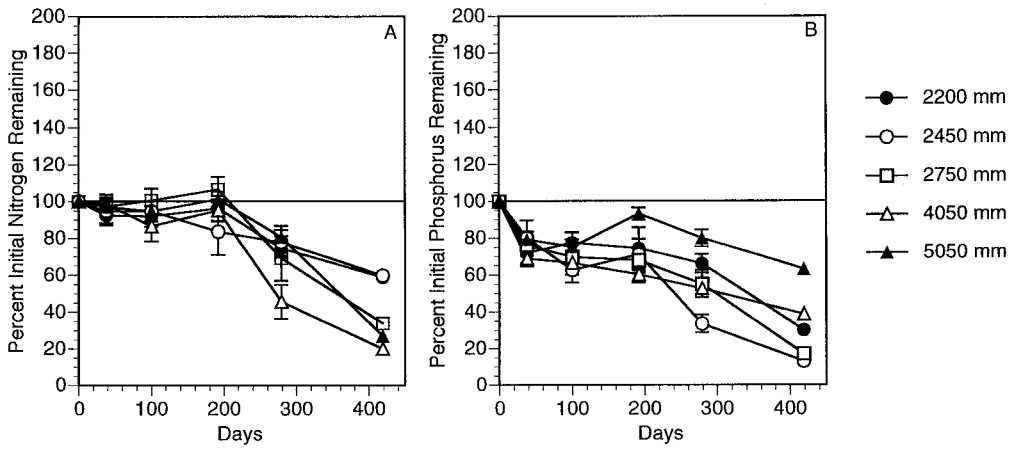

Figure 7. Nitrogen (**A**) and phosphorus (**B**) remaining in common leaf tissue from site 1, decomposed on the soil surface at all sites across the precipitation gradient. The horizontal line (y = 100) is the relative amount of N or P contained in the leaf tissue at the initiation of the experiment. Values below 100 indicate net mineralization of nutrients; values above 100 indicate net nutrient immobilization. Values are means (±1 SE).

Table 3. Nitrogen (N) and Phosphorus (P) Concentrations (% Dry Mass) of Living Foliage for Species Common to All Sites across the Precipitation Gradient

