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Soil nutrient dynamics in response to irrigation of a Panamanian tropical moist forest

JOSEPH B. YAVITT[1], R. KELMAN WIEDER[2] & S. JOSEPH WRIGHT[3]

[1] *Department of Natural Resources, Fernow Hall, Cornell University, Ithaca, NY 14853, USA;* [2] *Department of Biology, Villanova University, Villanova, PA 19085, USA;* [3] *Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Republic of Panama*

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Abstract. We measured concentrations of soil nutrients (0–15 and 30–35 cm depths) before and after the dry season in control and dry-season irrigated plots of mature tropical moist forest on Barro Colorado Island (BCI) in central Panama to determine how soil moisture affects availability of plant nutrients. Dry-season irrigation (January through April in 1986, 1987, and 1988) enhanced gravimetric soil water contents to wet-season levels (ca. 400 g kg^{-1}) but did not cause leaching beyond 0.8 m depth in the soil. Irrigation increased concentrations of exchangeable base cations (Ca^{2+}, Mg^{2+}, K^+, Na^+), but it had little effect on concentrations of inorganic N (NH_4^+, NO_3^- and S (SO_4^{2-}). These BCI soils had particularly low concentrations of extractable P especially at the end of the dry season in April, and concentrations increased in response to irrigation and the onset of the rainy season. We also measured the response of soil processes (nitrification and S mineralization) to irrigation and found that they responded positively to increased soil moisture in laboratory incubations, but irrigation had little effect on rates in the field. Other processes (plant uptake, soil organic matter dynamics) must compensate in the field and keep soil nutrient concentrations at relatively low levels.

Introduction

Although temperature and photoperiod are nearly constant in the tropics, extended drought can impose distinct seasonality (Richards 1952). For example, plant growth and reproduction decline whereas litter fall peaks during the dry season in lowland forests throughout the tropics (Breitsprecher & Bethel 1990; Wright 1991; Wright & Cornejo 1990 and references cited therein).

We hypothesized that seasonal drought also would affect soil nutrient dynamics in tropical forests. Since water stress limits microbial activity and decomposition of soil organic matter (Luizao & Schubart 1987),

nutrient release from detritus should be lower in the dry season than in the wet season. On the other hand since rainfall leaches dissolved ions (Franken et al. 1985; Russell & Ewel 1985), soil nutrients ought to accumulate during the dry season (Garcia-Mendez et al. 1991). As solutes concentrate in soil pore spaces upon soil drying (Uehara & Gillman 1981), weathering rates of soil minerals in the dry season should be lower than in the wet season. The wetting of dry soil (and vice versus) also could induce rapid changes in soil nutrient dynamics, especially for nitrogen (Birch 1964). There is evidence of an immediate increase in nitrogen mineralization following wetting of dry soil, particularly when the antecedent dry period is long (Davidson et al. 1993). Therefore, nitrogen availability might actually peak at the onset of the rainy season.

To evaluate the net effect of these processes, we added water to a 2.25 ha plot in each of two sites of mature forest on Barro Colorado Island (BCI) during successive dry seasons in 1986, 1987 and 1988. We tested the null hypothesis that moisture availability has no effect on soil nutrient concentrations by sampling soils late in the rainy season in December and again at the end of the dry season in April. We focused our studies on concentrations of exchangeable base cations (Ca^{2+}, Mg^{2+}, Na^{+}, and K^{+}), nitrogen (N), phosphorus (P) and sulfur (S). The latter three elements are of particular concern because they cycle rapidly through plant and microbial biomass (McGill & Cole 1981) and are important in the ecology of tropical forests (Cuevas & Medina 1988; Tanner et al. 1990; Vitousek 1984).

Study site

BCI (9°9′N, 79°51′W) is the largest island in Gatun Lake, Republic of Panama, a portion of the Panama Canal. The irrigation experiment was conducted in a mature (500-yr old) tropical moist forest (according to Holdridge & Budowski 1956) on BCI. Annual rainfall averages 2600 mm, but a predictable 4-mo dry season begins in December (or rarely in November or January) and ends in April or May. Total rainfall in January, February and March is just 84 mm (Windsor 1990). Soil in the study area is a well-drained Alfisol derived from sedimentary bedrock of the Caimito formation of late Oligocene age (Woodring 1958). The bedrock is a volcaniclastic sandstone composed largely of altered volcanic lithic fragments and plagioclase (Johnsson & Stallard 1989).

Irrigation water was drawn from Gatun Lake and delivered by sprinklers mounted 1.8 m above the ground and arranged in a hexagonal array. With this design, each point, except at plot borders, received water from

three or more sprinklers unless it was intercepted by vegetation. Irrigation lasted for 1.5 hr on each 5 d per week, resulting in a weekly deposition of 30 mm per plot (Wright 1991). Solute concentrations in Gatun Lake are exceedingly low (Gonzalez et al. 1975) and lower than solute concentrations in rain collected on BCI (R. Stallard, pers. comm.) so that irrigation did not cause a confounding fertilization. We estimated that weekly inputs did not exceed 45 mg m^{-2} for Ca, 7.5 mg m^{-2} for Mg, 15 mg m^{-2} for K, 45 mg m^{-2} for Na and 1.5 mg m^{-2} for P.

Dry-season irrigation maintained soil water potential (at 25 and 45 cm depths) above −0.04 MPa compared to values below −1.0 MPa in the control (not irrigated) plots each year (Wright 1991). Irrigation did not leach solutes from the soils during the dry season. Drainage lysimeters placed at 80-cm depth did not collect leachate in either the irrigated or control plots during any of the dry seasons (Stallard, Keller, and Wright, unpub. data).

Total rainfall, measured at the site, was 2069 mm in 1986, 2593 mm in 1987, and 2602 mm in 1988. Dry-season rainfall (that which occurred between our December sample and the following April sample) was 51 mm in 1986, 135 mm in 1987, and 122 mm in 1988. In April 1987, a 50 mm rain event occurred 5 days before we collected our soils, but several rainless weeks preceded collections in April 1986 and April 1988.

Methods

Soil collections

We established six sampling locations on a 15 × 15 m grid in each of the four plots prior to initiation of the first dry-season irrigation, and we sampled soil at each location six times: 15 December 1985, 5 April 1986, 14 December 1986, 16 April 1987, 9 December 1987, 19 April 1988. On each sampling date, we collected bulk soil samples (0—15 cm depth of mineral soil) within 2 m of each of the grid points and at least 1 m from any previously collected sample. We also collected subsurface samples (30—35 cm depth) on the first four dates. We did not include analyses for forest floor samples in the present paper because the forest floor is essential root-free at BCI, and we were interested in soil nutrient dynamics directly affecting plant growth. Analyses for forest floor samples are treated elsewhere (Yavitt & Wright, unpub. manuscript).

We initiated analyses of the soils within 36 h of collection. For the December 1985 samples, we determined particle-size distribution (< 2

mm fraction) by pipette, Fe and Al by selective extraction, total C and total S by dry combustion, total N by semimicro-Kjeldahl, and total P colorimetrically following HF digestion, all using standard methods (Soil Conservation Service 1984).

