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Seasonal drought and dry-season irrigation influence leaf-litter nutrients and soil enzymes in a moist, lowland forest in Panama

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Abstract Climatic conditions should not hinder nutrient release from decomposing leaf-litter (mineralization) in the humid tropics, even though many tropical forests experience drought lasting from several weeks to months. We used a dry-season irrigation experiment to examine the effect of seasonal drought on nutrient concentrations in leaf-fall and in decomposing leaf-litter. In the experiment, soil in two 2.25-ha plots of old-growth lowland moist forest on Barro Colorado Island, Republic of Panama, was watered to maintain soil water potential at or above field capacity throughout the 4-month dry season. Wet-season leaf-fall had greater concentrations of nitrogen (N, 13.5 mg g^{-1}) and calcium (Ca, 15.6 mg g^{-1}) and lower concentrations of sulfur (S, 2.51 mg g^{-1}) and potassium (K, 3.03 mg g^{-1}) than dry-season leaf-fall (N = 11.6 mg g^{-1}, Ca = 13.6 mg g^{-1}, S = 2.98 mg g^{-1}, K = 5.70 mg g^{-1}). Irrigation did not affect nutrient concentrations or nutrient return from forest trees to the forest floor annually (N = 18 g m^{-2}, phosphorus (P) = 1.06 g m^{-2}, S = 3.5 g m^{-2}, Ca = 18.9 g m^{-2}, magnesium = 6.5 g m^{-2}, K = 5.7 g m^{-2}). Nutrient mineralization rates were much greater during the wet season than the dry season, except for K, which did not vary seasonally. Nutrient residence times in forest-floor material were longer in control plots than in irrigated plots, with values approximately equal to that for organic matter (210 in control plots vs 160 in irrigated plots). Calcium had the longest residence time. Forest-floor material collected at the transition between seasons and incubated with or without leaching in the laboratory did not display large pulses in nutrient availability. Rather, microorganisms immobilized nutrients primarily during the wet season, unlike observations in tropical forests with longer dry seasons. Large amounts of P moved among different pools in forest-floor material, apparently mediated by microorganisms. Arylsulfatase and phosphatase enzymes, which mineralize organically bound nutrients, had high activity throughout the dry season. Low soil moisture levels do not hinder nutrient cycling in this moist lowland forest.

Key words: litter nutrients, microbial nutrient content, neotropics, nutrient residence time, soil enzymes, tropical moist forest.

INTRODUCTION

Nutrient return from forest trees to surface soil in litterfall and subsequent nutrient release from decomposing litter (mineralization) are crucial processes regulating nutrient availability and hence the rate of forest growth (Attiwill & Adams 1993). Based on biogeochemical theory, rates of nutrient mineralization vary as a function of both litter quality and climate (Berg 1986). Litter quality is the amount and types of organic carbon compounds in litter, nutrient concentrations themselves, and/or a ratio between carbon compounds and nutrients (Schlesinger 1997). Indeed, decomposer microorganisms can import nutrients from soil (immobilization) to support growth on poor quality litter, which results in a feedback with fewer nutrients available for uptake by plants (Fahey *et al.* 1985).

The evidence for litter quality versus climate control of nutrient mineralization in tropical forests is equivocal. Most litter-quality studies look at nitrogen (N) above all other nutrients, although phosphorus (P) is thought to play a more important role in litter quality in tropical forests (Vitousek 1984). Climatic conditions are assumed to be less constricting in the tropics (Couteaux *et al.* 1995), albeit that many tropical forests experience drought lasting from a few weeks to several months (Richards 1996). Drought affects decomposing litter in several ways. For example, during drought there is less nutrient input to decomposing litter in leaching from the forest canopy (throughfall).

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Under excessive drought conditions, the impact of decomposer microorganisms experiencing osmotic stress ranges from inactivity to solute accumulation (Kieft *et al.* 1987).

In the present paper, we describe a study of litter nutrient dynamics in a lowland tropical moist forest in central Panama. There were four objectives for the study: (i) to determine seasonal patterns in nutrient return from forest trees to surface soil in leaf-fall; (ii) to determine nutrient standing crops and residence time in decomposing litter; (iii) to measure mineralization rates in laboratory incubations in decomposing litter and activities of enzymes that carry out mineralization processes; and (iv) to assess the role of seasonal drought through a forest irrigation experiment.

METHODS

General description of the study area

The study area was on Barro Colorado Island (BCI, 9°9′N, 79°51′W), which is located in the Republic of Panama. The study area has a tropical monsoon climate in the Koppen system of climatic classification and supports tropical moist forest in the Holdridge life zone system (Holdridge & Budowski 1956). Soil in the study site is a well-drained Alfisol (Yavitt *et al.* 1993) derived from volcaniclastic sandstone (Johnsson & Stallard 1989). The mineral soil is rich in calcium (Ca), magnesium (Mg) and sulfur (S), but poor in potassium (K) and P, and it is 40% clay, 35% silt and 25% sand between 0- and 15-cm depth (Yavitt *et al.* 1993). The mean monthly maximum temperatures at 1 m in the forest understorey vary by just 1°C, from 22.4°C in January to 23.4°C in June (Windsor 1990). The annual precipitation is 2620 mm. A predictable 4-month dry season begins in December and ends in April, when only 84 mm of precipitation falls. As the dry season progresses, the gravimetric soil water content drops from 42 to 28% (Kursar *et al.* 1995) and soil water potentials can drop to −2.0 MPa (Becker *et al.* 1988). Community-wide rates of litterfall peak early in the dry season and remain high throughout the dry season (Haines & Foster 1977; Wright & Cornejo 1990). Many plants wilt by midday in the late dry season, and 12% of the species of trees are deciduous at some time during the dry season (Croat 1978).

To assess the effect of the dry season on forest ecology, we carried out a dry-season irrigation experiment for 5 years in an old-growth lowland tropical forest in Panama. It was a large-scale experiment in which two 2.25-ha plots were irrigated daily during the dry season, and two adjacent plots served as controls. Because water was added with sprinklers located 1.8 m above the soil surface, the experiment alleviated soil water stress but did not alter atmospheric moisture in the canopy, incident radiation, or throughfall nutrient flux. Previously, we have reported that irrigation does not affect the timing and magnitude of leaf-fall, but it does increase the rate of litter decomposition (Wieder & Wright 1995).

