Soil oxygen availability and biogeochemistry along rainfall and topographic gradients in upland wet tropical forest soils

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Abstract. We measured soil oxygen concentrations at 10 and 35 cm depths and indices of biogeochemical cycling in upland forest soils along a rainfall and elevation gradient (3500–5000 mm y^{-1}; 350–1050 masl) and along topographic gradients (ridge to valley, $\sim$150 m) in the Luquillo Experimental Forest, Puerto Rico. Along the rainfall gradient, soil O_2 availability decreased significantly with increasing annual rainfall, and reached very low levels (<3%) in individual chambers for up to 25 consecutive weeks over 82 weeks of study. Along localized topographic gradients, soil O_2 concentrations were variable and decreased significantly from ridges to valleys. In the valleys, up to 35% of the observations at 10–35 cm depth were <3% soil O_2. Cross correlation analyses showed that soil O_2 concentrations were significantly positively correlated along the topographic gradient, and were sensitive to rainfall and hydrologic output. Soil O_2 concentrations in valley soils were correlated with rainfall from the previous day, while ridge sites were correlated with cumulative rainfall inputs over 4 weeks. Soils at the wettest point along the rainfall gradient had very high soil methane concentrations (3–24%) indicating a strong influence of anaerobic processes. We measured net methane emission to the atmosphere at the wettest sites of the rainfall gradient, and in the valleys along topographic gradients. Other measures of biogeochemical function such as soil organic matter content and P availability were sensitive to chronic O_2 depletion along the rainfall gradient, but less sensitive to the variable soil O_2 environment exhibited at lower elevations along topographic gradients.

Introduction

Soil oxygen is an often ignored, but critical resource for plant and microbial processes, and plays an important role in ecosystem-level biogeochemical cycling (Gambrell & Patrick 1978; Crawford 1992). Decreased O_2 avail-

ability can change the composition and activity of soil microbial communities (Morris 1984; Magnusson 1992, 1994), lower redox potential (Gambrell & Patrick 1978; Hook 1984), and alter nutrient availability and utilization (Drew 1991; Crawford 1992; Silver et al. 1994). The degree to which these changes occur is dependent upon the severity and duration of O_2 depletion and the presence of alternative electron acceptors for microbial processes. For example, the O_2 content of the soil atmosphere has a direct impact on the form and/or mobility of N, Fe, P (through interactions with Fe and C), and C, as soil O_2 content and redox potential decline (Gambrell & Patrick 1978).

The occurrence and consequences of soil O_2 depletion have been widely reported in flooded soils (Patrick 1977; Hook 1984; Faulkner et al. 1989; Drew 1990, 1991; Crawford 1992), but few studies have evaluated soil O_2 concentrations and related them to biogeochemical cycling in upland ecosystems (Magnuson 1992, 1994; Kursar et al. 1995). Theoretically, under warm perhumid conditions, the combination of abundant rainfall or cloud input, clay or organic soils with high water-holding capacity, and high metabolic activity can lead to conditions where oxygen is rapidly and completely consumed from both liquid and gaseous-filled pore spaces, even in the absence of flooding (Frangi 1983). These factors can be highly variable over space and time, but frequently vary with regard to climate and topography. The cycling of N, P, and C have also been shown to vary with landscape position as a function of topography, temperature, and precipitation, and there has considerable recent interest in investigating the biogeochemical mechanisms controlling these patterns (Vitousek et al. 1992, 1994; Schimel et al. 1994; Silver et al. 1994).

In this study we examined the spatial and temporal variability of soil O_2 concentrations and indices of biogeochemical cycling along a rainfall gradient and localized topographic gradients in upland montane tropical forests on the island of Puerto Rico. Our goals were to determine: (1) how soil oxygen varies spatially and temporally in high rainfall environments; (2) how patterns in rainfall and hydrology are related to soil O_2; and (3) the implications of low soil O_2 concentrations for soil biogeochemistry.

Materials and methods

Study sites

The study was conducted in the Luquillo Experimental Forest (LEF) in northeastern Puerto Rico (Lat. 18°18′ N; Long. 65°50′ W). The Luquillo Mountains are characterized by steep and highly dissected topography, with distinct gradients in plant community composition and forest structure that

vary with regard to local topographic processes, and larger landscape-scale phenomenon such as rainfall and temperature (Beard 1941, 1949; Wadsworth 1951; Odum 1970). Precipitation increases with increasing elevation from 3500 mm yr^{-1} at 350 masl to 5000 mm yr^{-1} at 1050 masl, with a mean monthly minimum of approximately 200 mm at all elevations. Average annual temperature decreases along this gradient from 21 °C to 19°C (Brown et al. 1983; Weaver 1994).

For the rainfall gradient, we chose ridge top sites along a 650 m elevation gradient spanning three adjacent dicotyledenous plant communities and life zones (Wadsworth 1951; Brown et al. 1983). Ridge tops were the most readily comparable topographic zone along the elevation gradient, and are where the dominant species in each forest type reach their best development (Weaver et al. 1986; Weaver 1991; Scatena et al. 1993). All sites were located with a windward, northeastern aspect. Forests along the elevation and rainfall gradient differ dramatically in species richness, structure, and environmental conditions (Table 1). The lower elevation site was near the top of the Bisley Research Watersheds within the tabonuco ridge forest association at approximately 400 masl. The tabonuco forest is dominated by the tabonuco tree (*Dacryodes excelsa* Vahl), and receives approximately 3500 mm of rainfall annually (Brown et al. 1983). The mid elevation site fell within the colorado forest association at approximately 750 masl, is dominated by *Cyrilla racemiflora* L, and receives approximately 4500 mm of rainfall annually (Weaver & Murphy 1990). The upper elevation site occurred at approximately 1050 masl in the cloud forest zone. The cloud forest receives approximately 4700 mm of rainfall annually with an estimated 300–500 mm of additional cloud water input (Weaver & Murphy 1990; Silver et al. in prep.). The cloud forest is dominated by *Tabebuia ridgida* Urban.

For the localized topographic gradients, sites were located in the Bisley Research Watersheds (windward facing aspect), part of the Long Term Ecological Research project in Puerto Rico. Sites were located in the tabonuco forest type at approximately 350 masl. Topographic zones were identified as ridges, slopes or valleys based on geomorphologic descriptions by Scatena (1989). Tabonuco forest ridge top sites used for the rainfall gradient (hereafter referred to as "tabonuco forest") were nearby, but different than those used for the topographic study.

Soils in the LEF are derived from volcanoclastic sediments with quartz diorite intrusions (Beinroth 1982). The study sites were located on volcanoclastic sediments with a high clay content (up to 70%), with the possible exception of sites in the colorado forest which occurred near the contact between the volcanoclastic and dioritic sediments. The forest sites used here, however, were growing on a thick clay cap (>3 m) above a clay loam.

Table 1. Forest and climatic characteristics of 3 subtropical wet forests in the Luquillo Mountains, PR. Data are from Brown et al. (1983), and Weaver and Murphy (1990). Data on the topographic gradients are from the Bisley Research Watersheds (Scatena & Lugo 1995). Standard errors are in parentheses.

	Montane forest gradient: Luquillo Experimental Forest		
Life zone	Subtropical Wet	Lower Montane Wet	Lower Montane Rain
Forest type	Tabonuco	Colorado	Cloud
Elevation range (masl)	300–600	600–750	750–1050
Mean annual rainfall (mm)	3500	4500	5000
Tre species richness (ha^{-1})	50	40	15
Total tree species	170	90	40
Canopy height (m)	20–30	8–20	3–5
Mean no. stems (ha^{-1})	1750	1850	21900

	Topographic gradient: Tabonuco forest		
Topographic zone	Ridge	Slope	Valley
Tree species richness	7 (0.04)	6 (0.4)	4 (0.5)

Oxygen and methane measurements

Soil O_2 was sampled weekly along the rainfall gradient from Sept. 1992 through March 1994 using buried equilibration chambers. Preliminary tests showed that chambers equilibrated with the bulk soil air within 24–48 hours of insertion at all sites. Ten chambers per depth at 10 cm and 35 cm depths were randomly located across ridges within each forest type for a total of 20 chambers per forest type and 60 total chambers (n = approximately 2400 observations per depth). Depths were chosen to encompass the major rooting zone in all three forest types. Soil O_2 was sampled along topographic gradients in the Bisley Watersheds every two weeks from Feb. 1993 through July 1997. Six transects, each approximately 150 m long and perpendicular to the contour, were established from ridges to valleys. Valley sites were all associated with drainages, although chambers were located above the flood plain, in sites that rarely or never experience flooding. Three chambers each were randomly located at 10 cm and 35 depth along each transect, yielding 36 total chambers and 6 replicate chambers per depth in each topographic position (n = approximately 1900 measurements per depth).