We carried out all extractions on field-moist soils; soil moisture content was determined on separate subsamples to allow for expression of all data on a per gram dry soil basis. We measured soil pH on soil-water and soil-1M KCl suspensions (1—5 mass-to-volume ratio).

Concentrations of soluble, extractable and fumigation-released nutrients

We extracted base cations from 5 g of soil using 50 ml of 1 M ammomium acetate and determined concentrations using atomic absorption/emission spectrophotometry.

We extracted soil N, P and S using the following procedures. The designations given here for each form are used throughout this paper.

'*Soluble* NH_4^+, NO_3^-, P and S': 10 g of soil were extracted with 50 ml of 10 mM of $CaCl_2$ (Yavitt & Wieder 1988) and filtered through glass-fiber filters; concentrations of NH_4^+, NO_3^-, PO_4^{3-}, and SO_4^{2-} in the filtrates were determined by ion chromatography (Dionex Inc., Model 2010i).

'*Extractable* NH_4^+ and NO_3^-': 10 g of soil (December 1987 and April 1988 only) were extracted with 50 ml of 2M KCl, filtered through a glass-fiber filter, and concentrations of NH_4^+ and NO_3^- in the filtrate were determined colorimetrically by continuous-flow analysis (Stainton et al. 1977).

'*Extractable* P and S': 1 g of soil was extracted with an acid fluoride solution (Olsen & Sommers 1982), filtered, followed by colorimetric determination of the extracted PO_4^{3-} (Stainton et al. 1977). 5 g of soil was extracted with 50 ml of 16 mM NaH_2PO_4, filtered, followed by determination of the extracted SO_4^{2-} by ion chromatography.

'*Fumigation-released* N, P and S': We fumigated 20 g of soil overnight with chloroform (Jenkinson & Powlson 1976). On separate 5 g subsamples of both fumigated and unfumigated soil, we extracted total N, P and S using 0.5 M K_2SO_4, 0.5 M $NaHCO_3$, and 16 mM NaH_2PO_4, respectively (Brookes et al. 1982, 1985; Strick & Nakas 1984), determining extracted N concentrations by Kjeldahl digestion and colorimetric N determination, extracted PO_4^{3-} concentrations colorimetrically, and extracted SO_4^{2-} concentrations by ion chromatography. Differences in concentrations between fumigated and unfumigated subsamples are referred to as 'fumigation-released' rather than microbial biomass nutrient content, because appropriate conversion factors are unknown for soil on BCI. For such a conversion to microbial biomass nutrient content, our appropriate

values can be divided by 0.54 for N (Brookes et al. 1985), by 0.40 for P (Brookes et al. 1982), and by 0.34 for S (Strick & Nakas 1984).

Soil process studies

We incubated bulk field-moist soil using two different laboratory procedures, referred to throughout this paper as 'closed' and 'open' incubations. For closed incubations, we placed a 40 g subsample of soil into a polypropylene cup, which was covered and incubated for 28 d at 25 °C. We added distilled deionized water every 3 d to replace the amount lost by evaporation. Concentrations of soluble, extractable and fumigation-released N, P and S were determined on subsamples both prior to and following incubation. We refer to differences between preincubation and postincubation concentration of NO_3^- and S as net nitrification and net S mineralization, respectively (cf., Maynard et al. 1983). We also report changes in concentrations of fumigation-released N, P and S during the incubation period.

For open incubations, we placed a 40 g subsample of soil in a polypropylene Buchner funnel (70 mm diam.) and incubated it for 28 d at 25 °C. We percolated four 24 mL aliquots of distilled deionized water through the soil at the beginning of the incubation and at 3 d 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 all 96 mL of water had been drawn through the soil, thus simulating a 2.5 cm h^{-1} rain event. An aliquot of leachate was retained for analysis of NH_4^+, NO_3^-, PO_4^{3-}, and SO_4^{2-} by ion chromatography. Unfortunately, we did not determine the flux of organic N, P and S in the leachate. The sum of NO_3^- and S in leachate plus differences between preincubation and postincubation concentrations are referred to as net nitrification and net S mineralization, respectively. Following incubation, we also determined extractable and fumigation-released N, P and S.

Statistical analyses

We used repeated-measures analysis of variance (Winer 1971) to analyze soil properties across sampling dates and years. Treatment (irrigation versus control) was the grouping (or between subjects factor) in the statistical model. The repeated measures (or within subjects factors) were both season (April versus December) and year (December 1985/April 1986 = year 1, December 1986/April 1987 = year 2, December 1987/

April 1988 = year 3). Because we had a control and an irrigated plot in each of two sites, the true sample size per treatment was two (blocks). To test for the treatment effect, therefore, we nested the sampling locations within plots. However, if significance levels associated with the nested plot effect were > 0.25 (Sokal & Rohlf 1981, p. 285), we pooled the nested plot effect with the appropriate main effect or interaction effect.

Significance levels were evaluated with the conservative Greenhouse-Geisser correction for violations of the compound symmetry assumptions of repeated-measures ANOVA (Winer 1971). We also made a correction for the large number of tests in the ANOVA (11 nutrients × 7 main effects and interactions per nutrient = 77 tests) with the Bonferroni procedure that set the 0.05 significance level at 0.05/77 = 0.0006.

Results

Surface soil

We found no significant difference (by t-test, all P's < 0.05) in soil properties between the control and irrigated plots prior to the first irrigation (Table 1). We included the December 1985 samples in the ANOVA for all further analyses, assuming differences that arose through time were due only to the irrigation treatment.

pH. We found an average pH of 5.60 for the soil/water suspension, but pH of the 1M KCl suspensions was, on average, 1.15 units lower than that for the soil/water suspension, indicating release of acidity from soil exchange sites. Although we did not find a significant treatment effect for soil pH (Table 2), pH usually averaged 0.23 units higher in irrigated than in control soil (Fig. 1).

Exchangeable base cations. The sum of exchangeable base cations was, on average, 6.5 cmol kg^{-1} higher in irrigated than control soils, and in both treatments it decreased by about 5 cmol kg^{-1} from year 1 through year 3 (Fig. 2). We found significant effects of treatment and year on total exchangeable base cation concentrations, while most of the treatment interactions were not significant (Table 2), except the 3-way interaction.

The largest percentage contribution to total exchangeable base cation concentration was from exchangeable Ca^{2+} (55.6%), averaging 12.5 cmol kg^{-1} for control soil and 17.9 cmol kg^{-1} for irrigated soil. The next most common base cation was exchangeable Mg^{2+} (42.2%), averaging 11.0 cmol kg^{-1} for control soil and 12.1 cmol kg^{-1} for irrigated soil. Exchangeable K^{+} (1.4%) and exchangeable Na^{+} (0.8%) were minor soil components.

Nitrogen. In December 1987 and in April 1988, mean concentrations

Table 1. Soil properties of control and dry-season irrigated plots of mature lowland tropical moist forest on BCI, Panama. Values are means of 12 samples with standard error in parentheses.

