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Strong spatial variability in trace gasdynamics following experimental drought in a humid tropical forest

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[1] Soil moisture is a key driver of biogeochemical processes in terrestrial ecosystems, strongly affecting carbon (C) and nutrient availability as well as trace gas production and consumption in soils. Models predict increasing drought frequency in tropical forest ecosystems, which could feed back on future climate change directly via effects on trace gasdynamics and indirectly through changes in nutrient availability. We used throughfall exclusion shelters to determine effects of short-term (3 month) drought on trace gas fluxes and nutrient availability in humid tropical forests in Puerto Rico. Exclusion and control plots were replicated within and across three topographic zones (ridge, slope, valley) to account for spatial heterogeneity typical of these ecosystems. Throughfall exclusion reduced soil moisture in all sites and lowered exchangeable phosphorus (P) on ridges and slopes. Drought decreased soil carbon dioxide (CO_2) emissions by 30% in ridge sites and 28% in slope sites, and increased net methane (CH_4) consumption by 480% in valley sites. Both valley and ridge sites became net nitrous oxide (N_2O) sinks in response to soil drying. Emissions of CO_2 and N_2O, as well as CH_4 consumption were positively related to exchangeable P and the nitrate:ammonium ratio. These findings suggest that drought has the potential to decrease net trace gas emissions from humid tropical forest soils. The differential response of trace gas emissions and nutrients from different topographic zones to drought underscores the complexity of biogeochemical cycling in these ecosystems and the importance of considering spatial heterogeneity when estimating whole system responses.

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1. Introduction

[2] Tropical forest soils are the largest natural source of both carbon dioxide (CO_2) [*Raich and Schlesinger*, 1992] and nitrous oxide (N_2O) [*Matson and Vitousek*, 1990] globally, and wet tropical soils are a globally important source of methane (CH_4) [*Frankenberg et al.*, 2005]. Theory suggests that the ecological processes responsible for trace gas production and consumption in tropical soils are highly sensitive to soil moisture availability through its effect on soil redox dynamics, diffusion, and soil carbon (C) and nutrient pools [e.g., *Conrad*, 1996; *Davidson et al.*, 2004; *Holtgrieve et al.*, 2006]. As such, projected changes in precipitation for tropical regions are likely to significantly affect both the production and consumption of these trace gases, which could feed back on future climate change. Understanding how precipitation regimes might affect trace gas emissions from tropical forest soils is crucial to better predict the effects of, and feedbacks to, climate change in tropical forests.

[3] Although the magnitude of precipitation change is difficult to predict [*Malhi and Wright*, 2004], increased drought frequency and overall lower mean annual rainfall are frequently cited as likely future scenarios in tropical regions [*Cramer et al.*, 2004; *Cramer et al.*, 2001; *Hulme and Viner*, 1998; *Meehl et al.*, 2006]. Existing evidence suggests that the flux of trace gases from tropical soils is very responsive to changes in soil moisture status [*Butterbach-Bahl et al.*, 2004; *Holtgrieve et al.*, 2006; *Kieft et al.*, 1987; *van Haren et al.*, 2005; *Vasconcelos et al.*, 2004; *Werner et al.*, 2006]. However, the direction and magnitude of the trace gas response to experimental drought has been variable [*Cattânio et al.*, 2002; *Cleveland et al.*, 2010; *Davidson et al.*, 2004, 2008; *Metcalfe et al.*, 2007; *Sotta et al.*, 2007; *Wieder et al.*, 2011]. This variable response is likely due to the considerable spatial heterogeneity in edaphic conditions and biotic communities within and across these ecosystems [*Sotta et al.*, 2006]. The production and consumption of CO_2, N_2O, and CH_4 are largely

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Table 1. Plant and Soil Characteristics of the Three Forest Types

Variable	Forest Type		
	Ridge	Slope	Valley
Dominant species[a] (importance)	*Manilkara bidentata* (0.76) Dacryodes excelsa *(0.65)* Sloanea berteriana *(0.14)*	*Dacryodes excelsa* (0.46) *Prestoea montana* (0.44) *Tetragastris balsamifera* (0.37)	*Prestoea montana* (0.73) *Andira inermis* (0.26) *Cecropia schreberiana* (0.24)
Bulk density[b] (g/cm^3)	0.60 (0.05)	0.68 (0.06)	0.61 (0.11)
Organic matter[b] (%)	9.6 (2.2)$_x$	7.1 (0.6)$_{x,y}$	4.4 (0.5)$_y$
Exchangeable acidity[b] ($cmol^+/kg$)	5.5 (0.5)$_x$	4.2 (0.5)$_x$	2.0 (0.6)$_y$
Total N[b] (%)	0.34 (0.07)$_x$	0.31 (0.2)$_{x,y}$	0.25 (0.02)$_y$

[a]Data from this study. Importance value$_{spp}$ = relative frequency + relative density + relative basal area. n = 10.