    The equilibration chambers consisted of 60 cc inverted centrifuge tubes fitted with copper tubing and sealed with a three-way stopcock (Patrick 1977; Faulkner et al. 1989). Chambers were inserted into the ground using a soil

corer such that approximately 15–20 cc of chamber space was filled with soil. After insertion, soil was repacked into the hole so that a short length of tubing and a stopcock protruded above the surface. Sample gases were collected by first drawing and expelling five to ten cc of gas with a syringe to clear the tubing dead space, and then taking a 40 cc gas sample from each chamber, which was analyzed immediately in the field using a YSI O_2 meter (model 51B) and Clark-type electrode. The O_2 electrode was adapted with an air-tight cell with two ports, allowing for sample analysis without exposure to ambient air (Patrick 1977; Faulkner et al. 1989). We chose to use a 40 cc sample volume after determining that the dead space volume in the air tight cell was <3 cc, and that the meter required a minimum of 30 cc to achieve a stable O_2 reading. After determining the sample concentration, the electrode cell was flushed with ambient air until the O_2 meter response reached ambient levels (21%). Very rarely, a small amount of water was extracted with the gas sample. We did not re-inject the water into the chamber, as it had been mixed and aerated as a result of sampling.

As a further indication of the oxygen environment in the rhizosphere, we measured CH_4 and N_2O concentrations in the equilibration chambers used for O_2 sampling. Nitrous oxide concentrations were only measured along the topographic gradients. Along the topographic gradients, CH_4 and N_2O were sampled from equilibration chambers in Dec. 1993, July 1995, Dec. 1996, and July 1997. Soil CH_4 was sampled from the three sites along the rainfall gradient during Nov. 1993, and Mar. and July 1994 using the equilibration chambers. In addition, we measured soil CH_4 concentrations in the cloud forest in July 1993. Equilibration chambers were not sampled for soil O_2 during weeks when trace gases were sampled. After expelling air from the dead space, two 20 cc gas samples were taken from each equilibration chamber using nylon syringes. Samples were analyzed within 24 hr using flame ionization chromatography for CH_4 and electron capture gas chromatography for N_2O at the International Institute of Tropical Forestry (IITF). Sample peaks were compared with commercially prepared standard mixtures of CH_4 and N_2O (Keller & Stallard 1994; Keller & Reiners 1994).

We measured the net CH_4 efflux across the soil-atmosphere interface in March and July 1994 along the rainfall gradient, and in July 1997 from the topographic gradients. We used 10 randomly located static surface-flux chambers per forest type along the rainfall gradient ($n = 30$); along the topographic gradients we randomly located ten chambers per topographic zone ($n = 30$). Initial samples were taken immediately after placing the lid on the chamber, and at 10 minute intervals thereafter for 40 min. Gas samples were analyzed as discussed above. We note that these limited measurements represent only instantaneous fluxes and are not meant to quantify long-term fluxes for these

ecosystems. For soil-atmosphere CH_4 fluxes, we use the standard convention of a positive sign for net transfers of CH_4 from the soil to the atmosphere, and a negative sign for net transfers of CH_4 from the atmosphere to the soil.

Temporal patterns in soil O_2 concentrations were compared with daily or weekly rainfall at each of the sites. Rainfall data were collected using tipping bucket raingages located within each forest type along the rainfall gradient (Scatena 1997). For the topographic gradients, we also compared soil O_2 with throughfall and stream discharge from early 1993 through May 1996 to determine the possible relationships with hydrologic cycling. Data were collected as part of the US Forest Service long term monitoring program; details on sampling protocol and data management are given in Garcia-Martino et al. (1996). Throughfall and stream discharge measurements were not available for the other sites.

Other soil chemical and physical properties

Along the rainfall gradient, five composite soil samples were taken from both the 0–10 cm and 10–35 cm depths in each forest type using a 2.5 cm diameter soil corer ($n = 30$). Soils were air-dried and ground to pass through a 2 mm sieve. They were then extracted with a modified Olsen solution ($NaHCO_3$ with EDTA) for exchangeable Fe and extractable P (Wilde et al. 1979; Hunter 1982). Extracts were analyzed on a DCP Spectraspan V spectrophotometer at IITF in Puerto Rico. Soil pH was determined in 10:1 slurry of deionized H_2O (McLean 1982). Soil organic matter content was measured using the Walkley Black technique (Nelson & Sommers 1982), and total N using a modified Kjeldahl method (Bremner & Mulvaney 1982).

Along the topographic gradients, we used data from Silver et al. (1994). They did a detailed study of 87 small quantitative pits documenting patterns in soil chemical and physical properties in the Bisley watersheds as a result of methodological considerations and spatial heterogeneity. We re-analyzed the 'air dried and ground' soils data for exchangeable Fe, extractable P, SOM and total N using the three topographic zones identified here. Methods were the same used for the rainfall gradient soils.

Bulk density was estimated from $15 \times 15 \times 10$ cm deep pits (Silver et al. 1994). Two pits each were located in the cloud and colorado forests. For the tabonuco forest we used data from ridge top pits reported in Silver et al. (1994), which were sampled as above. As an estimate of the bulk density in the subsoil we took 3 bulk density cores (4.1 cm diameter) from 10–35 cm depth per forest type ($n = 9$). Moisture content and dry weight volume were determine from fresh and oven dry (105 °C) weights. Bulk density estimates of the 0–10 cm and 10–35 cm depths along the topographic gradients are from Silver et al. (1994).

Statistical analyses

Statistical analyses were performed using Systat (Wilkinson 1990). For the rainfall gradient, we used the Kruskal-Wallis non-parametric test to examine patterns in mean soil O_2 concentrations among sites within depths. The Mann-Whitney U test statistic was used to identify significant differences among depths within sites. We chose a non-parametric test because the data from the tabonuco forest (rainfall gradient) showed little spatial and temporal variability, and thus did not meet the assumptions for analysis of variance (ANOVA) with or without transformation. Within the cloud forest and the colorado forest we used repeated measures ANOVAs to test for changes in soil O_2 concentrations over time. The topographic data were also analyzed using ANOVAs. We examined the cumulative probabilities that soil O_2 would drop to $\leq 1\%$ and $\leq 3\%$ values, which have been identified as the critical oxygen concentrations for some herbs and wetland plants (Drew 1990), and to $\leq 10\%$, which is within a range that has been shown to result in reductions in growth and plant function (Stolzy 1974; Crawford 1989; Kramer 1992). These are conservative estimates of ecosystem thresholds that have the potential to affect plant and microbially mediated changes in biogeochemical cycling. Cross correlation analyses were performed to determine relationships among temporal and spatial patterns in mean soil O_2 and climate within and across sites. We used Pearson correlation matrices to determine the level of significant relationships between O_2 and rainfall for both topographic and rainfall gradients, and with throughfall, or stream discharge along the topographic gradients. We used regression analyses and one-way ANOVAs to examine patterns in other biogeochemical properties. Data were log-transformed where necessary to meet assumptions. We report significant differences as $P < 0.05$, unless otherwise noted.

Results

Patterns in soil oxygen concentrations

Average soil O_2 concentrations decreased significantly ($P < 0.001$ at 10 and 35 cm depths) from the low elevation tabonuco forest ($21\% \pm 0.03$ SE at both depths) to the mid elevation colorado forest ($13\% \pm 0.21$ at both depths), and further to the upper elevation cloud forest ($8\% \pm 0.19$ at 10 cm depth; $6\% \pm 0.18$ at 35 cm depth), corresponding to a gradient of increasing annual rainfall (Figure 1). Soil O_2 varied significantly over time within forest types, but the variability within forest types was always smaller than the differences among forest types (Figure 1). In the cloud forest, soil O_2 decreased signifi-

cantly with depth ($P < 0.001$). Cloud forest soils experienced very low soil O_2 concentrations for a high proportion of the 82 week study (Figure 2). In the surface depth, 10% of the measurements registered $\leq 1\%$ O_2; at 35 cm depth, 25% of the observations registered $\leq 1\%$ O_2. Approximately one-quarter and one-half of the observations registered $\leq 3\%$ soil O_2 at 10 cm and 35 cm depths, respectively. In the colorado forest, approximately one third of the observations were $\leq 10\%$ O_2 at both depths. The tabonuco forest soils were comparatively well aerated with 99% of the observations at or close to ambient concentrations (Figure 2).