	0—15 cm depth		35—45 cm depth	
	Control	Irrigated	Control	Irrigated
pH	5.4	6.0		
Carbon ($g\ kg^{-1}$)	44 (3.9)	46 (4.8)	3.0 (0.4)	2.0 (0.5)
Nitrogen ($g\ kg^{-1}$)	3.5 (0.2)	3.5 (0.2)	1.1 (0.1)	1.5 (0.1)
Phosphorus ($g\ kg^{-1}$)	0.64 (0.02)	0.59 (0.03)	0.20 (0.02)	0.26 (0.04)
Sulfur ($g\ kg^{-1}$)	0.51 (0.02)	0.50 (0.02)	0.31 (0.03)	0.30 (0.02)
Iron ($g\ kg^{-1}$)				
pyr[a]	4.6 (0.6)	4.4 (0.6)	8.0 (2.6)	6.5 (1.0)
oxalate[b]	7.6 (0.6)	7.0 (0.6)	3.9 (0.7)	3.3 (0.5)
CBD[c]	6.8 (0.4)	5.9 (0.6)	7.4 (1.1)	5.9 (0.7)
Aluminum ($g\ kg^{-1}$)				
pyr[a]	3.3 (0.3)	2.8 (0.2)	5.7 (0.9)	8.2 (1.0)
oxalate[b]	2.8 (0.4)	2.6 (0.1)	2.2 (0.4)	1.8 (0.1)
CBD[c]	0.7 (0.1)	0.6 (0.1)	0.7 (0.1)	0.4 (0.1)
Particle size				
% sand	25	25	28	25
% silt	36	35	29	27
% clay	39	40	43	48

[a] extracted with 0.1 M sodium pyrophosphate (Parfitt & Childs 1988)
[b] extracted with 0.2 M acid ammonium oxalate (Parfitt & Childs 1988)
[c] extracted with citrate-bicarbonate-dithionite (Parfitt & Childs 1988)

of extractable NH_4^+ were 2 to 10 times greater than the mean for soluble NH_4^+ (Fig. 3). We found that extractable NH_4^+ concentrations were higher at the end of the dry season than those at the end of the wet season, especially in the control plots. This seasonal pattern suggests that soil NH_4^+ accumulated during the dry season, whereas dry-season irrigation limited the amount amassed. The absence of consistently observed treatment effect for soluble NH_4^+ is evident both from the significant year-interaction terms of the ANOVA (Table 2) and from visual inspection of the data (Fig. 3).

Mean concentrations of soluble and extractable NO_3^- were similar. For soluble NO_3^-, values did not vary significantly between season (Table 2), but there was a marginally significant treatment × year interaction. The control soil had slightly lower NO_3^- concentrations than those in the irrigated soil in the first two years, but not in the third year (Fig. 3). On average, soluble NO_3^- comprised 84% of the total soluble inorganic N ($NH_4^+ - N + NO_3^- - N$). Concentrations of fumigation-released N were

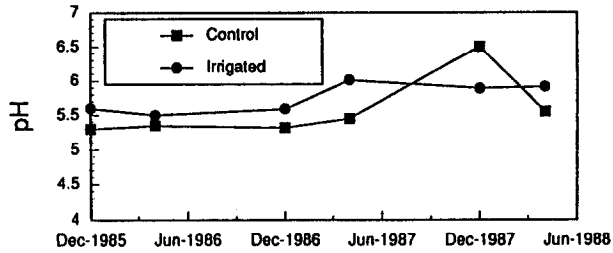

Fig. 1. Temporal trend for pH in control and irrigation soil on BCI, Panama.

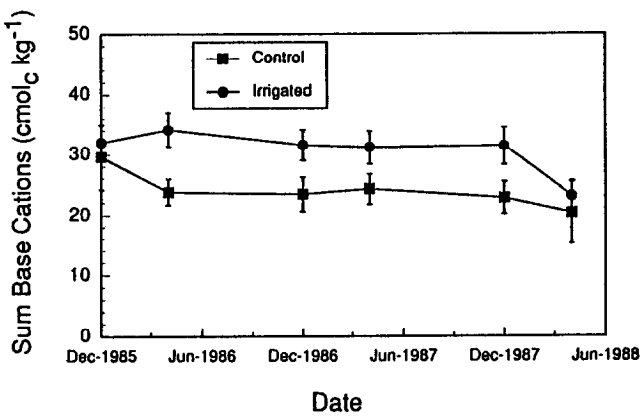

Fig. 2. Temporal trend for sum of exchangeable base cations in control and irrigated soil on BCI, Panama. Error bars represent one standard error.

considerably greater than that for soluble inorganic N (Fig. 3), averaging 140 mg N kg^{-1} for both irrigated and control soil. Neither treatment nor season affected fumigation-released N (Table 2).

Nitrification rates were generally higher in the open (42 mg N kg^{-1} 28 d^{-1}) than in the closed incubations (32 mg N kg^{-1} 28 d^{-1}; Fig. 4). For example, the maximum rate occurred in April 1987 for the open incubation, and it was two times that seen in closed-incubations. We also observed that nitrification rates were higher in April than in December, which was especially true for the open-incubation conditions. These patterns show up as significant incubation and season effects (P's < 0.0001 for main effects), but we did not find a significant difference in nitrification rates between irrigated and control soil and for all interactions with treatment (all P's > 0.05). During the laboratory incubations, changes in fumigation-released N were haphazard, with no clear relationship to incubation condition or initial concentration of fumigation-released N (Fig. 4). As a

Table 2. Significance (P values) of main effects and interactions in the repeated-measures ANOVAs for soil properties on BCI, Panama, measured every December and April between December 1985 and April 1988. Degrees of freedom are given in parentheses.

ANOVA Term	pH	Σ base cations	soluble NH_4^+	soluble NO_3^-	fum.-rel. N
Time (1, 22)	0.1868	0.0001	0.1818	0.9855	0.6005
Season (1, 22)	0.4720	0.5436	0.0027	0.7456	0.3123
Time × Season (1, 22)	0.8650	0.9000	0.0905	0.9015	0.5741
Year (2, 44)	0.0012	0.0001	0.0001	0.0001	0.0001
Time × Year (2, 44)	0.1260	0.1735	0.0010	0.0035	0.6930
Year × Season (1, 22)	0.0009	0.0570	0.0043	0.3341	0.0005
3-way interaction (2, 44)	0.5655	0.0001	0.0701	0.2406	0.5417

ANOVA Term	soluble P	ext. P	fum.-rel. P
Time (1, 22)	0.0864	0.0356	0.0301
Season (1, 22)	0.5711	0.0001	0.0519
Time × Season (1, 22)	0.0741	0.9719	0.4970
Year (2, 44)	0.0001	0.0029	0.0001
Time × Year (2, 44)	0.3417	0.3670	0.1939
Year × Season (1, 22)	0.7441	0.4369	0.0184
3-way interaction (2, 44)	0.0480	0.5222	0.2474

ANOVA Term	soluble S	ext. S	fum.-rel. S
Time (1, 22)	0.1966	0.9902	0.5397
Season (1, 22)	0.0001	0.0002	0.9564
Time × Season (1, 22)	0.0812	0.0045	0.0026
Year (2, 44)	0.0001	0.1046	0.0873
Time × Year (2, 44)	0.0336	0.8810	0.3784
Year × Season (1, 22)	0.0004	0.0001	0.1726
3-way interaction (2, 44)	0.5935	0.0006	0.0365

result, all main effects were not significant (all P's > 0.05), while interactions with season and year were significant (P's < 0.001).