The study plots were approximately 75 m from Gatun Lake, which was the source of irrigation water. Although solute concentrations in Gatun Lake are low (Gonzalez *et al.* 1975), irrigation resulted in weekly fertilization of 45 mg Ca m^{-2}, 7.5 mg Mg m^{-2}, 15 mg K m^{-2}, 45 mg N m^{-2} and 1.5 mg P m^{-2}.

Leaf-fall and forest-floor properties

Leaf-fall was collected in 10 0.25-m^2 screened traps located at randomly chosen positions in each plot. The screen was 1.2-mm mesh, and the trap was mounted 40 cm above the soil. Traps were emptied weekly over the period from 1 January 1989 to 31 December 1990, and plant material was dried at 60°C to a constant mass and weighed. Patterns in leaf-fall dynamics have been published previously in Wright and Cornejo (1990) and in Wieder and Wright (1995). However, nutrient dynamics in the material have not been reported. Species included in the analysis had at least 10 g of dried leaf material per year in each of the four study plots. Nine canopy trees, six subcanopy trees and five lianas met this criterion. Most of the species are distributed widely in Central and northern South America, and all are common on BCI (Croat 1978).

In addition, during the course of the experiment, 10 0.087-m^2 samples of forest-floor litter were collected monthly in 1989 close to 10 of the permanent grid posts on a 15 × 15 grid in each of the plots and at least 1 m from any previously collected sample. The material was dried at 60°C to a constant mass and weighed. Portions of each sample were ground to pass a 20-mesh cm^{-1} screen and archived for analyses.

For leaf-fall, we pooled portions from four contiguous weekly samples and analysed this for concentrations of N, P, S, Ca, Mg and K. For forest-floor litter, we analysed nutrient concentrations on each monthly collection.

The ground samples were dry-ashed in quartz crucibles at 450°C, dissolved in acid and heated to dryness. The ash was dissolved in an acid solution and analysed for Ca, Mg and K by atomic adsorption spectroscopy, for P colorimetrically on a continuous flow analyser, and for S by ion chromatography. N concentration of the ground samples was determined using a micro-Kjeldahl digestion method. Element pool sizes were obtained by multiplying the element concentration by the biomass.

We calculated a net mineralization rate for each nutrient (mg per square meter per day) using the mass

balance approach described in detail in Wieder and Wright (1995). Briefly, this was the nutrient mass in forest-floor material at the beginning of a 28-day sampling interval plus the nutrient inputs in leaf-fall during the interval minus the nutrient mass in forest-floor material at the end of the 28-day interval. We averaged monthly values within seasons (wet vs dry).

Transitions between seasons

In addition, we collected six samples of forest-floor material per plot as well as the underlying surface mineral soil (0–15-cm depth interval) and subsurface mineral soil (30–45-cm depth interval) in December and in April. Samples collected in December represented the period of nearly complete forest-floor litter decomposition, whereas samples collected in April represented maximum litter accumulation. These samples were processed in the laboratory within 3 days of collection. A portion of each sample was oven-dried at 70°C to determine its moisture content. Three other portions of each sample were used to estimate initial extractable concentrations of NH_4^+, NO_3^-, PO_4^{3-} and SO_4^{2-}. A 10-g portion was extracted in 50 mL of 2 mol L^{-1} KCl, which was analysed for NH_4^+ and NO_3^-. A separate 1-g portion was extracted in 7 mL of a dilute acid–fluoride solution and analysed for PO_4^{3-} (hereafter Bray P). A third 10-g portion was extracted in 50 mL of 16 mmol L^{-1} NaH_2PO_4 and analysed for SO_4^{2-}.

A fourth portion of each sample was used to characterize further the different forms of P using sequential P fractionation described by Tiessen and Moir (1993), with some modifications. The method extracts P of differing degrees of availability held in a variety of inorganic and organic forms. A 0.5-g sample was first extracted by shaking for 16 h in a 50-mL centrifuge tube with 30 mL of distilled water and a mesh bag containing 1 g of Dowex 1-X8 anion exchange resin. The resin bag was removed and P adsorbed to the resin was extracted with 20 mL of 0.5 mol L^{-1} HCl for 1 h; P in solution was analysed colorimetrically. The soil suspension was then centrifuged at 12 250 *g* for 10 min and the water decanted off through a Whatman 42 filter. Material on the filter was returned to the centrifuge tube and shaken for 16 h with 30 mL of 0.5 mol L^{-1} $NaHCO_3$ (pH = 8.5). Following centrifugation, the liquid was decanted off through a filter and analysed for total and inorganic P. Material on the filter was again returned to the centrifuge tube and shaken for a further 16 h with 30 mL of 0.5 mol L^{-1} NaOH. Following centrifugation, the liquid was decanted off through a filter and analysed for total and inorganic P. We did not measure the acid extractable fractions (Tiessen & Moir 1993). Total P in the liquid was determined following digestion with H_2SO_4, K_2SO_4 and HgO; hence, organic P was the difference between total P and inorganic P in the extract.

These data were labelled as 'available P', which is the resin extractable fraction; 'labile P', which is the sum of the inorganic P extracted with bicarbonate and NaOH; 'organic P', which is the sum of the organic P extracted with bicarbonate and NaOH; and 'resistant P', which is the difference between total P and the sum of P extracted with resin, bicarbonate and NaOH. These labels differ from those used for mineral soil extractions (Tiessen & Moir 1993).