Within the cloud forest, microsites experienced frequent, prolonged periods of continuously very low soil O_2 concentrations (Figure 3). Individual chambers registered $< 1\%$ O_2 for up to 6 consecutive weeks, and $\leq 3\%$ O_2 for up to 25 week intervals. Periods of O_2 concentrations $\leq 3\%$ lasting four or more weeks accounted for 15% and 25% of the observations at 10 cm and 35 cm depth, respectively. Reduced soils in the cloud forest did experience oxygenation events, but in general, O_2 concentrations fell to low levels within a week after these events. In the colorado forest, periods of O_2 depletion were generally shorter and less severe, with approximate one-fifth and one-quarter of the observations $\leq 10\%$ O_2 lasting 4 or more weeks in duration in the 10 and 35 cm depths, respectively (Figure 3).

Along topographic gradients, soil O_2 concentrations exhibited significant temporal and spatial variability in both the 10 cm and 35 cm soil depths (Figure 4). Average soil O_2 concentrations decreased significantly ($P < 0.01$) from ridges (19%$\pm$0.05) to slopes (16%$\pm$0.15) to valleys (10%$\pm$0.18), and with depth on ridges and in valleys, but not on slopes (Figure 4). In valleys, approximately 15% and 35% of the observations were $\leq 3\%$ O_2 at 10 cm and 35 cm depths, respectively (Figure 5). Intermediate levels of soil reduction ($\leq 10\%$ O_2) occurred frequently in valleys (49% and 63% at 10 cm and 35 cm depths, respectively), but were comparatively rare on slopes and ridges (Figure 5).

Relationships of soil O_2 to rainfall and hydrologic processes

Within the cloud and colorado forests, soil O_2 concentrations varied significantly ($P < 0.001$) over time at both depths (Figure 1). In the cloud forest, soil O_2 was not correlated with specific rainfall events or cumulative rainfall with lags of up to 8 weeks prior to O_2 sampling. In the colorado forest, O_2 was significantly negatively correlated with the cumulative rainfall 4 week prior to sampling.

Soil O_2 concentrations were also highly variable over time ($P < 0.001$) at both depths along the topographic gradients (Figure 4). Topographic zones were significantly positively cross correlated with each other over time, indi-
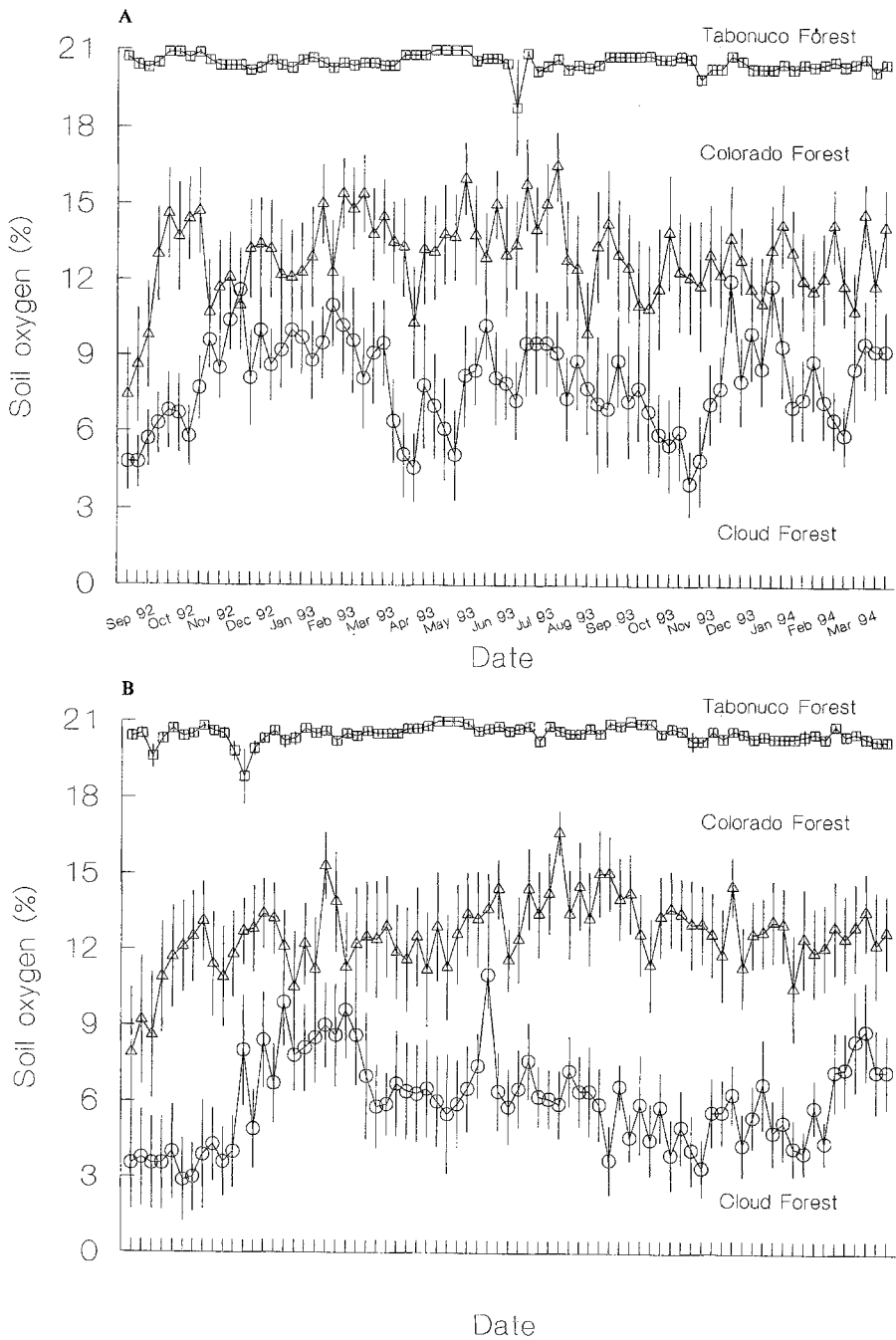
Figure 1. Mean soil O_2 concentrations (± 1 standard error) over time at (A) 10 cm depth and (B) 35 cm depth in the upper elevation cloud forest ($\bigcirc$), mid-elevation colorado forest ($\triangle$), and lower elevation tabonuco forest ($\square$) in the Luquillo Experimental Forest, Puerto Rico.