Phosphorus. Soluble P was present at or near the detection limit, with an average concentration of 0.1 mg P kg^{-1}; in contrast, extractable P levels were 25 times greater than those for soluble P (Fig. 5). Extractable P was consistently greater in irrigated (2.9 mg P kg^{-1}) than control soil (2.2 mg P kg^{-1}) and in December (3.4 mg P kg^{-1}) than April (1.7 mg P kg^{-1}). Moreover, extractable P exhibited a significant year effect (Table 2) with

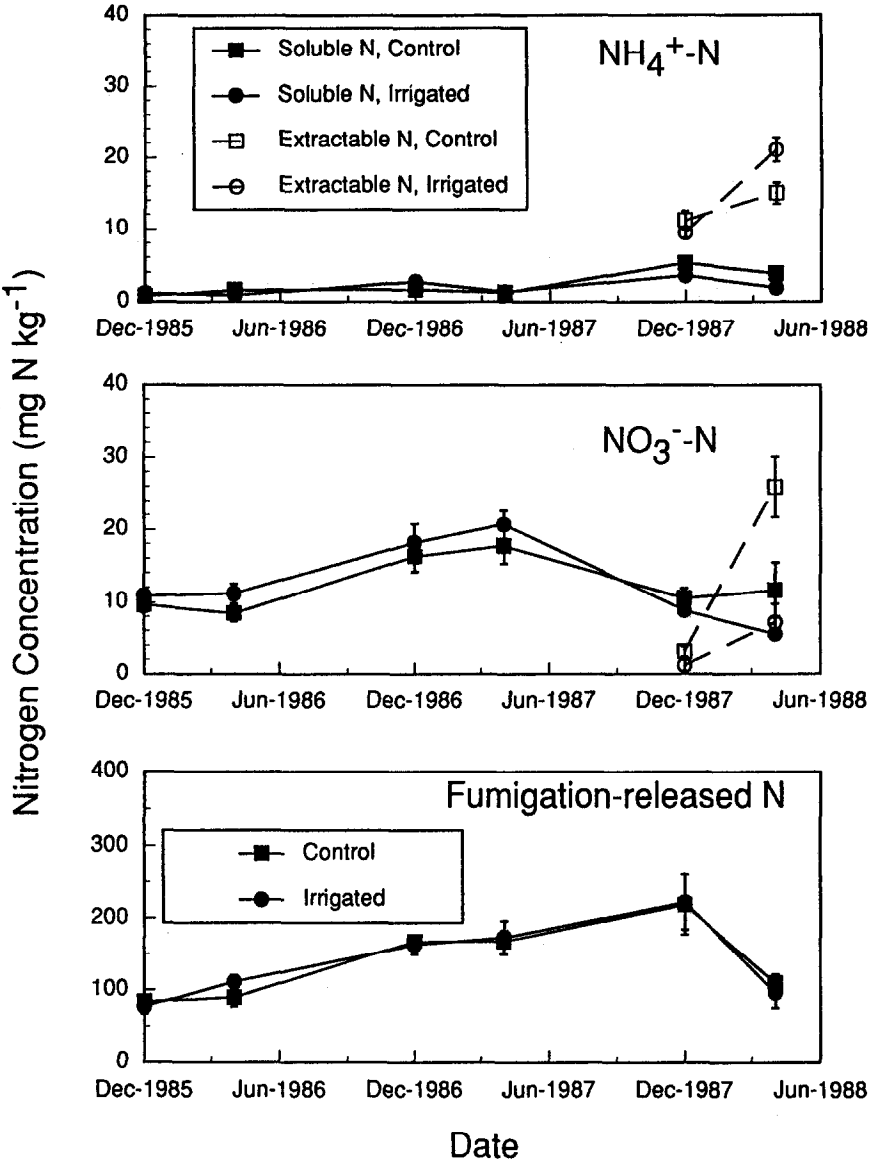

Fig. 3. Temporal trend for NO_3^-, NH_4^+ and fumigation-released N in control and irrigated soil on BCI, Panama. Error bars represent one standard error.

concentrations of 3.1 mg P kg^{-1} in year 1, 1.7 mg P kg^{-1} in year 2, and 2.5 mg P kg^{-1} in year 3. Concentrations of fumigation-released P were consistently greater than concentrations of either soluble or extractable P. Average fumigation-released P was 26.2 mg kg^{-1} for irrigated soil and