Three other portions of each sample were used to estimate the N, P and S contents of microbial biomass using chloroform fumigation–direct extraction techniques (Hedley & Stewart 1982; Strick & Nakas 1984; Brookes *et al.* 1985). A 10-g portion was extracted in 50 mL of 0.5 mol L^{-1} K_2SO_4, which was digested with acid and analysed for total N. Another 10-g portion was extracted with 0.5 mol L^{-1} $NaHCO_3$, digested with acid and analysed for total P. We used the initial SO_4^{2-} concentration for S content. The third 50-g portion was fumigated for 2 days with chloroform, dried briefly and then three separate portions were extracted with K_2SO_4, $NaHCO_3$ and NaH_2PO_4 as described above. The nutrients in the microbial biomass were calculated by subtracting the initial N, P and S extracted in each sample from the N, P and S extracted after chloroform fumigation. Soil scientists often use conversion coefficients to convert these values to microbial biomass nutrient pools. We used correction factors of $K_n = 0.54$ for N (Brookes *et al.* 1985), $K_p = 0.37$ for P (Hedley & Stewart 1982), and $K_s = 0.25$ for S (Strick & Nakas 1984).

Finally, two portions of each forest-floor litter sample were used to estimate the net nutrient mineralization rates in two different ways. For one estimate, we placed a 50-g portion in a plastic cup and incubated it for 28 days at 23°C. Distilled water was added twice each week to maintain the water content at field levels during the incubation period. At the end of the incubation period, several different portions were extracted as described above for concentrations of nutrients as well as fumigation-released nutrients. Net nutrient mineralization was calculated as the difference between nutrient concentration in the incubated and initial samples, and the result is referred to hereafter as 'closed' incubation.

For the second measure, a different 50-g portion was placed in a polypropylene Buchner funnel and incubated for 28 days at 23°C. Four 135-mL samples of distilled water were percolated through the sample at the beginning of the incubation and at 3-day intervals thereafter. Each aliquot was allowed to equilibrate for 15 min before being slowly drawn into a flask suspended below each funnel. We repeated this procedure immediately, until the entire 540 mL of water had

been drawn through the material, thus simulating a 2.5-cm h^{-1} rain event. An aliquot of leachate was retained for analysis of the base cations $NH4^+$, NO_3^-, PO_4^{3-} and SO_4^{2-}. At the end of the incubation, the forest-floor litter was extracted as described above for concentrations of nutrients as well as for fumigation-released nutrients. Net nutrient mineralization was calculated as the difference between nutrient concentration in the incubated and initial samples plus the sum of nutrients leached during the incubation period,

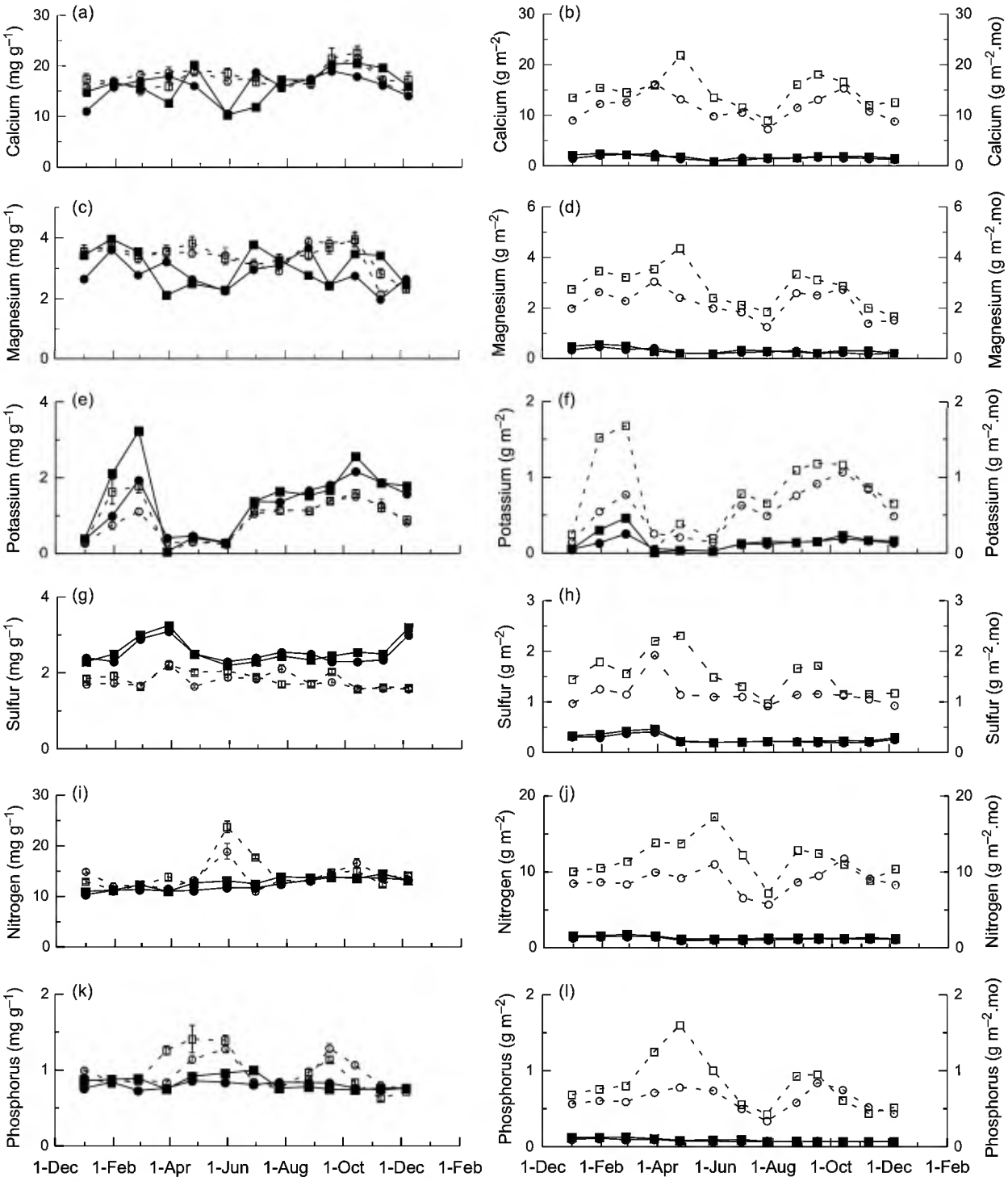

Fig. 1. (a, c, e, g, i, k) Concentrations and (b, d, f, h, l) standing crops of nutrients in (■,●) leaf-fall and (□,○) forest-floor material collected in (■,□) control and (●,○) irrigated plots.

and the result is referred to hereafter as 'open' incubation.