○ Cloud Forest 10 cm
● Cloud Forest 35 cm
△ Colorado Forest 10 cm
▲ Colorado Forest 35 cm
□ Tabonuco Forest 10 cm
■ Tabonuco Forest 35 cm
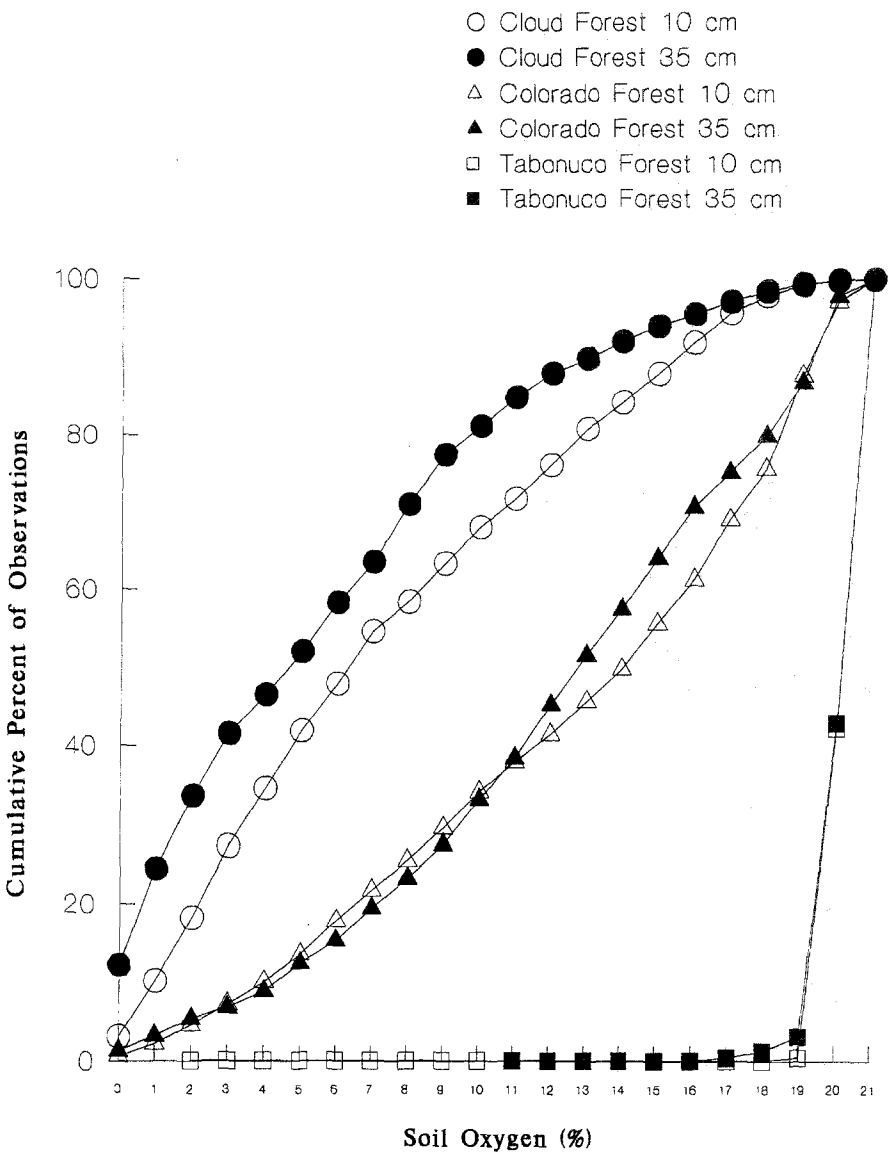
Figure 2. The cumulative percent of observations of soil O_2 concentrations ranging from 0–21% along a rainfall and elevation gradient in the Luquillo Experimental Forest, PR. (○) upper elevation cloud forest 10 cm depth; (●) cloud forest 35 cm depth; (△) mid elevation colorado forest 10 cm depth; (▲) colorado forest 35 cm depth; (□) lower elevation tabonuco forest 10 cm depth; (■) tabonuco forest 35 cm depth.
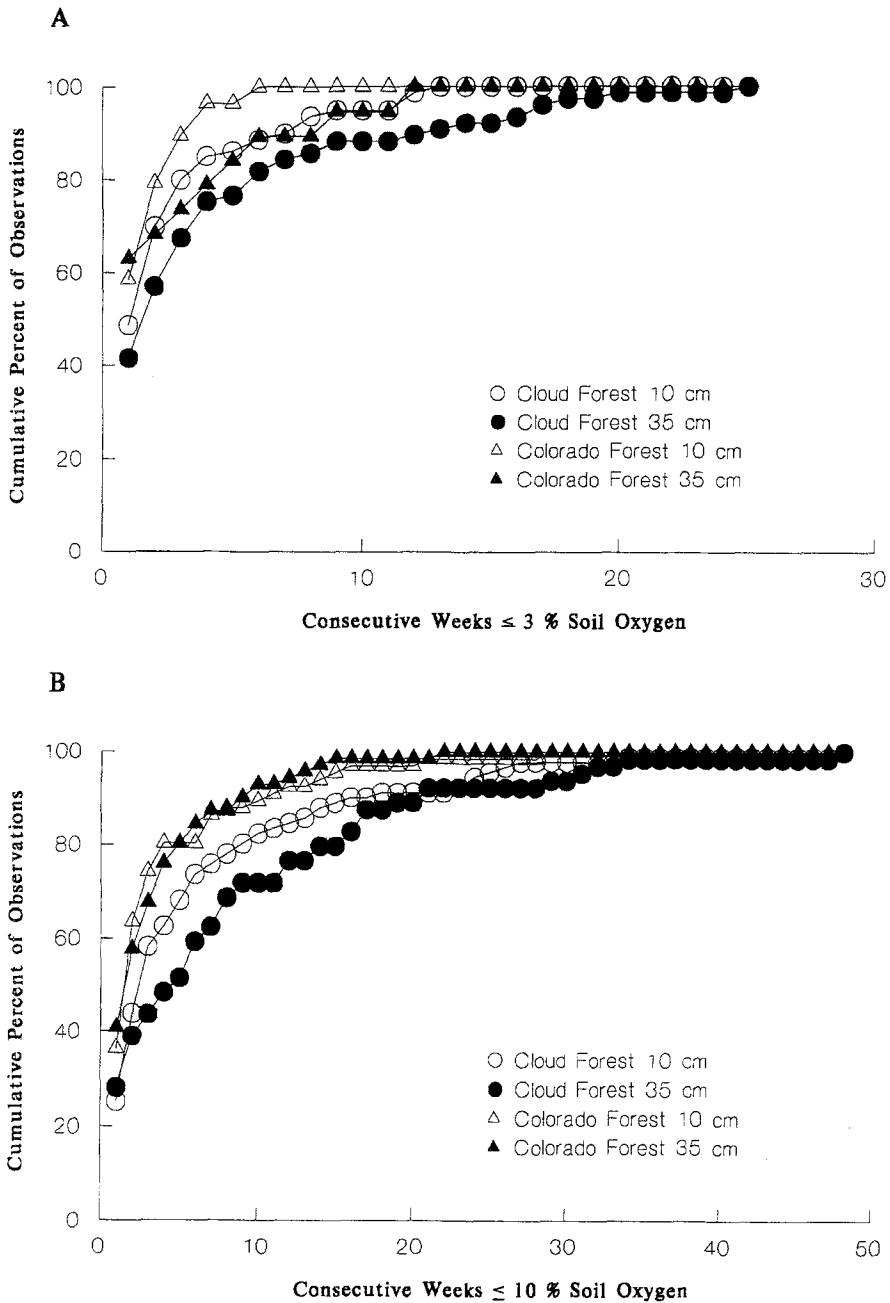
A