[b]Data from *Silver et al.* [1994]. Soils are 0–10 cm. Subscript letters indicate significant differences among forest types. ±S.E. is given in parentheses. n = 24 (ridge), 41 (slope), 9 (valley).

mediated by biological processes, which in turn respond to their physical (e.g., soil texture, drainage) and chemical (e.g., nutrients, pH, redox potential) environment [*Burgin et al.*, 2011; *Townsend et al.*, 2011]. These physical and biological characteristics occur within a heterogeneous landscape characterized by variability in topography, disturbance history, and biodiversity. The response of trace gas emissions to reduced soil moisture is thus also likely to vary with physical, chemical, and biological heterogeneity.

[4] Carbon and nutrient availability have been shown to directly affect trace gas emissions from soils [*Cleveland and Townsend*, 2006; *Cleveland et al.*, 2011; *Cusack et al.*, 2010; *Holtgrieve et al.*, 2006; *Townsend et al.*, 2011; *Wieder et al.*, 2011]. Therefore, drought can have an indirect effect on trace gas flux via direct effects of drought on C and nutrient availability. There are several mechanisms by which drought can affect C and nutrient availability. First, reduced water availability may slow decomposition and nutrient mineralization rates [*Aerts*, 1997; *Lodge et al.*, 1994; *Townsend et al.*, 2011]. Second, soil moisture could affect C and nutrient availability via changes in soil redox potential [*Chacon et al.*, 2006; *Silver et al.*, 1999, 2001; *Wieder et al.*, 2011]. Phosphorus (P), which is generally considered the primary limiting nutrient in tropical ecosystems, can react with iron (Fe) oxides and hydroxides generally formed under well aerated conditions, decreasing its mobility and availability to roots and microbes [*Crews et al.*, 1995; *Walker and Syers*, 1976]. Internal nitrogen (N) transformations and rates of N_2O emissions are also directly affected by changing redox conditions [*Enquist*, 2002; *Silver et al.*, 2001], as N_2O production can be derived from both nitrification (under aerobic conditions) and denitrification (under anaerobic conditions) [*Firestone and Davidson*, 1989]. Finally, drought could increase soil C and nutrient concentrations by reducing loss from leaching and the lysing of microbial cell walls [*Cleveland et al.*, 2010; *Lodge et al.*, 1994].

[5] Here, we report on the effects of soil drying on the emissions of CH_4, N_2O and CO_2 from three humid tropical forest sites in Puerto Rico. These sites were stratified by ridge, slope, and valley to account for the major topographic zones in the region. Our goals were to evaluate the role of soil moisture in mediating the emissions of CO_2, N_2O, and CH_4 from these different forests, and investigate soil physical and chemical changes accompanying reduced soil moisture that affect ecosystem biogeochemical cycling.

2. Materials and Methods

2.1. Study Area

[6] The study was conducted in the Bisley Research Watersheds, approximately 350 m above sea level in northeastern Puerto Rico (18°18′N, 65°50′W). The Bisley Watersheds are part of the NSF-sponsored Long-term Ecological Research Program in the Luquillo Experimental Forest (LEF), and are classified as subtropical wet forest [*Scatena*, 1989]. The watersheds receive an average of 3500 mm of rainfall per year with every month receiving over 200 mm. The forest canopy intercepts approximately 40% of rainfall [*Heartsill-Scalley et al.*, 2007]. Mean annual temperature is 23°C with little seasonal variation [*Scatena*, 1989]. Soils are classified as ultisols in the Humatus-Cristal-Zarzal series. The soils are derived from volcanic sediments with Tertiary-age quartz-diorite intrusions of the Rio Blanco stock. They are deep, clay-rich and acidic, with high aluminum (Al) and Fe content [*Scatena*, 1989]. Root biomass is concentrated (>60%) in the top ten centimeters of mineral soil [*Silver and Vogt*, 1993].

2.2. Experimental Design

[7] We worked in three topographic zones within a 1 ha area of the Bisley Watersheds including riparian valley dominated by *Prestoea montana* R. Graham Nichols (Palmaceae), ridge dominated by *Dacryodes excelsa* Vahl (Burseraceae), and moderate slope dominated by *Sloanea berteriana* Choisy (Elaeocarpaceae) [*Scatena*, 1989]. While the dominate species varied among sites, this forest is quite diverse with approximately 190 tree species identified in this region. Several soil properties also vary predictably across these topographic zones. In the surface soils, exchangeable base cation concentrations increase along a gradient from ridge tops to riparian valleys, while soil organic matter, exchangeable Fe, total N and exchangeable acidity decrease along this gradient (Table 1) [*Silver et al.*, 1994].