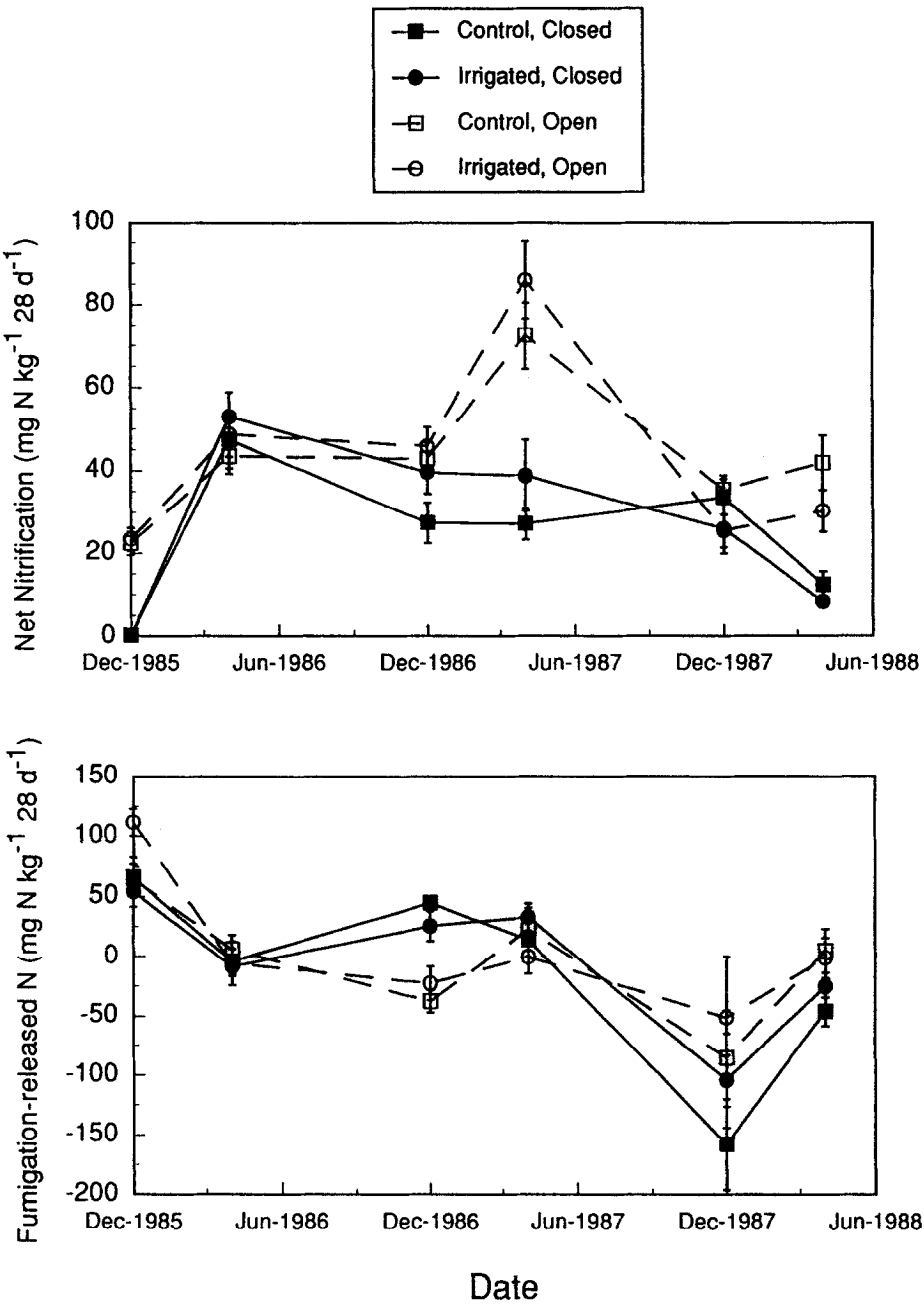

Fig. 4. Temporal trend for net nitrification and changes in fumigation-released N during laboratory incubation of control and irrigated soil from BCI, Panama. Error bars represent one standard error.

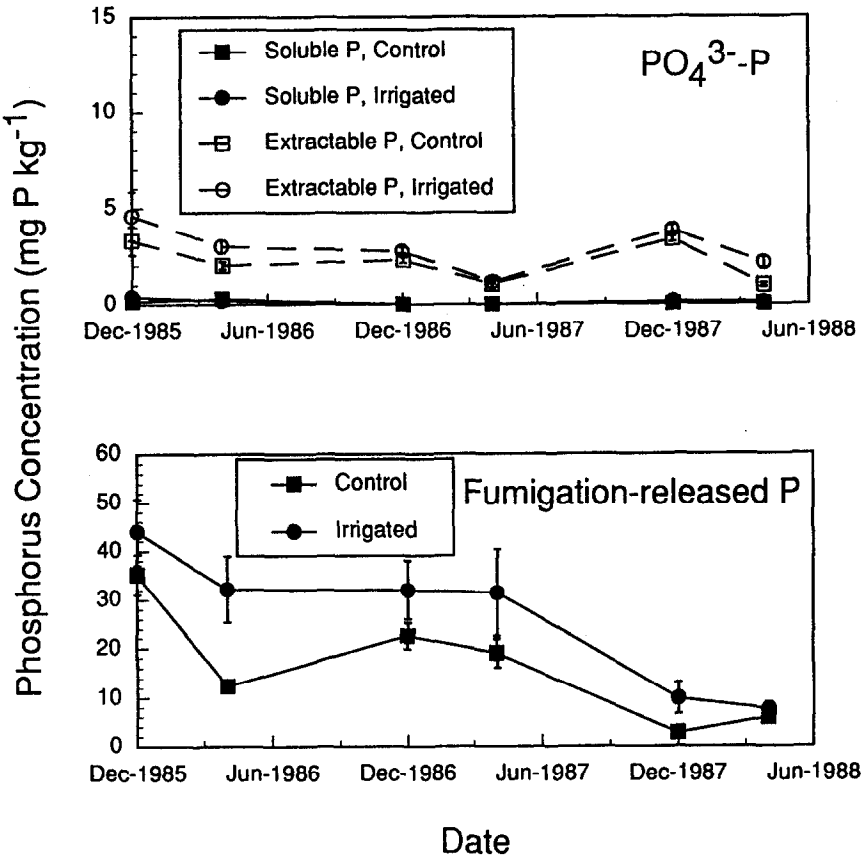

Fig. 5. Temporal trend for soluble, extractable and fumigation-released P in control and irrigated soil on BCI, Panama. Error bars represent one standard error.

16.3 mg kg^{-1} for control soil. Only the effect of year was significant (Table 2), however, and concentrations of fumigation-released P decreased progressively and by almost 80% between December 1985 and April 1988.

Changes in fumigation-released P (Fig. 6) during incubation were not affected by incubation condition, treatment or season (all *P*'s > 0.05 for main effects). There was a strong year-to-year trend ($P < 0.0001$), however, with decreases in concentration in December 1985 that gradually changed to increases in concentration by April 1988.

Sulfur. Within treatment and months, extractable S concentrations were about 2.4 times greater than those for soluble S (Fig. 7). The average concentrations of extractable S was 13.6 mg S kg^{-1} in both irrigated and control soil. The data suggest some effect of moisture availability on extractable S, as values for April and December were not always similar;

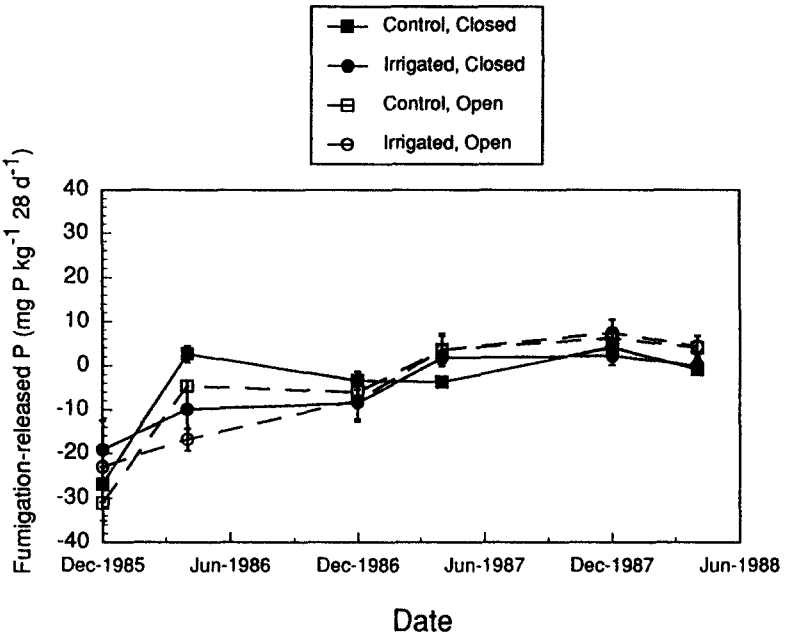

Fig. 6. Temporal trend for changes in fumigation-released P during laboratory incubation of control and irrigated soil from BCI, Panama. Error bars represent one standard error.

however, there was no consistent pattern from one year to the next (Fig. 7). Although on average, concentrations of fumigation-released S were about 1.7 times greater than those for extractable S, there were occasions (December 1985 in irrigated soils; April 1987) where extractable S concentrations exceeded fumigation-released S (Fig. 7). Although the treatment × season interaction was marginally significant for fumigation-released S (Table 2), suggesting a treatment effect, this was due in part to a large apparent treatment difference in December 1985 prior to irrigation.

Net S mineralization rates varied considerably due to incubation and season (both P's < 0.0001) but not treatment ($P > 0.05$). Net S mineralization (Fig. 8) was always higher for the open counterpart, especially in April. Closed incubations had low rates of net S mineralization, regardless of treatment, season and year.