	%N						%P					
Species	**Site 1**	**Site 2**	**Site 3**	**Site 4**	**Site 5**	**Site 6**	**Site 1**	**Site 2**	**Site 3**	**Site 4**	**Site 5**	**Site 6**
Metrosideros polymorpha var. glabberima[a]	1.33 (0.03)	1.29 (0.07)	0.90 (0.08)	1.11 (0.06)	0.98 (0.04)	0.84 (0.05)	0.074 (0.005)	0.068 (0.005)	0.052 (0.005)	0.064 (0.003)	0.058 (0.003)	0.074 (0.002)
Broussaceae arguta[b]	1.75 (0.02)	1.67 (0.06)	1.55 (0.14)	1.61 (0.05)	1.38 (0.06)	1.28 (0.09)	0.122 (0.005)	0.109 (0.007)	0.097 (0.010)	0.116 (0.005)	0.087 (0.003)	0.182 (0.004)
Cibotium chamissoi[c]	2.01 (0.08)	2.06 (0.13)	1.70 (0.11)	1.90 (0.11)	1.42 (0.08)	1.35 (0.12)	0.105 (0.005)	0.097 (0.006)	0.089 (0.004)	0.106 (0.007)	0.081 (0.004)	0.119 (0.010)
Cibotium glaucum[c]	2.08 (0.14)	1.78 (0.08)	1.62 (0.12)	1.86 (0.06)	1.46 (0.08)	1.42 (0.02)	0.113 (0.006)	0.082 (0.005)	0.087 (0.005)	0.110 (0.004)	0.090 (0.013)	0.107 (0.020)
Carex alligata[d]	1.25 (0.16)	1.42 (0.03)	1.67 (0.17)	1.53 (0.03)	1.60 (0.07)	1.04 (0.11)	0.081 (0.011)	0.078 (0.003)	0.102 (0.014)	0.111 (0.015)	0.161 (0.018)	0.092 (0.007)
Alyxia olivaforma[d]	2.06 (0.11)	1.61 (0.04)	1.51 (0.09)	1.89 (0.01)	1.35 (0.04)	1.08 (0.09)	0.092 (0.004)	0.074 (0.003)	0.066 (0.001)	0.090 (0.002)	0.059 (0.004)	0.084 (0.009)
Cheirodendron trigynum[a]	1.64 (0.01)	1.35 (0.12)	1.29 (0.06)	1.46 (0.09)	1.18 (0.05)	1.32 (0.10)	0.122 (0.009)	0.078 (0.008)	0.077 (0.005)	0.102 (0.011)	0.080 (0.005)	0.102 (0.010)
Clermontia arborescens[b]	2.00 (0.20)	1.85 (0.11)	1.88 (0.14)	1.92 (0.25)	1.65 (0.18)	1.82 (0.04)	0.172 (0.033)	0.103 (0.011)	0.095 (0.009)	0.131 (0.013)	0.106 (0.016)	0.259 (0.082)
Vaccinium calycinum[b]	1.32 (0.03)	0.95 (0.09)	1.14 (0.03)	1.13 (0.04)	1.06 (0.03)	1.03 (0.09)	0.075 (0.003)	0.042 (0.005)	0.058 (0.004)	0.066 (0.002)	0.051 (0.001)	0.053 (0.004)
Styphelia tameiameiae[b]	1.29 (0.10)	1.00 (0.04)	1.10 (0.11)	1.16 (0.05)	1.10 (0.06)	0.48 (0.09)	0.068 (0.001)	0.042 (0.002)	0.036 (0.004)	0.050 (0.001)	0.053 (0.007)	0.037 (0.012)
Melicope clusiifolia[e]	1.63 (0.07)	1.36 (0.07)	1.68 (0.11)	1.54 (0.09)	1.42 (0.13)	1.13 (0.03)	0.095 (0.004)	0.070 (0.002)	0.084 (0.007)	0.084 (0.005)	0.076 (0.008)	0.120 (0.029)
Dryopteris spp.[c]	2.64 (0.20)	2.31 (0.11)	2.26 (0.13)	2.61 (0.03)	1.99 (0.06)	1.45 (0.24)	0.153 (0.012)	0.120 (0.004)	0.116 (0.014)	0.176 (0.012)	0.121 (0.016)	0.136 (0.016)

Values are means (SE) of a minimum of three replicate individuals per species, per site.
[a]*Canopy tree*
[b]*Understory shrub*
[c]*Fern*
[d]*Herb*
[e]*Understory tree*