[8] The study was designed to determine the effects of decreased soil moisture availability associated with short-term (seasonal) drought on soil nutrient dynamics and trace gas fluxes. Our goals were to reduce, but not eliminate, water input to the soil, which would be an unrealistic scenario for this region. To do this, we used small shelters

(1.54 m^2 plots; 1.24 m × 1.24 m each) located between tree stems; plots were not trenched to allow lateral water flow into the plots. This also minimized soil disturbance and allowed root activity, which plays a key role in soil C dynamics, CO_2 production and can influence N_2O and CH_4 fluxes [*Brienen et al.*, 2010; *Keller et al.*, 2000]. Roots of mature trees were able to access water outside of the exclusions, potentially decreasing the effects of soil moisture loss on root respiration. We established ten plots in each of the three topographic zones (10 plots × 3 sites = 30 plots total). The forest sites were not located along a catena, where hydrology would potentially cause treatment interactions. Within each zone, five plots were designated as controls and five as treatment plots. Plots were established a minimum of 4 m apart and were randomly interspersed to avoid treatment interactions. To minimize the effect of repeated soil sampling, we divided each plot into four equal square quadrants. We then randomly selected one quadrant within each plot to be reserved for destructive sampling (e.g., soil nutrients, gravimetric soil moisture, pH). To evaluate the community composition of the different sites, we measured the diameter at breast height (DBH) and identified all tree species (DBH > 5 cm) within a 5 m radius of all 30 plots (Table 1).

[9] We excluded throughfall using clear, corrugated plastic panels (1.54 m^2) that were 0.5 m above the ground. Each panel drained into a polyvinyl chlorate (PVC) gutter that was used to transfer water away from the treatment plots. The panels were flipped every 3–7 days to transfer litter back onto the forest floor beneath. The shelters were installed on June 4, 2008 and removed August 26, 2008 (12 weeks total). We chose this period as it represented the length of a typical dry season in the adjacent, moist forest life zone [*Holdridge*, 1967].

2.3. Throughfall

[10] We sampled throughfall to determine the amount of water and nutrients excluded from the treatment plots. While most rainfall exclusion experiments focus only on water reduction, decreased rainfall can also potentially reduce nutrient inputs by excluding the nutrients dissolved in throughfall. We measured throughfall adjacent to each of the 30 plots using identical 24.6 mm^2 funnels attached to sterile 1-gallon plastic containers [*Heartsill-Scalley et al.*, 2007]. Throughfall was measured weekly for each plot. Subsamples from a composite of five throughfall collectors in each topographic zone were analyzed every two weeks. The composite samples were filtered using methods described in *Heartsill-Scalley et al.* [2007] and frozen at −21°C until analysis. Solutions were digested in persulfate and analyzed colorometrically on a spectrophotometer for N and P (Milton Roy, Ivyland, PA, USA) according to *McDowell et al.* [1990].

2.4. Soil Sampling and Analyses

[11] We used time domain reflectometery (TDR, Campbell Scientific Model CS616) to estimate volumetric soil moisture in each of 6 plots per forest site (3 control, 3 treatment; 0–30 cm depth). We additionally installed one soil temperature probe (10 cm depth; Campbell Scientific, Model 108L) in one control and one exclusion plot in each topographic zone. Volumetric soil moisture and temperature were measured hourly starting one month prior to throughfall exclusion and ending three months after the shelters were removed (May through November 2008).

[12] Soils (0–10 cm depth) were collected once every two weeks concomitantly with trace gas sampling (see below) from all plots using 2.5 cm diameter corer. The soil was immediately processed for gravimetric soil moisture, inorganic N [*Hart et al.*, 1994], sodium bicarbonate extractable P (a widely used index of exchangeable P, and thus generally considered biologically available), exchangeable Fe, and soil pH. Gravimetric soil moisture was determined on 5 g of field-wet soil dried in a 105°C oven for 24 h. Soil pH was determined in a slurry of 2:1 potassium chloride (KCl) and deionized (DI) water and measured with a pH meter. We used a KCl extraction to estimate inorganic nitrogen (N) [*Hart et al.*, 1994; *Yang et al.*, 2012]. Samples were analyzed on a Lachat QuickChem FIA + 8000 series (Lachat Instruments, Loveland, CO, USA) for ammonium (NH_4^+) and nitrate plus nitrite (NO_3^- and NO_2^-). Approximately 10 g field-wet soil samples were processed and analyzed the day of collection at the International Institute of Tropical Forestry (IITF). Exchangeable P and Fe were measured using an Olsen-EDTA (NH_4-EDTA-$NaHCO_3$) extraction [*Anderson and Ingram*, 1993] followed by analysis on an ICP-Spectro Ciros CCD (Spectro Analytical Instruments, Kleve, Germany). We measured Fe because previous research at this site identified significant relationships among redox, Fe and P availability [*Chacon et al.*, 2006; *Liptzin and Silver*, 2009].