Subsurface soil

Concentrations of exchangeable base cations and S were much higher in the subsurface than surface soil, while N and P had higher concentrations in surface than subsurface soil (Table 3 versus data presented above). All

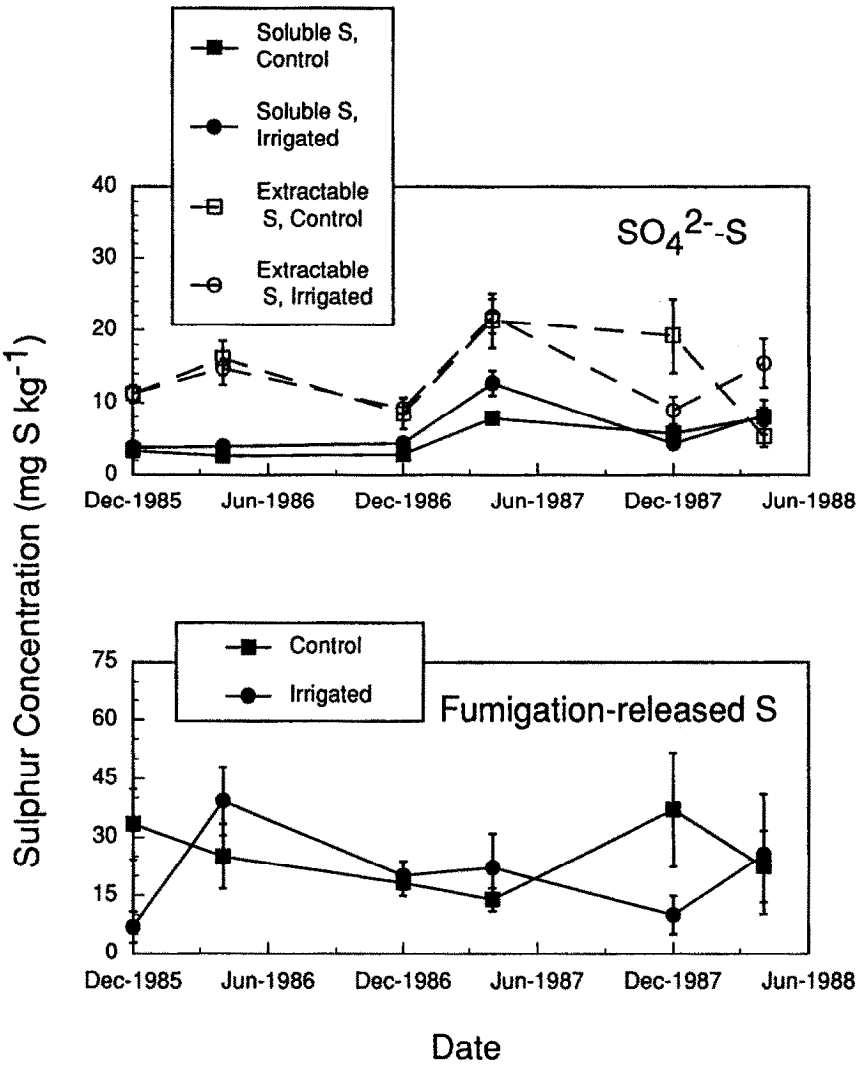

Fig. 7. Temporal trend for soluble, extractable and fumigation-released S in control and irrigated soil on BCI, Panama. Error bars represent one standard error.

parameters measured in subsurface soil showed no difference between irrigated and control soil (Table 3), while most of the parameters measured had significantly different values in April than December. Although season was often significant for N and P, their low concentrations suggest that any seasonal differences were not biologically important. On the other hand, S was so abundant in subsurface soil it is difficult to ascribe seasonal differences exclusively to biological processes.

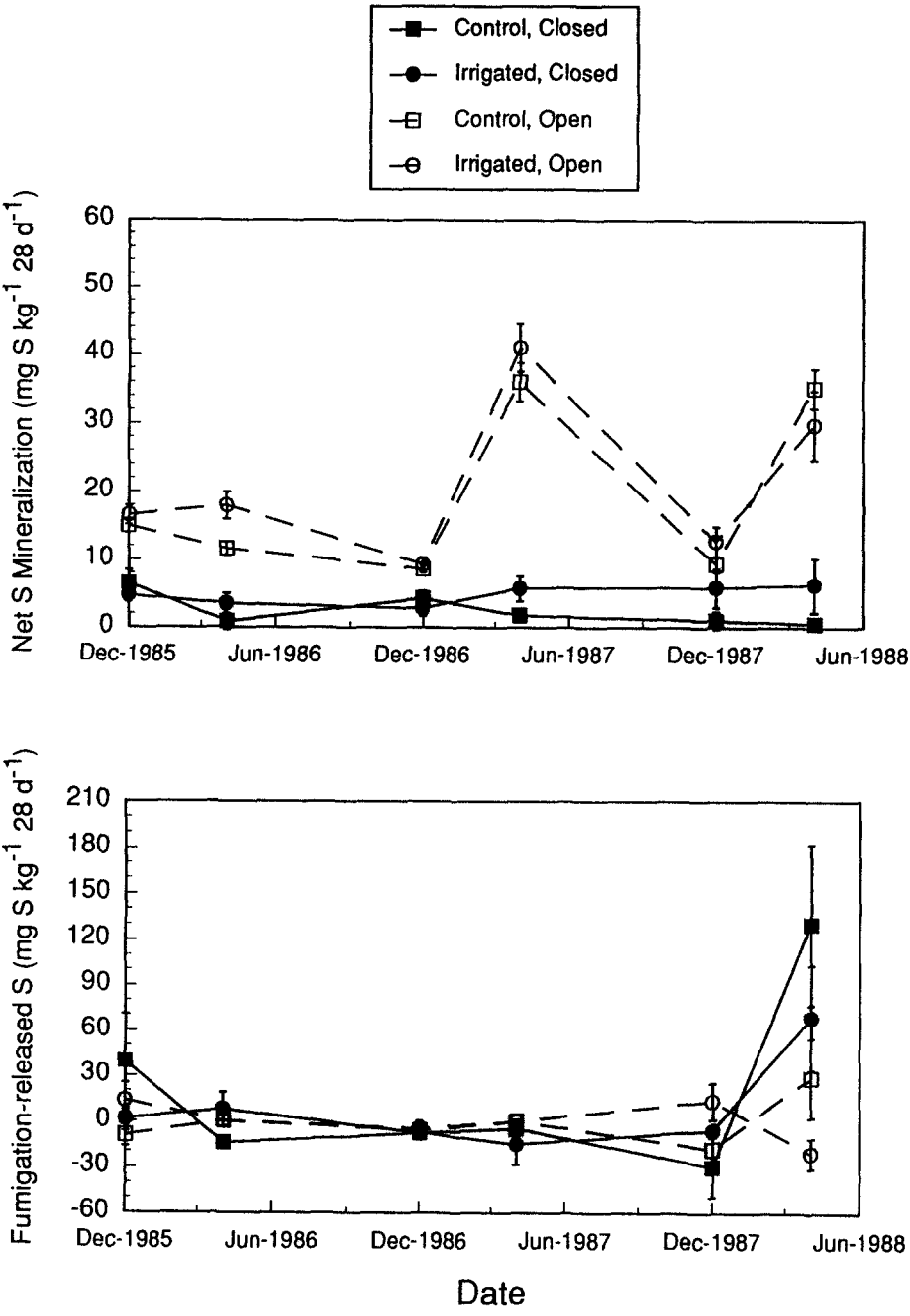

Fig. 8. Temporal trend for net S mineralization and changes in fumigation-released S during laboratory incubation of control and irrigated soil from BCI, Panama. Error bars represent one standard error.