Consecutive Weeks ≤ 3 % Soil Oxygen

B

Consecutive Weeks ≤ 10 % Soil Oxygen

Figure 3. The cumulative percent of observations of (A) consecutive weeks ≤3% soil O_2 and (B) ≤10% soil O_2 in the upper elevation cloud forest and the mid elevation colorado forest, Luquillo Experimental Forest, PR. (○) Cloud Forest 10 cm depth; (●) Cloud Forest 35 cm depth; (△) Colorado Forest 10 cm depth; (▲) Colorado Forest 35 cm depth. Tabonuco forest soils did not experience sustained low O_2 events and so are not included here.
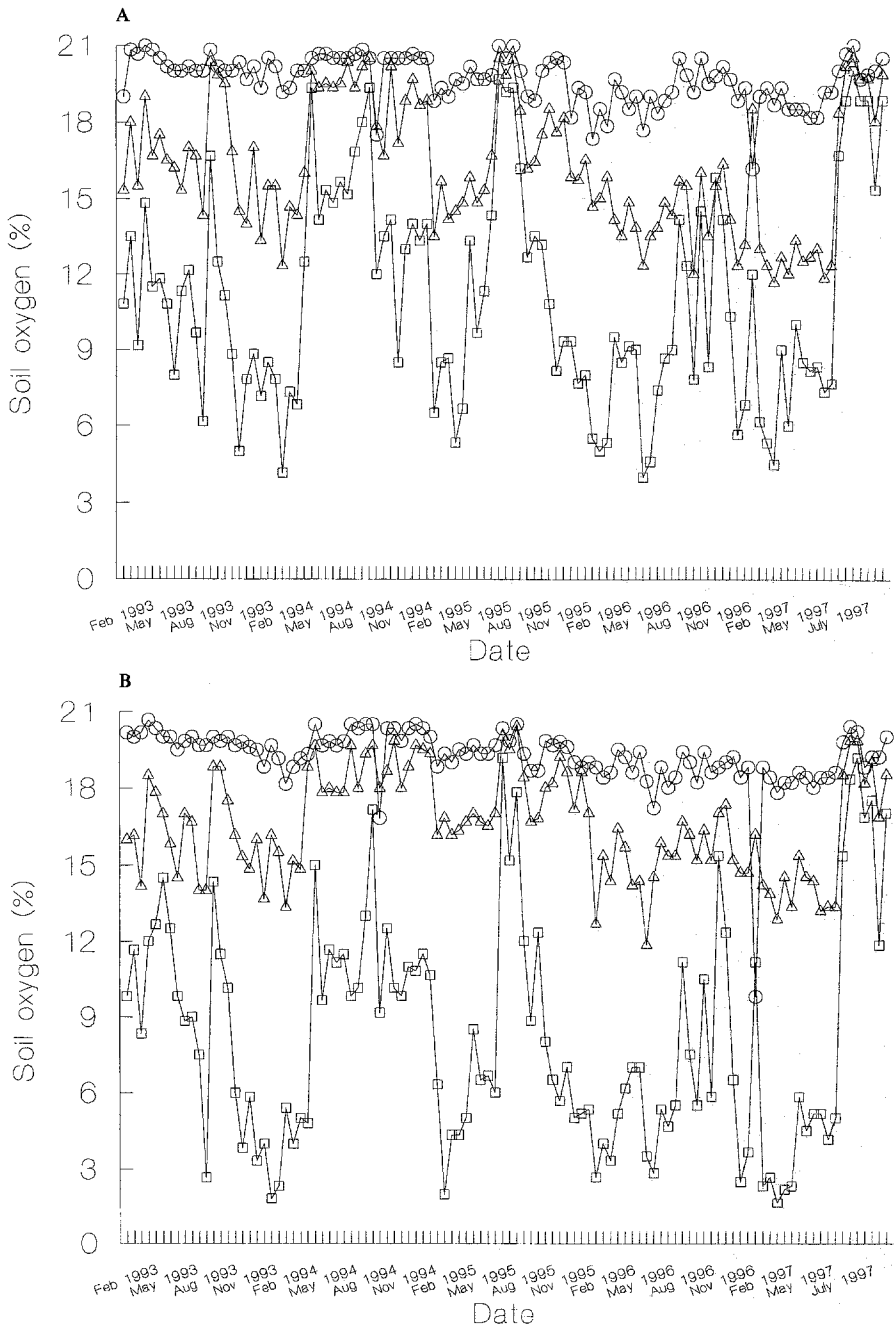
Figure 4. Average soil O_2 concentrations at (A) 10 cm depth and (B) 35 cm depth on ridges (○), slopes (△), and valleys (□) in the Bisley Research Watersheds, Luquillo Experimental Forest, Puerto Rico. Error bars were excluded for clarity; soil O_2 content decreases significantly from ridges to slopes to valleys (see text).
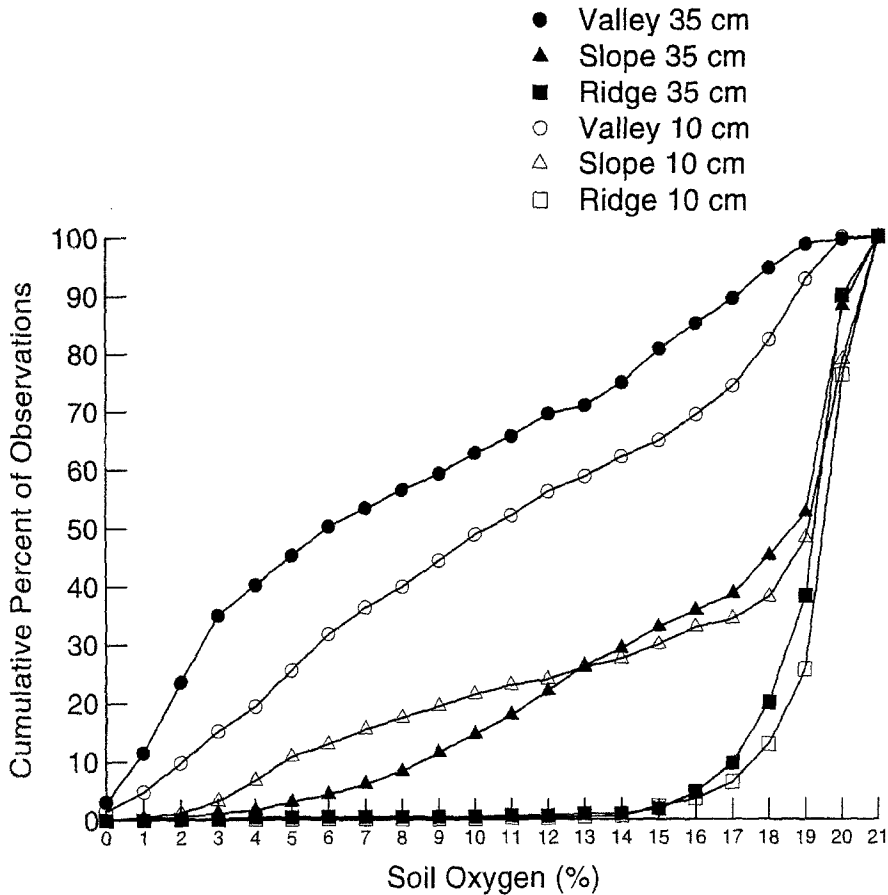
Figure 5. The cumulative percent of observations of soil O_2 concentrations ranging from 0–21% along a topographic gradients in the Luquillo Experimental Forest, PR. (○) valleys 10 cm depth; (●) valleys 35 cm depth; (△) slopes forest 10 cm depth; (▲) slopes 35 cm depth; (□) lower elevation ridges 10 cm depth; (■) ridges 35 cm depth.

cating that similar processes are likely to regulate soil O_2 concentrations along the gradients. At 10 cm depth, soil O_2 was significantly negatively correlated with rainfall the day prior to sampling on slopes and in valleys, and with the total rainfall that had fallen the 4 week prior to sampling on ridges and slopes (Table 2). Soil O_2 concentrations at 10 cm depth from all topographic zones were negatively correlated with stream discharge at almost all time steps examined (Table 2). At 35 cm depth, slopes were negatively correlated with stream discharge at all time steps, and with valleys at longer time steps of 2, 3, and 4 weeks. Soil O_2 concentrations at 10 cm depth in slope and valley zones were negatively correlated with throughfall the day prior to sampling only (Table 2).

Table 2. Pearson correlations of soil oxygen concentration with cumulative stream flow, rainfall, and throughfall over 1–7 d, 14 d, 21 d, and 28 d by topographic zone and depth in the Bisley Research Watersheds, Luquillo Experimental Forest, Puerto Rico. Asterisks identify statistically significant differences at the 95% level using Bonferroni probabilities.

Days prior to sampling	Stream flow			Rainfall			Throughfall		
	Ridge	Slope	Valley	Ridge	Slope	Valley	Ridge	Slope	Valley
				Soil oxygen at 10 cm depth					
1	−0.35*	−0.50*	−0.47*	−0.21	−0.41*	−0.35*	−0.22	−0.40*	−0.36*
2	−0.36*	−0.46*	−0.45*	−0.08	−0.25	−0.23	−0.07	−0.24	−0.24
3	−0.37*	−0.47*	−0.44*	−0.15	−0.31	−0.23	−0.14	−0.29	−0.23
4	−0.36*	−0.46*	−0.43*	−0.09	−0.27	−0.16	−0.08	−0.25	−0.17
5	−0.34*	−0.45*	−0.42*	−0.02	−0.27	−0.16	−0.01	−0.24	−0.17
6	−0.33*	−0.46*	−0.45*	−0.04	−0.28	−0.20	−0.03	−0.25	−0.20
7	−0.32	−0.45*	−0.46*	−0.07	−0.27	−0.18	−0.07	−0.24	−0.19
14	−0.33*	−0.45*	−0.47*	−0.03	−0.22	−0.21	−0.02	−0.19	−0.20
21	−0.30	−0.45*	−0.45*	−0.01	−0.20	−0.19	0.02	−0.13	−0.17
28	−0.33*	−0.49*	−0.46*	−0.34*	−0.34*	−0.31	−0.32	−0.26	−0.28
				Soil oxygen at 35 cm depth					
1	−0.22	−0.49*	−0.30	−0.31	−0.22	−0.25	−0.31	−0.21	−0.25
2	−0.27	−0.45*	−0.29	−0.12	−0.19	−0.16	−0.10	−0.17	−0.16
3	−0.31	−0.44*	−0.27	−0.14	−0.23	−0.17	−0.12	−0.21	−0.17
4	−0.30	−0.45*	−0.26	−0.03	−0.24	−0.05	−0.01	−0.21	−0.05
5	−0.27	−0.44*	−0.25	0.02	−0.25	−0.03	0.04	−0.22	−0.04
6	−0.26	−0.46*	−0.28	−0.01	−0.24	−0.08	−0.02	−0.20	−0.08
7	−0.25	−0.46*	−0.30	−0.05	−0.25	−0.04	−0.04	−0.21	−0.04
14	−0.26	−0.48*	−0.39*	0.05	−0.26	−0.17	0.07	−0.22	−0.15
21	−0.24	−0.46*	−0.41*	0.09	−0.22	−0.17	0.13	−0.15	−0.15
28	−0.27	−0.49*	−0.42*	−0.28	−0.37	−0.30	−0.23	−0.29	−0.26

Soil methane concentrations and methane efflux

Methane concentrations in the equilibration chambers were inversely related to O_2 concentrations, and increased significantly along the elevation and rainfall gradient ($P < 0.001$). The cloud forest soils exhibited very high CH_4 concentrations (up to 2.4×10^5 ppmv) (Figure 6). Depth to the parent material is generally less than 50 cm in these soils, so it is probable that methane is produced *in situ* rather than at depth. Methane concentrations

fluctuated over time, but always averaged above ambient atmospheric concentrations (approximately 1.7 ppmv) in the cloud and colorado forests (Figure 6). Methane concentrations in the cloud forest dropped significantly in March 1994 ($P < 0.01$), during a drought in Puerto Rico (Figure 6), although concentrations still averaged approximately 0.3×10^5 ppmv in the surface soil. Following one high rainfall event (105 mm in two days) in July 1994, we measured significantly elevated methane concentrations ($P < 0.001$) that were a factor of 10 above ambient levels in the normally well-oxygenated tabonuco forest (Figure 6). We resampled the chambers within 12 hr and the levels had returned to sub-ambient concentrations.