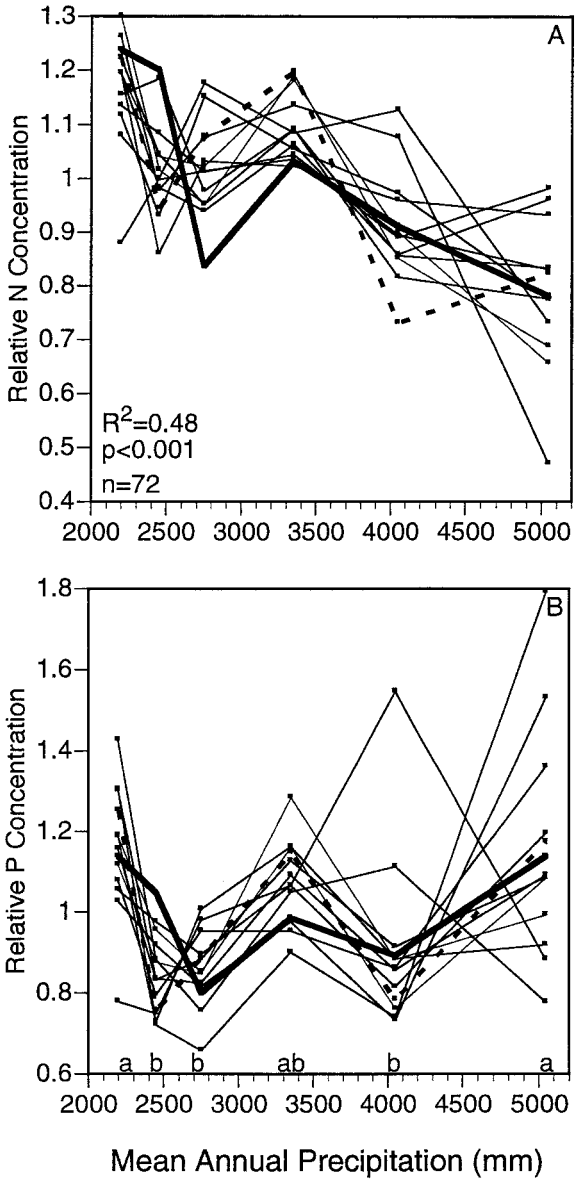

Figure 8. Relative concentration of nitrogen (**A**) and phosphorus (**B**) in live leaves from 12 taxa common to all sites on a precipitation gradient. Actual N and P concentrations were divided by the mean for that species across the gradient. Heavy solid lines represent live *M. polymorpha* leaves; heavy dashed lines represent senescent *M. polymorpha* leaves used in the decomposition experiments. Each point is the mean of three to five individuals.

posed; the relative effect of these two components differed depending on tissue type. Root decomposition was not affected by changes in tissue chemistry and was primarily controlled by changes in the environment. For leaves, changes in tissue quality that occurred across the precipitation gradient appeared to have an effect on decomposition rates similar in magnitude to the effect of changes in the environment. Because the ratio of decomposition rates of high- and low-lignin leaves remained similar in all sites on the gradient (Figure 5A), the relative effect of changes in tissue chemistry appears to be generalizable to all sites on the gradient.

Leaf decomposition rates in the common site were correlated with both N and lignin content, but evidence from root decomposition suggests that lignin alone exerts the strongest direct effect on decomposition in terms of tissue quality effects. In leaves, N and lignin covary inversely, making it difficult to separate the effect of each variable. In contrast, roots varied in N but not in lignin; this variation in N alone did not affect the decomposition rates when roots were decomposed in the common site. When leaves decomposed below ground in the common site were included in the root analysis, lignin alone correlated with decomposition rates. This finding suggests that the effect of lignin and the apparent lack of effect of N are consistent between tissue types.

However, it is possible that N availability affects decomposition rates indirectly by influencing lignin concentration in leaves. Because nutrient concentrations of senescent leaves generally followed nutrient concentrations of live leaves across the precipitation gradient, decreased N concentration with increased MAP (Figure 8A) appeared to be a result of the production of leaves with low N concentration in wetter sites rather than differences in nutrient retranslocation or leaching. Lower N concentrations in wet forests vs mesic forests have been observed elsewhere in the Hawaiian Islands (Vitousek and others 1995) and could be a result of lower N turnover in ecosystems with higher MAP (Table 4). In turn, increased lignin concentration in leaves may reflect excess C relative to N supply (Garnier 1991), increased protection of tissue, and longer leaf life spans as a consequence of low-N conditions (Chapin 1980; Aerts and Van der Peijl 1993; Austin and Vitousek 1998; Bruijnzeel and Veneklaas 1998). Although lignin appears to exert the strongest direct effect on decomposition of all the tissue chemistry indexes. N may influence decomposition indirectly if increased lignin is a feedback from low ecosystem N availability (Vitousek 1982).

The environment for decomposition changed dramatically as MAP increased in these mesic to wet forests. Low soil redox potentials indicated that depletion of oxygen and other electron acceptors occurred in all of these soils, but with increasing frequency in wetter sites. Silver and other (1999) observed similar patterns of low soil oxygen with increased precipitation in upland tropical forests in

Table 4. Soil Nitrogen N and Phosphorus P Availability, Redox Potential, and pH for Soils across the Precipitation Gradient

Site	In situ resin P ($\mu g \cdot bag^{-1} \cdot d^{-1}$)	In situ resin NO_3-N ($\mu g \cdot bag^{-1} \cdot d^{-1}$)	In situ resin NH_4-N ($\mu g \cdot bag^{-1} \cdot d^{-1}$)	Redox Potential (mV)			pH
				Upper Quartile	Median	Lower Quartile	
1	2.62 (0.66)	33.2 (4.1)	4.3 (0.46)	499	417	304	3.2 (0.04)
2	0.87 (0.43)	33.6 (5.9)	5.0 (0.66)	468	380	242	3.5 (0.12)
3	0.24 (0.04)	48.4 (11.3)	4.7 (0.61)	441	323	144	3.8 (0.09)
4	1.02 (0.23)	38.0 (3.8)	5.0 (0.67)	442	321	145	3.7 (0.04)
5	0.85 (0.23)	10.8 (2.2)	5.4 (1.08)	224	10	–229	3.3 (0.09)
6	4.10 (0.47)	2.8 (0.3)	5.0 (0.69)	86	–139	–270	3.2 (0.04)