Table 3. Soil properties (30–35 cm depth) of mature lowland tropical moist forest on BCI, Panama. Values are averaged across treatment and are means of 16 samples.

Soil factor	April	December	*p*
pH	4.34	4.83	n.s.
Exchangeable base cations ($cmol_c\ kg^{-1}$)			
Ca^{2+}	9.5	12.9	<0.05
Mg^{2+}	11.5	16.6	<0.05
K^+	2.0	2.1	n.s.
Na^+	2.2	1.9	<0.05
Nitrogen ($mg\ N\ kg^{-1}$)			
soluble NH_4^+	2.26	1.96	n.s.
soluble NO_3^-	1.13	2.22	n.s.
fumigation-released N	3.07	7.03	n.s.
Net nitrification ($mg\ N\ kg^{-1}\ 28\ d^{-1}$)			
open incubation	5.34	3.78	n.s.
closed incubation	4.62	0.01	<0.01
Δ fumigation-released N ($mg\ N\ kg^{-1}\ 28\ d^{-1}$)			
open incubation	3.55	9.84	<0.05
closed incubation	−0.22	14.70	<0.01
Phosphorus ($mg\ N\ kg^{-1}$)			
soluble	0.07	0.34	<0.05
extractable	0.42	1.86	<0.05
fumigation-released	1.65	2.29	n.s.
Δ fumigation-released P ($mg\ P\ kg^{-1}\ 28\ d^{-1}$)			
open incubation	0.06	−1.53	n.s.
closed incubation	0.69	−1.98	<0.05
Sulfur ($mg\ S\ kg^{-1}$)			
soluble	5.41	8.85	<0.05
extractable	64.40	61.70	<0.05
fumigation-released	50.10	20.20	<0.05
Net S mineralization ($mg\ N\ kg^{-1}\ 28\ d^{-1}$)			
open incubation	0.03	−1.65	n.s.
closed incubation	2.86	−7.10	n.s.
Δ fumigation-released S ($mg\ S\ kg^{-1}\ 28\ d^{-1}$)			
open incubation	−9.75	13.40	<0.05
closed incubation	42.10	24.21	<0.05

n.s. = value is not significantly different among seasons

Discussion

Cation dynamics

These BCI soils are moderately fertile with respect to Ca and Mg but are infertile with respect to K. Concentrations of exchangeable Ca^{2+} and Mg^{2+}

are much greater than typical values of < 1 cmol kg^{-1} reported for tropical Ultisols and Oxisols (Cochrane & Sanchez 1982; Sanchez et al. 1983) and 5—10 cmol kg^{-1} for tropical Alfisols (Lathwell & Grove 1986). The relatively high levels of exchangeable Ca^{2+} and Mg^{2+} undoubtedly reflect soil development from a marine facies of the sedimentary formation (Woodring 1958). Concentrations of exchangeable K^+ are similar to relatively infertile soils of the humid tropics and only slightly above the level that seems to limit plant growth (0.2 cmol kg^{-1}), as established by Cano (1973).

The irrigated soil had consistently higher pH and a 39% increase in the concentration of exchangeable base cations compared to control soil. If we assume that the total number of soil exchange sites did not change as a result of irrigation, then base cations replaced exchangeable acidity (H^+, Al^{3+}) on the exchange sites of the irrigated soil. It is certainly possible that irrigation caused the amount of exchangeable base cations to increase due to increased rates of weathering and cation release from decomposing soil organic matter. A 40% change in concentration of exchangeable base cations during a 3 yr period has been observed in other studies (cf. Johnson et al. 1988).

On the other hand, the assumption that the total number of soil exchange sites did not change might not be true. Unfortunately, we did not measure all of the components of soil exchange capacity, which includes exchangeable acidity. Thus, we do not know the total cation exchange capacity (CEC = sum of exchangeable base cations plus acidity) of these soils. In most tropical soils, however, there is a positive relationship between pH and CEC (Uehara & Gillman 1981), with an increase in pH causing an increase in the pH-dependent component of CEC. Both variable-charge minerals (allophane, imogolite, gibbsite) and soil organic matter have pH-dependent charge, but the mineralogy of these BCI soils is not consistent with variable-charge minerals (Johnsson & Stallard 1989). Thus, soil organic matter probably contributed most of the pH-dependent charge. It is possible that irrigation leached soluble organic acids away from the surface soils, causing both the pH and CEC to increase.

Nitrogen dynamics

Soil in our study area was moderately fertile with respect to N. Concentrations of NO_3^- (12.5 mg N kg^{-1}) and NH_4^+ (15 mg N kg^{-1}) are near the high end of literature values for inorganic N in other tropical soils (2 to 15 mg N kg^{-1}) reported by Vitousek & Matson (1988). Nitrification of BCI is somewhat lower than that for old-growth tropical forest sites in Costa Rica (Robertson 1984; Zou et al. 1992) but higher than that in old-growth forests of the Venezuelan Amazon (Montagnini & Buschbacher 1989).

These differences in nitrification among regions might be related to high soil fertility in the Costa Rican site, moderate soil fertility in Panama and low soil fertility in the Amazonian site.

The level of fumigation-released N measured (140 mg N kg^{-}) falls midway among values for other tropical forest soils (40 to 270 mg N kg^{-1}) reported by Vitousek & Matson (1988). There are numerous studies focusing on fumigation-released N (microbial biomass N) in soil (Wardle 1992), even though few have considered tropical moist forest. The range of values in the literature suggests that there is no relationship between inorganic N and fumigation-released N (Wardle 1992). Thus the moderately high level of fumigation-released N we found is probably related to high soil fertility and lack of soil disturbance in this old-growth forest (cf., Ayanaba et al. 1976).

Phosphorus dynamics

We expected a low level of soluble P, give that most soils have a high P-fixing capacity (Larsen 1967). However, we also found extractable P levels near the low end of values for tropical soil (3 to 73 mg P kg^{-1}; Sharpley et al. 1989) and near to the level that seems to limit plant growth ($<$ 3.0 mg P kg^{-1}; Vitousek & Denslow 1987). We did observe a seasonal trend for extractable P, in which concentrations declined during the dry season (Fig. 5), suggesting that the lowest availability for plant growth occurs at the start of the rainy season. However, if water was the sole factor responsible for the seasonal trend, then we should have seen enhanced concentrations in the irrigated soil in April, and this was not true. Hence, extractable P concentrations fluctuate in response to some other trait of season; for example a fluctuation in plant productivity and/or root activity.

We measured much higher levels of fumigation-released P than those seen in other tropical soils (7 to 14 mg P kg^{-1} dry soil; Srivastava & Singh (1988)). Moreover, our ratio of fumigation-released P to extractable P of $>$ 3:1, except in April 1988, is much greater than that for weathered forest soils of the temperate zone, as reported by Walbridge et al. (1991). Unlike soil N, in which levels of inorganic N and fumigation-released N are unrelated, it is likely that extractable P levels determine fumigation-released P, with low levels acting as a cue for microbes to sequester P. The combination of low levels of extractable P and high levels of fumigation-released P (microbial biomass P) suggest that microbes compete effectively with plants for a limited supply of soil P.