Enzyme activity

We used a slight modification of conventional *p*-nitrophenylester-based assays (Tabatabai & Bremner 1969, 1970) to estimate potential activity of acid phosphatase (phosphomonoesterase, EC 3.1.3.2) and arylsulfatase (EC 3.1.6.1). Portions of forest-floor litter and mineral soil were analysed before and after both of the incubations. Portions at field moisture content (1 g) were mixed with 10 mL of either 10 mmol L^{-1} *p*-nitrophenyl-phosphate or *p*-nitrophenyl-sulfate and incubated for 1 h at 30°C. We did not use conventional buffers as we wanted to perform the assays at field conditions rather than at optimal pH and ionic strength. After the incubation, 0.5mol L^{-1} NaOH was added to stop the reactions. Litter or soil was removed by centrifugation before concentrations of *p*-nitrophenol in the solution were measured by absorbency at 410 nm. Controls were slurry without substrate and substrate without slurry.

Statistical analyses

Monthly nutrient concentrations in leaf-fall and forest-floor material were analysed using a repeated measures ANOVA. Treatment (irrigated vs control) was the between-subjects effect and plot was nested within treatment. Each leaf-fall trap and forest-floor collection site was a subject ($n = 10$ per plot). Within-subjects effects were the season and the interaction term. Extractable nutrient concentrations, mineralization rates and enzyme activities were also analysed with repeated measures ANOVA. The within-subjects effect was the sampling date (December vs April). All estimates of variance are 99% confidence intervals.

Table 1. Mean concentrations and standing crops of nutrient elements in leaf-litter and forest-floor material, reported separately by season

	Nitrogen	Phosphorus	Sulfur	Calcium	Magnesium	Potassium
Litter						
Concentration (mg g^{-1})						
Wet season	13.50[a]	0.79[a]	2.51[b]	15.60[a]	4.80[a]	3.03[b]
Dry season	11.60[b]	0.87[a]	2.98[a]	13.60[b]	4.95[a]	5.70[a]
Return (g m^{-2} a^{-1})						
Wet season	11.60[a]	0.60[a]	1.90[a]	11.60[a]	3.73[a]	2.38[a]
Dry season	6.40[b]	0.46[a]	1.59[a]	7.30[b]	2.75[a]	3.33[a]
Total	18.00	1.06	3.49	18.90	6.48	5.70
Forest floor						
Concentration (mg g^{-1})						
Wet season	14.10[a]	0.90[a]	1.59[b]	17.90[a]	3.10[a]	1.27[a]
Dry season	12.80[b]	0.90[a]	1.90[a]	18.40[a]	3.25[a]	1.25[a]
Standing crop (g m^{-2})						
Wet season, control plots	9.80	0.56	1.18	12.20	2.20	0.79
Wet season, irrigated plots	7.00	0.43	0.89	9.10	1.55	0.58
Dry season, control plots	12.00	0.90	1.93	16.90	3.10	1.40
Dry season, irrigated plots	9.20	0.60	1.23	13.60	2.30	0.71
Average, control plots	10.50[c]	0.67[c]	1.42[c]	13.70[c]	2.50[c]	0.99[c]
Average, irrigated plots	7.80[d]	0.49[c]	1.00[d]	10.60[d]	1.80[d]	0.62[e]
Residence time (days)						
Control plots	223	224	146	256	155	59
Irrigated plots	151	173	106	211	93	43

[a,b]Significant season effects at $P = 0.05$; [c,d]significant treatment effects at $P = 0.05$.

Table 2. Net nutrient mineralization rates in forest-floor material (mg m^{-2} day^{-1}), reported separately by season and treatment

	Nitrogen	Phosphorus	Sulfur	Calcium	Magnesium	Potassium
Wet season						
Control plots	119.0–132.0	6.9–10.5	20.2	141.0	35.8–49.7	28.0
Irrigated plots	104.0	6.3	17.2	123.0	42.7	17.4
Dry season						
Control plots	8.5–42.0	–0.2–3.3	13.0	7.6–56.8	10.0	21.7
Irrigated plots	33.0	2.6	12.2	19.2–49.8	16.0	21.9

RESULTS

Leaf-fall and forest-floor properties

Element concentrations in leaf-fall varied seasonally (Fig. 1). Concentrations of N and Ca increased gradually during the year and peaked at the end of the wet season, just prior to the maximum rate of leaf-fall, before decreasing sharply to the lowest values in the dry season. Temporal changes in S and K concentrations were the reverse of N and Ca, peaking in the dry season. P and Mg concentrations showed no significant seasonal variability. Although leaf-fall rates peaked during the dry season (Wright & Cornejo 1990), more than 50% of the nutrient return from forest trees to the surface soil in leaf-fall occurred during the wet season, expect for K (Table 1). Irrigation did not have a significant effect on either concentrations in leaf-fall or the amount of nutrient return annually by leaf-fall.

The temporal patterns in nutrient element concentrations in forest-floor material tended to parallel those in leaf-fall (Fig. 1), although the range of values was lower in forest-floor material. Because irrigation had a large impact on the standing crop of forest-floor material (Wieder & Wright 1995), there were large differences in the standing crop of nutrients in forest-floor material in irrigated versus control plots. Overall, nutrient standing crops were 29–60% greater in control than in irrigated plots (Table 1). Ca had the smallest irrigation effect, whereas K had the largest irrigation effect. As expected, a large irrigation effect on standing crop of nutrients in the forest floor was observed during the dry season. However, the irrigation effect persisted into the wet season, and the standing crop of nutrients in forest-floor material was, on average, 36% greater in control than in irrigated plots.