Along the topographic gradients, CH_4 concentrations increased significantly ($P < 0.05$) from a mean of below-ambient concentrations (1.02 ppmv) on ridges to an order of magnitude greater than ambient concentrations (28.16 ppmv) in the valleys for the 10 cm soil depth (Figure 7). A similar trend was found at 35 cm depth ($P < 0.01$), and CH_4 concentrations decreased significantly with depth in all topographic positions (Figure 7). Methane concentrations varied significantly among sampling periods ($P < 0.05$). Samples collected in December 1993 and 1995 yielded significantly higher soil methane concentrations than samples collected in July 1995 and 1997 for both soil depths.

We measured significantly greater net methane efflux across the soil atmosphere interface ($P < 0.01$) from the cloud forest soils than the other forests along the rainfall gradient (Table 3). In the well oxygenated soils of the tabonuco forest, we measured net CH_4 consumption from the atmosphere (-0.48 mg m^{-2} day^{-1}). Net CH_4 efflux also varied significantly along the topographic gradients ($P < 0.05$). Ridges and slopes consumed methane from the atmosphere, and valleys exhibited an average net flux to the atmosphere of 4.6 mg CH_4 m^{-2} d^{-1} (Table 3).

Patterns in N_2O concentrations along topographic gradients

Nitrous oxide concentrations in equilibration chambers increased significantly ($P < 0.05$) from near ambient concentrations on ridges to above-ambient concentrations on slopes and in valleys (Figure 7). Nitrous oxide concentrations in the surface soils were twice as high as concentrations in the deeper soil depth, but differences were not statistically significant at the 95% level. Soil N_2O concentrations varied significantly among sampling periods ($P < 0.05$), but did not follow any consistent trends across topographic positions over time.
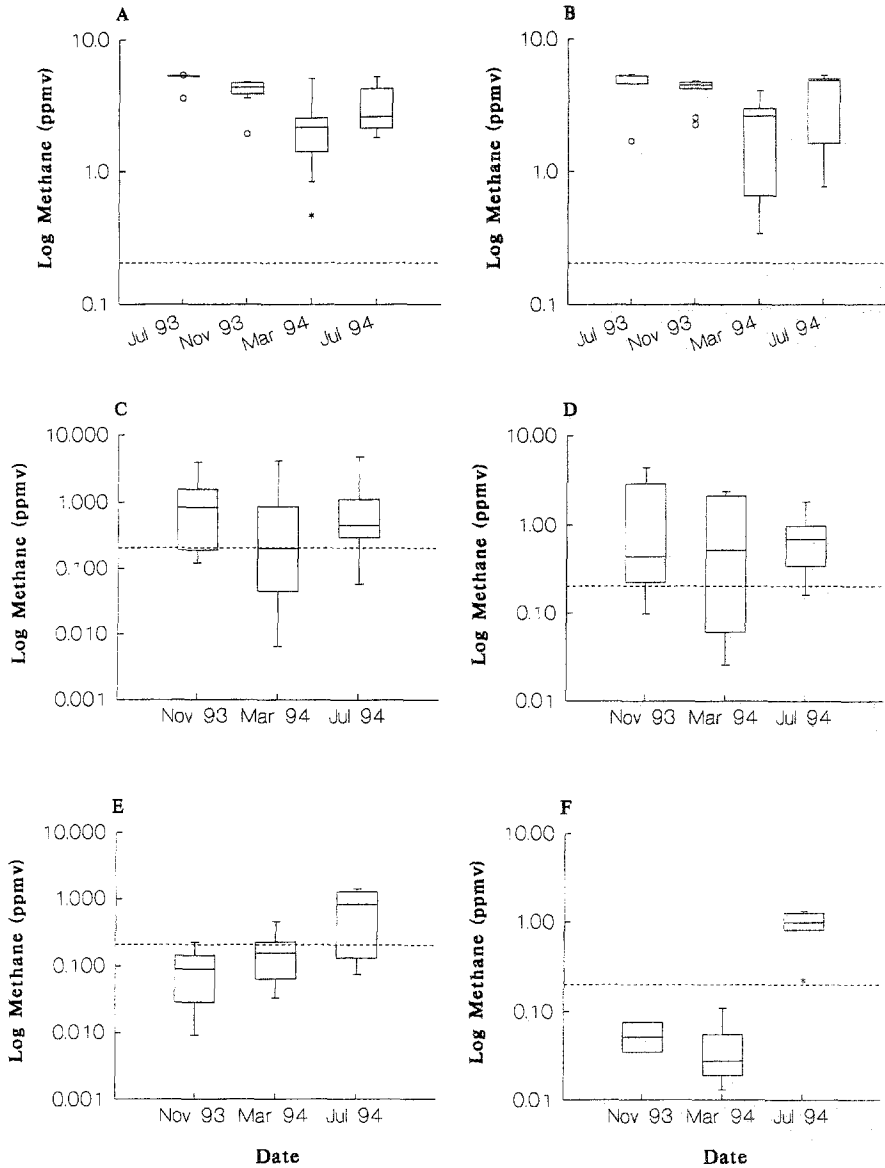
Figure 6. The range of CH_4 concentrations (Log_{10}) in equilibration chambers along an elevation and rainfall gradient in the Luquillo Experimental Forest, PR. (A) upper elevation cloud forest at 10 cm depth; (B) cloud forest at 35 cm depth; (C) mid elevation colorado forest at 10 cm depth; (D) colorado forest at 35 cm depth; (E) lower elevation tabonuco forest at 10 cm depth; (F) tabonuco forest at 35 cm depth. Horizontal bars dissecting the boxes represent the median values between the whiskers (the range of values minus the outliers), boxes enclose the innerquartile range, stars represent outliers, and dots represent far outside values. The dotted line identifies ambient concentrations.
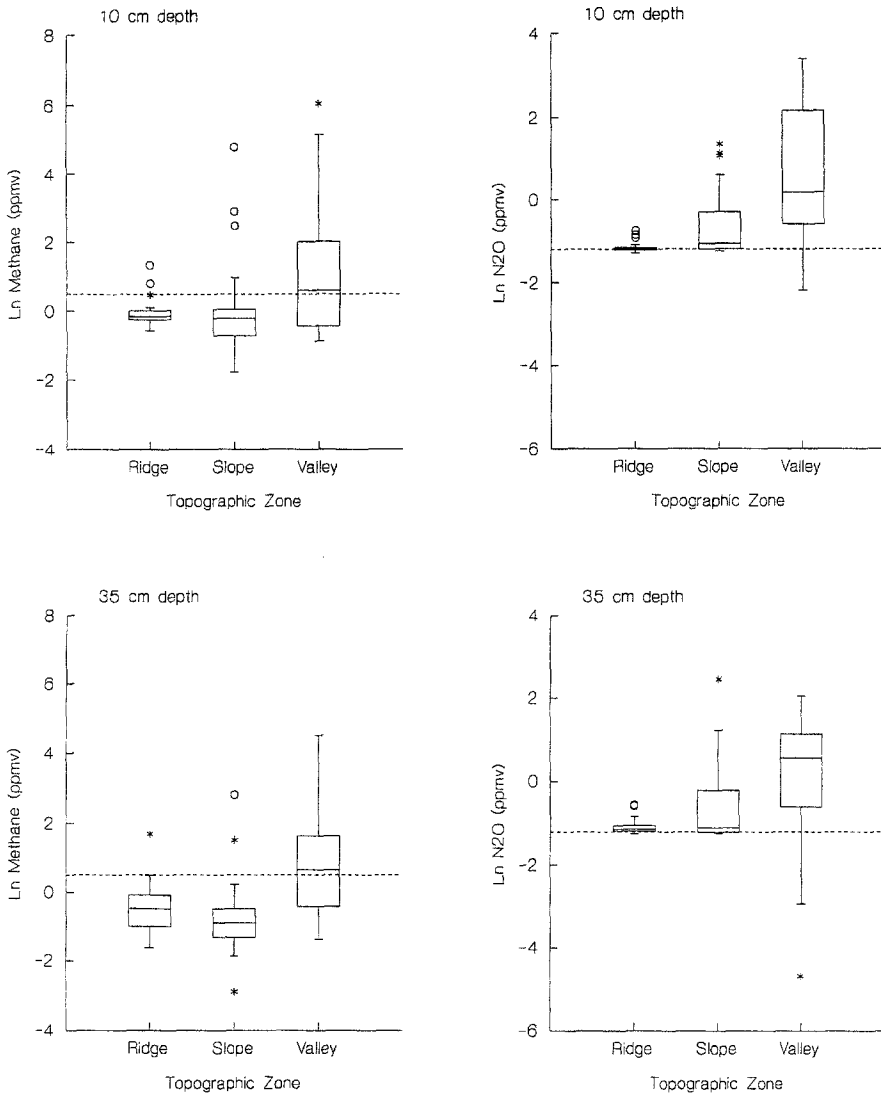
Figure 7. The range of CH_4 and N_2O concentrations (natural Log) by depth in equilibration chambers along topographic gradients in the Bisley Research Watersheds, Luquillo Experimental Forest, PR. See Figure 6 for explanation of the symbols and lines.