Fumigation-released P decreased from one sampling date to the next (Fig. 5). This coincided with a somewhat opposite trend for fumigation-

released P during the laboratory incubations (Fig. 6). There we measured a large decrease in concentration initially, but the decreases gradually lessened from one sampling to the next, and fumigation-released P actually increased during the incubation for the last two samplings. Hence microbial biomass appeared to be a source of P when fumigation-released P levels were high, but microbes immobilized P when fumigation-released P levels were low. These results suggest that microbes become stronger competitors for P as P availability in the soil decreases. The large amounts of P that cycle through different soil pools even though instantaneous concentrations remain low agrees with some previous findings (Lee et al. 1990; Sharpley 1985).

Sulfur dynamics

The average extractable S concentration in our study area is higher than the level that seems to cause S deficiency in tropical plants (< 8.0 mg S kg^{-1}; Hasan et al. 1970). Although 'extractable' suggests that the S binds more tightly to soil exchange sites than soluble S, extractable S is still probably plant available (Curtin & Syers 1990). Therefore, it seems unlikely that plants on this BCI soil are S deficient, even though most tropical soils have high capacity to fix S (Bornemisza & Llanos 1967) and cause S deficiency.

We found net S mineralization rates near the high end of values for tropical soil (10—20 mg S kg^{-1} 28 d^{-1}; Nor 1981) and much higher than those for temperate-region soil (< 5 mg S kg^{-1} 28 d^{-1}; Maynard et al. 1983; Pirela & Tabatabai 1988). Higher S mineralization rates under open than closed incubation is consistent with the accepted mechanism of S mineralization in soil (McGill & Cole 1981), in which the accumulation of mineralized S in the soil (i.e. closed incubation) inhibits further mineralization.

We found no consistent pattern in fumigation-released S during the laboratory incubation (Fig. 6). In this regard, our measured values for fumigation-released S seemed unrealistically high, at least compared to literature values (cf., Strick & Nakas 1984). This was especially true for subsurface soil where fumigation-released S was extremely high while fumigation-released N and P were quite low, as expected. It is possible that the relatively high level of extractable S complicates the assay for fumigation-released S, similar to that observed for fumigation-released N in fertilized soil (Widmer et al. 1989).

Water effect on soil nutrients

Our goal was to isolate water as a factor controlling nutrient concentrations. As such we designed our research around two analogies. The first analogy was between open versus closed incubations and dry-season irrigated versus dry-season control values. The second analogy was between open versus closed incubations and wet versus dry season values. With this information we can relate net changes in the incubations to concentrations prevailing under the appropriate field conditions. If incubation trends differ from field trends, then water alone does not explain field trends. Three other explanations are possible: (i) other current mechanisms (plant uptake, root turnover, rhizosphere activity), (ii) long-term trends, or (iii) date-to-date variability.

With regard to the first analogy — the effect of dry-season irrigation — we measured much higher rates of net nitrification and net S mineralization in open than closed incubations in the dry season (April). This suggests that water stimulates soil N and S transformations. As a result, one might expect a 'pulse' of nutrient availability occurring with the onset of the rainy season, thereby coinciding with plant growth following drought (Wright & Cornejo 1989). However, concentrations of N and S in the field were no different between control and irrigated plots in April. Accordingly, some other factor, such as plant uptake of N and S, must have been strong enough in the irrigated plot to prevent increases in soil N and S concentrations.

Dry-season irrigation was strong enough to prevent soil cracking that was evident by the end of each dry season in the control soil. Cracking, caused by shrinkage of soil clays during drying (Murray & Quirk 1990), is of considerable interest to soil nutrient cycling, because it determines the partitioning and movement of water and solutes within the soil system. Moreover, soil drying increases the concentrations of solutes in soil pore spaces (cf., Zabowski & Ugolini 1990), thereby decreasing weathering rates of soil minerals. Irrigation, which dilutes solute concentrations in soil pore waters, could enhance weathering rates of soil minerals.

With regard to our second analogy — seasonality — few of the soil factors we measured changed predictably with season. In contrast, few studies in temperate regions (Gupta & Rorison 1975; Haines & Cleveland 1981; Johnson et al. 1988; Vaughn et al. 1986) have shown that soil nutrient concentrations change seasonally in a predictable pattern, with minimum concentrations found at the end of the growing or rainy seasons and higher levels during the non-growing and dry seasons. In our case, it appears that the factors affecting loss and gain of soil nutrients offset each

other so that concentrations do not fluctuate seasonally. Certainly, we must constrain our conclusion about seasonality because we sampled only two times per year. However, we sampled at those times when maximum differences should have occurred, i.e. at the transitions of wet-to-dry and dry-to-wet seasons.

The non-significant effect of season on fumigation-released N, P and S at BCI is not consistent with previous studies in tropical dry forest showing a flush of plant-available nutrients following wetting of dried soils (Singh et al. 1989). This flush has been attributed to rapid rewetting of dried soil causing osmotic stress and microbial death (Kieft et al. 1987). Dead microbes represent a substantial pool of available plant nutrients (Bottner 1985; Powlson & Jenkinson 1976). However, our soils dry to only −1.25 MPa, and only −0.75 MPa in some years (Wright 1991), whereas soil drying to less −2.8 MPa seems necessary to generate osmotic stress (Kieft et al. 1987; Sparling et al. 1989).

It also seems from a comparison of values in the literature (Wardle 1992) that boreal rather than tropical climates support the highest seasonal change in the nutrient pool held in soil microbes. This is ascribed to extensive microbial growth in response to spring warming, followed by microbial death in the autumn and winter. In the tropics with seasonal rainfall, there is evidence of a negative relationship between soil moisture level and microbial nutrient content (Srivastava & Singh 1988; Raghubanshi 1991); although, Kinsbursky & Steinberger (1989) reported a positive relationship. In our study, seasonal changes in the nutrient content of soil microbes were either too small, inconsistent from one year to the next, or part of a year-to-year trend for us to offer much of a conclusion.

Nearly all soil factors measured in December showed remarkably similar values for open and closed incubations. This suggests that water alone does not affect nutrient concentrations, at least during the first month of the dry season (closed incubation). Hence marked changes in nutrient concentrations across the dry season such as the decrease in extractable P (Fig. 5) must be the result of drought and other mechanism(s). Given the complexity in soil factors controlling P concentrations in soil (Vitousek 1984; Walbridge & Vitousek 1987), biological and/or physiochemical factors could be responsible.

Finally, our results do show significant date-to-date variation in soil nutrient concentrations during the 3 years of the study. The variability we observed emphasizes the importance of multi-year studies to determine accurate patterns in soil nutrient concentrations. If we had compared and contrasted soil nutrient concentrations after only one year of treatment, different conclusions would have resulted. Moreover, the gradual declines

in concentrations of exchangeable base cations and P and increase in concentrations of soil N and S that we observed during the three years of study would not have been apparent in single-year measurements.

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