Assuming nutrients in forest-floor material are at steady state conditions, maintained by input in litterfall and output following mineralization, the nutrient residence time can be estimated by dividing standing crop by nutrient return in leaf-fall. Standing crop pool size was a weighted average calculated using the pool size during the 8-month-long wet season and the 4-month-long dry season. N, P and Ca had the longest residence times, whereas K had the shortest residence time. Irrigation reduced the residence time by 40–70 days. We also calculated a daily nutrient mineralization rate and found that rates were much greater during the wet season than during the dry season, except for K (Table 2). Mineralization rates were quite variable during the dry season, especially in the control plots, presumably in response to periodic dry-season rain events.

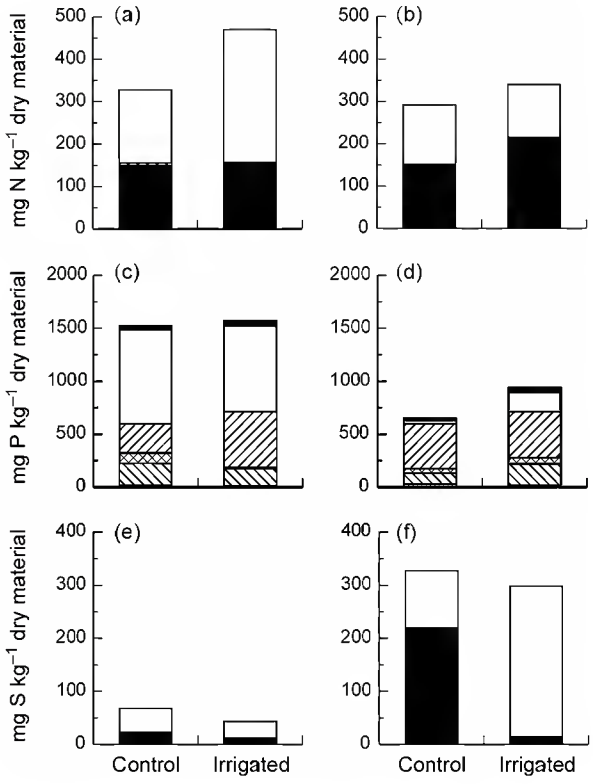

Fig. 2. Mean concentrations of nutrients extracted from forest-floor material collected at (a, c, e) the end of the wet season in December and again at (b, d, f) the end of the dry season in April. (a, b) nitrogen (N): (□), microbial N; (▨), nitrate; and (■), ammonium. (c, d) phosphorus (P): (■), phosphate; (□), microbial P; (▨), resistant; (▧), organic; (▧), labile; and (X), available. (e, f) sulfur (S): (□), microbial S; and (■), sulfate.

Transitions between seasons

Extractable N was mostly $NH4^+$ and microbial N (Fig. 2). Overall, extractable N was greater in December than in April Concentrations of NH_4^+ were significantly greater in irrigated than in control plots in April, whereas concentrations of microbial N were significantly greater in irrigated versus control plots in December (i.e. significant treatment–season interactions for each). Extractable P was twofold greater in December than in April (Fig. 2), driven by much greater concentrations of microbial P in December. Moreover, in April, microbial P was significantly greater in irrigated than in control plots. Resistant P was the largest of the four sequentially extracted fractions, being greater than labile P and organic P combined. Extractable S was fivefold greater in April than in December (Fig. 2), driven by greater SO_4^{2-} in control plots versus greater microbial S in irrigated plots.

Rates of net N mineralization and net nitrification were significantly greater in closed than in open incubations, whereas net S mineralization was significantly greater in open than in closed incubations (Fig. 3).

Rates did not differ significantly between control and irrigated plots; net N mineralization was slightly greater in control than in irrigated plots in April (data not shown). Net nitrification was significantly greater in April than in December for both incubation conditions. Net S mineralization rates were also significantly greater in April than in December (Fig. 3). Indeed, S was immobilized (negative net S mineralization) in the closed incubations in December.

Measuring net P mineralization is not straightforward (Walbridge & Vitousek 1987). Nevertheless, we found large net transfer of P into the organic fraction during incubations, except in the open incubation in April (Fig. 4). This occurred at the expense of resistant P in the closed incubations versus resistant and labile P in the open incubations. The largest change in microbial P occurred in April, with loss occurring during the open incubations versus increases during the closed incubation of material from the control plot (i.e. the driest material). Changes of greater than 80% are significant.

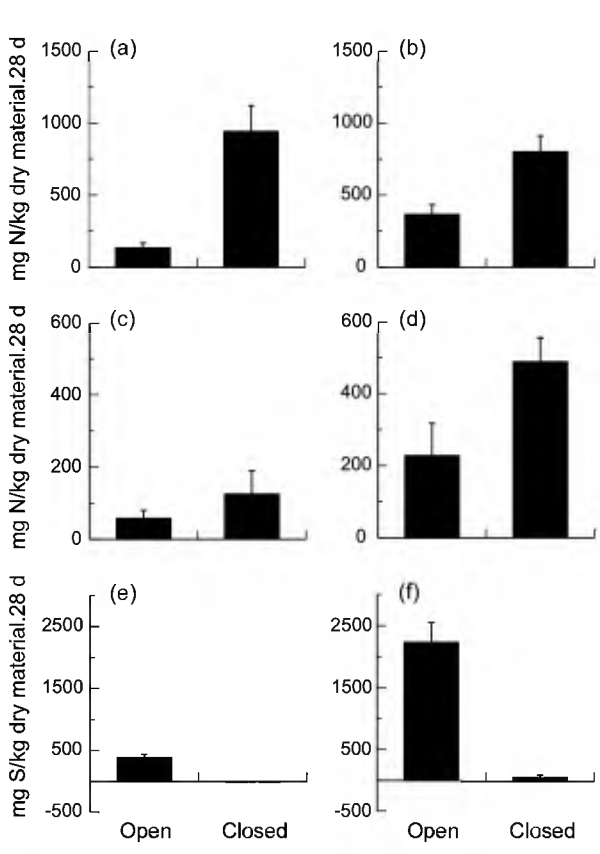

Fig. 3. Mean (±99% confidence interval) rates of (a, b) net nitrogen (N) mineralization, (c, d) net nitrification, and (e, f) net sulfur (S) mineralization in forest-floor material collected at (a, c, e) the end of the wet season (December) and again at (b, d, f) the end of the dry season (April).