Other soil chemical properties

In the top 10 cm of mineral soil, the upper elevation cloud forest exhibited significantly higher mean concentrations of total N, soil organic matter, and pH than the lower elevation forests (Table 4). The concentrations of extractable Fe and P decreased significantly with depth in the colorado forest,

Table 3. Net methane efflux (mg CH_4 m^{-2} d^{-1}) across the soil-atmosphere interface along a landscape-scale rainfall gradient and localized topographic gradients in the Luquillo Experimental Forext, P.R. Standard errors in parentheses. Different lower case letters signify statistically significant differences among forest types along the rainfall graidnet, or among topographic zones along the localized gradients.

Site	CH_4 efflux	(se)
Cloud	97.66	(49.78) a
Colorado	0.32	(0.24) b
Tabonuco	−0.48	(0.07) c
Ridge	−0.78	(1.23) a
Slope	−2.62	(1.68) a
Valley	4.55	(1.19) b

and only P decreased with depth in the cloud forest (Table 4). Soil P was positively correlated with SOM in the tabonuco forest ($r^2 = 0.89$, $P < 0.001$), but not in the other forest types. On a soil mass basis, the upper elevation cloud forest soils had significantly larger pools of extractable P ($P < 0.005$) total N ($P < 0.001$), and exchangeable Fe ($P < 0.01$) in the top 35 cm of mineral soil than lower elevation forests. Pools of extractable P were positively correlated with exchangeable Fe pools ($r^2 = 0.71$, $P < 0.01$). Bulk densities in the top 10 cm of mineral soil decreased with increasing elevation (Table 4). Values were generally low in the surface soils reflecting the high macropore volume in the LEF soils (Silver et al. 1994), and the high soil organic matter content in upper elevation soils.

Along the topographic gradients, extractable Fe ($P < 0.01$) and soil organic matter concentrations ($P = 0.05$) decreased significantly from ridges to valleys in the 0–10 cm soil depth (Table 5). Extractable soil P concentrations were significantly greater in the valleys than on ridges or slopes ($P < 0.01$) for the 10–35 cm soil depth. Soil organic matter concentrations decreased with depth ($P < 0.01$) in all topographic zones (Table 5). Pools of extractable P (kg ha^{-1}) and exchangeable Fe (kg ha^{-1}) increased with depth in the valleys. At 0–10 cm depth, soil P content was significantly correlated with SOM in all topographic zones, and the variability in soil P content explained by SOM increased from 42% on the ridges to 57% in the valleys. Soil P and Fe were weakly, but significantly positively correlated on slopes ($r^2 = 0.17$) and in valleys ($r^2 = 0.26$). In the 10–35 cm depth, soil Fe and SOM content were highly significantly correlated in valleys ($r^2 = 0.76$). Soil

Table 4. Total N, extractable P, exchangeable Fe, soil organic matter (OM), pH, and bulk density (±1 standard error) in the 0–10 cm and 10–35 cm soil depths along a rainfall and elevation gradient in the Luquito Experimental Forest, PR. Different lower case letters signify statistically significant differences among forest types within depths. Upper case letters signify statistically significant differences between depths within forests. na = not available.

Life zone	Subtropical Wet		Lower Montane Wet		Lower Montane Rain	
Forest type	Tabonuco		Colorado		Cloud	
Depth	0–10 cm	10–35 cm	0–10 cm	10–35 cm	0–10 cm	10–35 cm
N (%)	0.32 ± 0.03aA	0.14 ± 0.01aB	0.20 ± 0.02bA	0.13 ± 0.01aB	0.61 ± 0.02cA	0.33 ± 0.04bB
P (μg g^{-1})	12.69 ± 2.46A	2.66 ± 0.68aB	8.90 ± 0.51A	4.36 ± 0.46aB	12.38 ± 0.75A	9.17 ± 1.08bB
Fe (cmol$^+$ kg^{-1})	17.72 ± 5.54A	5.35 ± 1.4aB	9.53 ± 0.57A	6.61 ± 0.24aB	12.99 ± 0.63	12.69 ± 0.35b
OM (%)	9.00 ± 0.10aA	3.59 ± 0.26aB	8.00 ± 1.00aA	4.27 ± 0.32aB	25.00 ± 1.00bA	15.91 ± 1.81bB
pH	3.96 ± 0.08a	4.21 ± 0.12a	4.81 ± 0.06bA	5.00 ± 0.05bB	5.41 ± 0.15c	5.75 ± 0.08c
Bulk density (g cm^{-3})	0.60 ± 0.05	1.23 ± 0.30	0.55 na	1.44 ± 0.18	0.52 na	1.47 ± 0.16

P content in the 10–35 cm depth was significantly positively correlated with both SOM and Fe in all topographic positions. In valleys, 46% of the variability in soil P content was explained by SOM, while 67% of the variability was explained by extractable Fe content.

Discussion

Several studies have described O_2 depletion of the soil atmosphere as a result of flooding (see reviews by Stolzy 1974; Gambrell & Patrick 1978; Crawford 1992), but few studies have documented soil O_2 concentrations in upland forest ecosystems (Magnusson 1992, 1994; Kursar et al. 1995). We know of no other studies that have reported such low levels of soil O_2 and sustained periods of reduction in non-flooded surface soils. In this study, soil O_2 decreased significantly with increasing annual rainfall. Soil O_2 concentrations dropped to 0–3% in soil chambers for up to 25 consecutive weeks, and averaged only 6–8% O_2 in the cloud forest over the 82 week study period. Oxygen levels that were less than half of ambient concentrations were observed for >30% of the sampling periods in the colorado forest and >60% of the 18 month study in the cloud forest within 10 cm of the soil surface.

Drainage characteristics often vary with regarded to slope position, and evidence of probable O_2 depletion along topographic gradients has been documented indirectly through assays of denitrification (Davidson & Swank 1986; Livingston et al. 1988; Grofffman & Tiedje 1989). In the LEF, soil O_2 concentrations decreased significantly along the localized topographic gradients from ridge to slope to valley. Although periods of O_2 depletion were shorter and less frequent along the topographic gradients than in the upper elevation forests, we still found that 5–12% of the measurements yielded $\leq 1\%$ O_2 in the valleys and 15–35% yielded $\leq 3\%$ O_2 at 10 cm and 35 cm depth, respectively.

Under flooded conditions, chemical and microbial O_2 demand can exceed the rate of O_2 diffusion through an aqueous medium resulting in anaerobiosis (Gambrell & Patrick 1978). In this study, high rainfall and hydrologic through-flow created similar conditions at the scale of the soil aggregate, leading to O_2 depletion of the bulk soil air. Soil O_2 concentrations appeared to respond to long term (annual) precipitation patterns along the elevation and rainfall gradient, and were sensitive to shorter term precipitation events along the localized topographic gradients. Soil O_2 concentrations were negatively correlated with weekly rainfall totals in the colorado forest for a lag of 4 weeks. It is unclear why the cloud forest soil O_2 concentrations were not cross correlated with weekly rainfall, but might be explained by the near constant soil saturation in these ecosystems. If soils remain saturated, additional mois-

Table 5. Extractable P, extractable Fe, and soil organic matter by depth in different topographic zones of the Bisley Research Watersheds, PR. Values are means ± one standard error. Different lower case letters signify statistically significant differences within depths among topographic zones ($P < 0.05$). Different upper case letters signify statistically significant differences between depths, within topographic zones. Bulk density in the 10–35 cm depth was only measured on slopes. Data are recalculated from Silver et al. 1994.