Values are mean (SE) of five replicates per site averaged over 12 monthly intervals for resin N and P, and 10 replicates per site over 12 monthly intervals for redox potentials. Medians, upper quartiles (lowest value for upper 25% of measurements), and lower quartiles (highest value for lowest 25% of measurements) are presented for all redox measurements (n = *120) taken over 1 year. Mean pH values (in 0.01M* $CaCl_2$*) of the top 15 cm of soil are for four to five replicates per site.*

Puerto Rico. Soil nutrient availability, particularly the availability of N, also decreased with increased precipitation (Table 4). In theory, both oxygen and nutrient supply together could play a role in the negative effect of MAP on the environment for decomposition in these forests. Because N and P were mineralized from liter at all time points (Figure 7) with no apparent immobilization of the soil nutrient supply, it is likely that low soil oxygen availability is the main environmental factor limiting decomposition rates both above and below ground. Fertilizer additions of N or P in other Hawaiian montane forest sites also showed little or no stimulation of leaf and root decomposition rates (Ostertag and Hobbie 1999; Hobbie and Vitousek 2000).

Oxygen limitation to decomposition makes immediate sense for litter decomposing within the soil profile in these high-rainfall forests, but what about litter on the soil surface? It appears that the decomposer community could be affected by low oxygen not only within the soil profile but also at the surface of the soil, perhaps as the habitat for obligate aerobic decomposers becomes unfavorable. In support of a common mechanism above and below ground, the decrease in common leaf decomposition rates with increased MAP observed above ground (Figure 3A) was identical not only to the decrease in decomposition rates of common leaves decomposed below ground (Figure 3B), but also to the decrease in decomposition rates of roots decomposed below ground that were affected only by changes in the environment (Figure 2B). Fungi are an important component of the decomposer community because of their ability to degrade large macromolecules, but most fungi require oxygen for metabolism or as a substrate for extracellular enzymes (Sinsabaugh and others 1993). The exclusion of important functional groups of decomposing organisms such as fungi could feed back to affect ecosystem scale C cycling (Schimel 1995).

Large differences in total mass loss caused differences in the percentage of nutrient released from leaves on the soil surface overall (Figure 6). Not only do leaves from wetter sites have lower N concentrations (Table 2), but they also mineralized a smaller proportion of the N that they contained. Thus, slow decomposition rates help to explain the observed low levels of soil N availability (Table 4). This may create a positive feedback from increased MAP and low levels of soil oxygen to reduced rates of litter decomposition. Slower decomposition limits nutrient mineralization rates, potentially leading to lower tissue quality of leaves, which in turn further reduces decomposition rates (Vitousek 1982). Both the effect of tissue quality and the effect of low soil oxygen in combination appeared to decrease rates of litter decomposition with increased precipitation in these upland systems.

According to current empirical models, climate has little effect on decomposition dynamics in humid tropical ecosystems. However, AET as a composite climate index has little sensitivity in describing variation in decomposition rates when water supply is in excess of plant demand. The experiments described here demonstrate that changes in the precipitation regime can affect decomposition in humid ecosystems by altering other environmental factors, such as soil oxygen availability. Across the entire global range of precipitation, decomposition rates are probably best described by a unimodal curve that has a maximum at an intermediate level

of precipitation and is lower in both drier and wetter rainfall regimes. The interactive control of lignin concentration and precipitation modeled in Figure 5B is similar to the findings of Meentemyer (1978b, but it is important in extending those results to wetter environments where water no longer has a positive effect on decomposition. Despite the potential for soil oxygen limitation and lignin concentration to interact in a nonlinear fashion, these experiments suggest that the linear relationship between climate variables, lignin concentration, and decomposition rates also applies to ecosystems where water is in excess. This type of linear relationship suggests that the relative effect of changes in litter quality is similar in all environments. The results of this study—that variation in rainfall can play an important role in decomposition dynamics in the humid tropics—helps to explain the general pattern of increased soil organic matter storage with increased precipitation that has been observed in a wide range of humid ecosystems.

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