Enzyme activity

Enzyme activities in forest-floor material (Table 3) did not differ significantly among collections made in December versus April and among control and irrigated plots. Upon incubation in the laboratory, however, enzyme activities decreased significantly following the open incubation and increased following the closed incubations. Arylsulfatase activity was significantly greater in material from the irrigated versus control plots following the closed incubation.

Arylsulfatase activity was significantly greater in surface mineral soil than in either forest-floor material or subsurface mineral soil (Table 3). Phosphatase activity was significantly greater in forest-floor material than in mineral soil. On incubation in the laboratory, phosphatase activity showed the same behaviour in the mineral soil as in forest-floor material, with lower rates following the open incubation. However, arylsulfatase activity in the mineral soil increased in both the open and closed incubations.

DISCUSSION

The question of whether nutrient concentrations in leaf-fall vary systematically with seasonal drought in

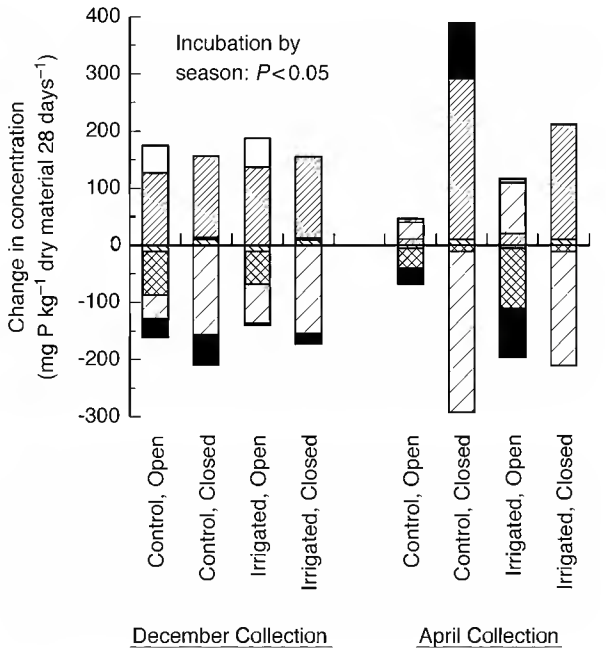

Fig. 4. Changes in phosphorus (P) fractions in forest-floor material collected at the end of the wet season (December) and again at the end of the dry season (April) from control and irrigated plots, following incubation in the laboratory under closed or open conditions. (□), P in leachate; (■), microbial P; (▨), resistant; (□), organic; (▩), labile; and (▩), available.

tropical forests is still open to debate. Some have concluded that nutrient concentrations in leaf-fall vary haphazardly during the year (Lips & Duivenvoorden 1996; Herbohn & Congdon 1998). In contrast, others have found relatively strong evidence for lower K concentrations and greater N concentrations in wet-season leaf-fall (Scott *et al.* 1992; Cuevas & Lugo 1998; Chuyong *et al.* 2000). The results of the present study suggest greater N and Ca concentrations and lower S and K concentrations in wet-season versus dry-season leaf-fall.

Increasing concentrations of both N and Ca as leaf-fall reached peak rates were not expected. It is generally believed that Ca and Mg concentrations increase while N and P concentrations decrease as leaf-fall approaches peak rates (Reiners & Reiners 1970), albeit that most data come from non-tropical forest ecosystems. The decrease in N and P has been attributed to translocation of the elements from green leaves to twigs prior to leaf-fall as well as to greater accumulation of organic matter than N and P as green leaves grow, thereby diluting their concentrations. Conversely, Ca and Mg are not removed from leaves prior to leaf-fall. We have no explanation of why N and Ca behaved so similarly in the present study. Because leaves that fell during the dry season grew during the wet season, apparently these leaves had a lower Ca requirement than leaves grown earlier in the wet season. In contrast, lower K and S concentrations in wet-season litter probably reflect leaching from green leaves, as both elements are quite mobile.

Although leaf-fall rates peak during the dry season (Wieder & Wright 1995), the larger return of nutrients from forest trees to the forest floor during the wet season than during the dry season (Table 1) coincides with 65% of the annual leaf-fall during the longer wet season. Overall, nutrient return in leaf-fall was at the high end of values published in reports for other lowland tropical forests (Lips & Duivenvoorden 1996); in a large part, this reflects the large litter mass in the study area.

In contrast, nutrient standing crops in forest-floor material were not excessively high compared with values published for other lowland tropical forests. This indicates rapid nutrient mineralization rates once organic matter decomposition begins. For comparison, we use residence time values, even though the residence time concept assumes steady-state conditions between

Table 3. Mean (±99% confidence interval) activity of phosphatase and arylsulfatase enzymes (μmol *p*-nitrophenol (PNP) produced g^{-1} h^{-1}) in mineral soil