	Ridge ($n = 24$)		Slope ($n = 41$)		Valley ($n = 22$)	
P (μg g^{-1})	33.6 ± 7.0A	7.1 ± 0.9aB	23.1 ± 1.7A	6.4 ± 0.8aB	23.3 ± 2.3A	13.5 ± 2.1bB
Fe (cmol$^+$ kg^{-1})	7.2 ± 0.8aA	3.8 ± 0.6aB	5.2 ± 0.5bA	2.0 ± 0.3bB	3.3 ± 0.4cA	2.4 ± 0.5bB
S.O.M. (%)	9.6 ± 2.2aA	3.1 ± 0.3B	7.1 ± 0.5aA	2.6 ± 0.2B	5.3 ± 0.4bA	3.0 ± 0.5B
Bulk density (g cm^{-3})	0.64 ± 0.05	0.98 ± 0.03	0.72 ± 0.05	0.98 ± 0.03	0.68 ± 0.03	0.98 ± 0.03

ture input may not have a direct or additional effect on diffusivity of O_2 into soil (Kursar et al. 1995).

Soil O_2 concentrations were significantly negatively correlated with rainfall and stream flow along the topographic gradients. Rainfall, irrigation, and snow melt have been shown to temporarily lower soil O_2 concentrations, although, generally by only a few percent in the surface soil horizons (Magnuson 1992, 1994; Kursar et al. 1995). In the valleys and slopes, soil O_2 was strongly negatively correlated with the previous day's rainfall. Slopes and ridges were also negatively correlated with rainfall over 28 day periods suggesting that longer term rainfall trends may adequately characterize soil aeration in the upper topographic positions, but that aeration and reduction are dynamic on shorter time scales in the valleys. We used stream flow as a means to integrate soil moisture with drainage rates, both of which are likely to feed back on soil aeration. In humid tropical environments, changes in soil moisture can be difficult to detect due to the high water holding capacity of clay and organic particles (Silver 1992; Silver et al. 1994). Soil O_2 concentrations in the surface soils were highly sensitive to stream flow the day prior to sampling, as well as over longer time periods. These results suggest that hydrologic flow may be a key mechanism controlling soil aeration in this ecosystem.

Periods of O_2 depletion signal an increased probability of anaerobically-mediated biogeochemical processes in the bulk soil. We measured soil CH_4 and N_2O concentrations, CH_4 efflux, and other soil chemical and physical properties to identify any potential biogeochemical consequences of periodic or chronic anaerobiosis. Nitrous oxide is produced as a result of both nitrification and denitrification, and thus concentrations are not necessarily indicative of anaerobiosis (Bremner & Blackmer 1978). However, at low O_2 availability, the production of N_2O through denitrification is thought to predominate (Goreau et al. 1980; Davidson & Swank 1986; Riley and Vitousek 1995). Along the topographic gradients, above ambient N_2O was measured in the equilibration chambers on slopes and in valleys consistent with the periodic declines in O_2 content and above ambient CH_4 concentrations observed. Although we did not measure N_2O fluxes here, Bowden et al. (1992) reported higher net N_2O emission rates in valleys relative to ridges in the Bisley Watersheds.

Because CH_4 is so readily oxidized in the presence of O_2, above-ambient CH_4 concentrations and efflux are perhaps the best indicators of strongly reducing conditions in soils (Gambrell & Patrick 1978). Methane concentrations in the cloud and colorado forests averaged above ambient levels at all sampling periods, and exceeded ambient levels by over four orders of magnitude in the cloud forest. The juxtaposition of CH_4 and O_2 within

chambers illustrates the different processes occurring at the scale of soil microsites. Although CH_4 and O_2 can not coexist at the microsite scale, they can coexist in the bulk soil atmosphere. The dominance of anaerobic microsites is evidenced by the high CH_4 concentrations. In the surface soils along the topographic gradients, above-ambient methane was measured in valleys, and sub-ambient concentrations were measured on slopes and ridges. Surface soils in the cloud and colorado forests and in the valleys of the tabonuco forest were sufficiently reduced to result in net methane emission across the soil-atmosphere interface. Keller et al. (1986) reported similar net methane consumption rates from a one time sampling of the tabonuco forest, but found higher emission rates in the colorado forest (87 mg CH_4 m^{-2} d^{-1}) and lower rates in the cloud forest (1.5 mg CH_4m^{-2} d^{-1}) than we report here. Upland tropical forests are typically thought to be net consumers of methane from the atmosphere (Keller & Matson 1994), but these data suggest that in high rainfall environments net methane efflux to the atmosphere can occur for all or part of the year. Low soil O_2 and high methane concentrations indicate a strong dominance of anaerobic over aerobic microsites in the soil.

In this study, CH_4 concentrations appeared to be particularly sensitive to changes in rainfall. The rapid flush of methane observed in the tabonuco forest soils in July 1994 suggests that the potential exists for short-term anaerobiosis to occur, even in normally well-oxygenated sites. Such a rapid flush of methane production has not been previously reported for tropical forest soils, and may result from a combination of decreased gas transport, increased activity of methanogens in the anaerobic microsites, and suppression of the activity of aerobic methanotrophs (Reeburgh et al. 1993). Such a short-term change indicates that upland tropical forest soils are dynamic with regards to methane production and consumption, and that methanogenic bacteria can respond quickly to changes in microsite conditions. This result may also have important implications for the magnitude of tropical forest soils as a sink for atmospheric CH_4.

The degree of soil oxidation or reduction affected other soil chemical and physical properties. Because we did not measure soil biogeochemistry simultaneously with weekly or bi-weekly O_2 measurements, our results can only indicate potential effects of anaerobiosis in these ecosystems, and do not describe the dynamics of these processes over time. Nitrous oxide and CH_4 concentrations and efflux are likely to vary at short temporal scales of hours to days. Measures such as SOM, total N, extractable P, and exchangeable Fe are not likely to vary significantly at such short temporal scales. Soil organic matter pools increased with decreasing soil O_2 along the rainfall gradient, probably due to the slower metabolism of anaerobic decomposers (Day & Megonigal 1993), and lower temperatures. This process results in a negative

feedback between soil O_2 and SOM, increasing soil water holding capacity and metabolic O_2 demand, decreasing gaseous diffusion, and enhancing the potential for anaerobiosis (Gambrell & Patrick 1978; Frangi 1983). It is interesting to note that net primary productivity (NPP) decreases with increasing annual rainfall in the LEF (Weaver & Murphy 1990); therefore it is unlikely that NPP directly explains patterns in SOM, and supports the hypothesis of potential O_2 limitations on decomposition. Soil organic matter accumulation also led to an associated increase in total soil N, but may not explain the patterns in extractable soil P along the rainfall gradient. In the tabonuco forest, extractable soil P was positively correlated with SOM; in well aerated soils, iron oxides and hydroxides strongly sorb P in the mineral soil, leaving the organic fraction as the dominant extractable and plant available pool (Tiessen et al. 1994). In the anaerobic cloud forest soils, P was not significantly correlated with organic matter, probably due to higher P mobilization and availability in mineral soils where Fe^{3+} is reduced to Fe^{2+} (Shapiro 1958). The amount of extractable P in the top 35 cm of soil decreased significantly with decreasing annual rainfall as soils became more oxidized.

Along the topographic gradients, SOM, exchangeable Fe, and extractable P all decreased from ridges to valleys. We expected that the variable O_2 environment in the valleys would lead to high SOM content, similar to what we saw along the rainfall gradient. Instead, SOM decreased, potentially due to lower rates of C stabilization and greater DOC and POC losses in lower topographic positions. The tabonuco forest of the LEF has high rates of DOC export (up to 109 kg ha^{-1} y^{-1}) relative to other tropical montane watersheds (McDowell & Asbury 1994). We also expected to see more labile P in the lower topographic zones as the strength of Fe and P bonds decreased with Fe reduction. Again, this was not the case in the surface soils. We speculate that the lower SOM content, and possibly increased DOP losses as P was mobilized during reduction might explain these patterns, but more research would be needed to confirm if these mechanisms are important here. The temporal dynamics of Fe and P reactions are not well described for tropical forest soils, and may be particularly sensitive to soil O_2 concentrations.

In summary, our results show that soil O_2 can drop to very low levels for extended time periods in upland, non-flooded soils, and result in changes in biogeochemical cycles. The patterns in soil O_2 availability with rainfall and stream flow, and the changes in soil C, N, Fe, and P in both well and poorly aerated soils provides some intriguing evidence for the sensitivity of humid tropical ecosystems to climate. Wet tropical forests are often referred to as aseasonal environments and the relationships of soil and plant processes to climate is often ignored within these ecosystems. Here we use soil O_2 concen-

trations to show how high rainfall environments differ from one another in an ecological sense with regard to soil resource availability and biogeochemical cycling.

Acknowledgments

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