	December collection		April collection	
	Control	Irrigated	Control	Irrigated
Phosphatase				
Forest-floor material				
Pre-incubation	12.1 ± 2.0[b]	13.2 ± 2.3[b]	16.0 ± 2.4[b]	19.3 ± 2.6[b]
Open incubated	10.1 ± 1.0[b]	12.1 ± 1.4[b]	8.0 ± 0.6[c]	9.3 ± 1.4[c]
Closed incubated	24.3 ± 3.5[a]	24.8 ± 4.4[a]	34.7 ± 2.9[a]	40.5 ± 5.6[a]
0–15-cm depth				
Pre-incubation	6.6 ± 1.1[b]	6.7 ± 0.7[b]	8.8 ± 0.9[a]	8.4 ± 1.2[a]
Open incubated	3.8 ± 0.4[c]	3.8 ± 0.4[c]	3.9 ± 0.6[b]	6.1 ± 0.8[b]
Closed incubated	9.1 ± 0.5[a]	8.6 ± 0.4[a]	8.9 ± 0.6[a]	10.2 ± 1.1[a]
30–45-cm depth				
Pre-incubation	2.0 ± 0.4[b]	3.1 ± 0.6[a]	2.5 ± 0.7[b]	3.8 ± 0.7[a]
Open incubated	1.4 ± 0.2[b]	0.9 ± 0.1[c]	1.4 ± 0.1[c]	0.6 ± 0.2[c]
Closed incubated	3.4 ± 0.4[a]	2.4 ± 0.2[b]	3.3 ± 0.1[a]	2.9 ± 0.2[b]
Arylsulfatase				
Forest-floor material				
Pre-incubation	2.0 ± 0.4[b]	3.1 ± 0.6[b]	2.5 ± 0.7[b]	3.8 ± 0.7[b]
Open incubated	0.5 ± 0.1[c]	0.6 ± 0.1[c]	0.7 ± 0.1[c]	2.1 ± 0.5[c]
Closed incubated	4.4 ± 0.8[a]	7.5 ± 1.0[a]	5.1 ± 0.8[a]	8.2 ± 1.2[a]
0–15-cm depth				
Pre-incubation	6.1 ± 0.9[b]	7.6 + 1.0[a]	6.1 + 1.0[b]	6.9 + 1.5[b]
Open incubated	3.9 ± 0.4[c]	4.7 + 0.4[b]	7.0 + 0.6[b]	8.3 + 0.6[b]
Closed incubated	7.7 ± 0.6[a]	8.3 + 0.6[a]	8.4 + 0.8[a]	10.1 + 0.9[a]
30–45-cm depth				
Pre-incubation	1.0 ± 0.3[a]	0.6 ± 0.1[a]	1.5 ± 0.3[b]	0.9 ± 0.3[b]
Open incubated	0.5 ± 0.1[b]	0.4 ± 0.1[b]	1.5 ± 0.1[b]	1.4 ± 0.2[a]
Closed incubated	1.1 ± 0.2[a]	0.8 ± 0.1[a]	1.9 ± 0.2[a]	1.5 ± 0.1[a]

[a,b]Significant incubation effects at $P = 0.05$.

input in litter and output following mineralization. Although we realize that some of the assumptions about steady-state conditions are questionable with such rapid turnover of litter, residence time is a good variable for comparison. The values for N were nearly identical to the organic matter in leaf-litter of 210 days in the control plot and 170 days in the irrigated plots (Wieder & Wright 1995). Therefore, N was lost at the same rate as mass, at least on an annual basis. Residence times for P and Ca were a bit longer than that for organic matter, indicating some net immobilization. The longer values for Ca might be an accumulation rather than slow mineralization, as Ca accumulation in forest-floor material has been attributed to fungi that need to dispose of oxalate – a metabolic product – as a calcium salt to prevent osmotic imbalance (Sollins *et al.* 1981). The very short residence times for S, K and Mg, notably shorter than that for organic matter, suggests rapid mineralization and is in agreement with the mobility of the elements in leaf-litter (Gosz *et al.* 1973). We also found that nutrient residence times were shorter in irrigated than in control plots in accordance with the irrigation effect on faster organic-matter decomposition rates.

The incubation of forest-floor material in the laboratory allowed us to test whether changes in water availability at the transitions between seasons cued pulses in nutrient mineralization. Our approach was to collect samples just prior to the change in season and apply water flux (open incubation), or not (closed incubation), simulating wet-season versus dry-season conditions. For the transition from the dry season to the wet season, there was no evidence for pulses in net N mineralization or net nitrification, as rates were lower in open than in closed incubations, with material collected in April. Pulses in net N mineralization and/or net nitrification at the onset of the wet season appear to occur more commonly in montane than in lowland tropical forests (Kiese *et al.* 2002) and after long dry seasons (Marrs *et al.* 1991). Conversely, we found significantly larger net N mineralization rates in the closed than in open incubation with material collected in December, possibly suggesting a pulse of N mineralization when the dry season was extended, at least artificially. The reason might be related to both elevated N concentrations in leaf-litter falling during the later part of the wet season and the lack of leaching that removes nutrients.

Although net S mineralization was much greater in the open than in the closed incubation in material collected in April (dry-to-wet-season transition), the phenomenon occurred in material from both the control and the irrigated plots, suggesting that the onset of the wet season was not responsible for the phenomenon. No pulse in S mineralization occurred in material collected in December, as was found for net N mineralization. Unfortunately, P mineralization cannot be measured in the same manner because mineralized P can be fixed very quickly in inorganic reactions (Walbridge & Vitousek 1987). Nevertheless, we observed large changes in the distribution of P between different fractions during incubation (Fig. 3), indicating that P is not static in these fractions at the transitions between seasons. The transformation of resistant P to organic P and fumigation-release P, especially in the closed incubations, suggests that microorganisms synthesize organic P from inorganic P during litter decay. It has been suggested that microorganisms mediate conversion of P from inorganic to organic forms to prevent leaching, for later immobilization (Mueller-Harvey & Wild 1986). The transformation of labile P in the open incubations suggests that leaching promotes a different mechanism of P transformations. The data in the present study are also unusual in that microorganisms used resistant P. However, there was a major pool of P in the forest floor (Fig. 2), whereas litter P occurs primarily in labile and fumigation-released fractions in dry tropical forests (Campo *et al.* 1998) versus the organic fraction in wet rainforests (Tiessen *et al.* 1994).

Estimates of nutrients in microbial biomass suggested greater N, P and S immobilization during the wet season than the dry season and greater nutrient immobilization in irrigated than in control plots (Fig. 2). In contrast, soil microorganisms in dry tropical forests immobilize nutrients primarily during the dry season (Singh *et al.* 1989; Campo *et al.* 1998), apparently because they remain active in soil that is too dry for plants and microbial grazers (Campo *et al.* 1998). There are certainly several factors that affect nutrient immobilization, and we can only speculate about the reasons for the different finding in the present. The results indicate a molar N : P ratio in microbial biomass of 1.2:1.0, which is closer to the expected value of 1.0:1.0 for soil fungi than the 3.0:1.0 for bacteria (Anderson & Domsch 1980). This suggests that fungi dominate nutrient immobilization in the wet season. Cornejo *et al.* (1994) found more bacteria on wet than on dry leaf-litter and more microfungi on dry than on wet leaf-litter. However, our method for measuring the nutrient content of microbial biomass includes filamentous fungi that Cornejo *et al.* (1994) did not measure. Further experiments measuring fungal and bacterial biomass specifically would be necessary to identify tradeoffs between bacterially and fungally mediated decomposition as litter oscillates between the wet and dry seasons.

In contrast, forest-floor litter collected in April from the control plots showed an unusually high N : P ratio, but the explanation is probably that there was a large decrease in microbial P as soil dried gradually (Srivastava 1998). When the April samples from the control plots were incubated under closed conditions, which prolonged the drought, microbial biomass P levels

Table 4. Residence times for litter mass and nutrients in the forest floor in several lowland tropical forests

Location	MAP (mm)	Dry season (months)	Mass (days)	Nitrogen (days)	Phosphorus (days)	Sulfur (days)	Calcium (days)	Magnesium (days)	Potassium (days)	Reference
Sarawak	5100	0	281	192	304	NA	203	159	107	Anderson *et al.* (1983)
Borneo	2800	5	139	155	164	NA	128	119	60	Burghouts *et al.* (1998)
BCI, Panama (control)	2600	4	210	223	224	146	256	155	59	Present study
BCI, Panama (irrigated)	3900	0	151	151	173	106	211	93	43	Present study
Australia	2100	3	294	255	276	NA	276	173	58	Brasell and Sinclair (1983)
Australia	1560	3	302	215	320	NA	276	217	71	Brasell and Sinclair (1983)
Maraca, Brazil	1800	6	182	152	130	NA	183	124	62	Scott *et al.* (1992)
Belize	1720	6	208	152	36	NA	280	278	173	Lambert *et al.* (1980)
India	821	9	NA	484	463	NA	438	NA	507	Singh and Singh (1991)
Mexico	679	7	519	NA	382	NA	646	427	314	Campo *et al.* (1998, 2000)

BCI, Barro Colorado Island; MAP, mean annual precipitation; NA, not applicable.

rebounded, but interestingly not under open conditions, suggesting P accumulated again under extended drought (i.e. >4 months).

A comparison of results provides insight into microbial control of soil nitrogen cycling. Greater nitrification rates in April than in December coincided with lower amounts of N in microbial biomass. The inverse relationship occurs when soil microbes are limited by the availability of carbon (C) for growth, and thus some carry out autotrophic nitrification for energy (Fisk & Fahey 2001). Knops *et al.* (2002) suggested that the most labile source of C for microbial growth is soluble organic molecules released from fine roots. As expected, fine roots are dying towards the end of the dry season in April (Yavitt & Wright 2001) and, presumably, exuding little fresh carbon to the soil. In contrast, fine roots are still active in December, supplying soil microbes with carbon and suppressing nitrification. The results of the present study also show that net S mineralization followed the opposite pattern. This was expected, as S mineralization is a heterotrophic, not an autotrophic process, and the SO_4^{2-} formed is excess after metabolic needs are met.

Both seasonal drought and dry-season irrigation had little effect on soil enzyme activities, although activity was sensitive to laboratory incubation conditions. This was not expected, as the accumulation of end product (PO_4^{3-}, SO_4^{2-}) has been shown to inhibit enzyme activity, much more so for phosphatase than for arylsulfatase (McGill & Cole 1981). Accordingly, leaching in the open incubations should shave stimulated enzyme activities, whereas we found greater enzyme activities after closed than after open incubation. For phosphatase, the highest activity in forest-floor material, combined with a large fraction of organic-P formation, suggests that microorganisms decomposing relatively fresh litter can immobilize P and synthesize phosphatase enzymes. Less enzyme activity following open incubation might relate to 'aging' of the litter under prolonged wet-season conditions. The 'age' of litter helps explain other reported observations that phosphatase activity increases (Spiers & McGill 1979) or decreases (Pang & Kolenko 1986) during incubation.

Arylsulfatase activity was not much different seasonally, even though litter collected in December had a very low concentration of extractable S. In contrast, lower activity following open incubation coincided with very high rates of net S mineralization, suggesting the mineralization inhibited activity. Net S mineralization can derive from organic matter decomposition by heterotrophic microorganisms that encounter S in proteins in excess of metabolic needs, and might not involve arylsulfatase enzymes directly (McGill & Cole 1981). In contrast, data from the subsoil suggests end-product inhibition of arylsulfatase (Table 3), where activity was lower in April (no leaching) than in

December (well leached). The results of the present study are consistent with the notion that arylsulfatase produced by microorganisms (i.e. in forest-floor material) is inhibited by inorganic S accumulation to a lesser degree than arylsulfatase produced by plant roots (i.e. in the subsoil; Ganeshamurthy & Nielsen 1990).

Overall, nutrient residence times in forest-floor material are similar to values from other moist tropical forests and, generally, are shorter than values from tropical dry forests with a 6-month dry season (Table 4). The somewhat longer residence time for nutrients in the very wet forest of Sarawak (Table 4) indicates that nutrient residence times do not change monotonically with precipitation or drought period. Although dry-season irrigation resulted in even shorter nutrient residence times, there was no indication that seasonal drought hindered nutrient cycling. Indeed, rates of nutrient cycling might peak in moist forests in which soil does not experience anoxic conditions and the dry season is not too harsh. This analysis supports the notion that Oikawa (1986) advanced on theoretical grounds that seasonal drought in moist tropical forests is distinctly different from protracted (>6-month) drought in dry tropical forests.

Although drought-induced water stress is seemingly the most important trigger for seasonal rhythms observed in many moist tropical forests (Lodge *et al.* 1994; Leigh *et al.* 1996), other exogenous triggers, such as incident radiation or atmospheric moisture could play important roles. For example, although leaf-fall peaks in the dry season, it also coincides with low levels of atmospheric moisture that could trigger the event through the relationship between transpiration and atmospheric moisture (Eamus & Prior 2001).

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