2.5. Trace Gas Measurements

[13] We measured CO_2 fluxes on a weekly basis in all 30 plots using the Li-Cor LI-6400 Soil Respiration System (Li-Cor Biosciences, Lincoln, NE, USA). We consistently sampled during the morning hours to control for time of day. On days when there was rainfall, we waited 30 min before sampling CO_2 emissions once the rain stopped. On days when rainfall persisted for more than 20 min, we sampled CO_2 the following day. We randomly selected one of the three remaining quadrants for initial CO_2 sampling (excluding the quadrant designated for destructive soil sampling). After the initial sampling, we followed a clockwise rotation for each subsequent collection to minimize any sampling bias within the shelter. We began CO_2 measurements one month prior to throughfall exclusion to quantify background fluxes and continued measurements three months after the shelters were removed (April 29 through November 18) to determine if throughfall exclusion had lasting effects. Soil collars for the LI-6400 were installed a minimum of 30 min prior to CO_2 measurements. The collars were removed following sampling to avoid artifacts from permanent chamber bases [*Varner et al.*, 2003].

[14] The soil-atmosphere exchange of N_2O and CH_4 was estimated in each plot using a standard and well-tested static flux chamber method [*Davidson*, 1993; *Keller et al.*, 1993; *Livingston et al.*, 2005; *Silver et al.*, 2005], rotating quadrats as above. Chambers consisted of a polyvinyl chloride (PVC) ring (25.4 cm diameter × 20 cm height) and a vented PVC cover. The PVC rings were pushed into the soil to a depth of 2–3 cm and a minimum of 30 min prior to sampling. We re-deployed the chambers during each field campaign to avoid artifacts from permanent chamber bases [*Varner et al.*, 2003]. We controlled for time of day and the timing of

Table 2. Mean Treatment Differences in Throughfall and Soil Characteristics During the Exclusion Period (±S.E.; n = 5 Unless Otherwise Specified)[a]

		Forest Site		
Variable	Treatment	Ridge	Slope	Valley
Throughfall (mm)	control	$463 \pm 46_x$	$577 \pm 81_x$	$512 \pm 150_x$
	exclusion	577 ± 81	393 ± 65	453 ± 65
Throughfall N (mg N/L)	–	$0.70 \pm 0.11_x$	$0.75 \pm 0.16_x$	$2.79 \pm 0.59_y$
Throughfall P (mg P/L)	–	$0.02 \pm 0.005_x$	$0.02 \pm 0.006_x$	$0.23 \pm 0.05_y$
Soil pH (in KCl)	control	$3.8 \pm 0.04_x$	$3.9 \pm 0.04_y$	$4.1 \pm 0.05_z$
	exclusion	3.7 ± 0.02*	3.8 ± 0.05*	4.0 ± 0.07*
Exchangeable Fe (μg Fe/g)	control	$3364 \pm 83_x$	$2552 \pm 86_y$	$805 \pm 42_z$
	exclusion	2738 ± 87*	2552 ± 63	788 ± 50*
Exchangeable P (μg P/g)	control	$10.2 \pm 0.20_x$	$8.9 \pm 0.20_y$	$11.6 \pm 0.4_z$
	exclusion	9.2 ± 0.30*	8.4 ± 0.20*	11.7 ± 0.4
Inorganic NO_3^- (μg N/g)	control	$0.19 \pm 0.03_x$	$0.16 \pm 0.02_x$	$1.29 \pm 0.08_y$
	exclusion	0.20 ± 0.02	0.16 ± 0.02	1.38 ± 0.28
Inorganic NH_4^+ (μg N/g)	control	$0.77 \pm 0.12_x$	$1.12 \pm 0.32_x$	$1.30 \pm 0.16_y$
	exclusion	0.84 ± 0.13	0.81 ± 0.12	2.15 ± 0.23*
Inorganic NO_3^-:NH_4^+	control	$0.61 \pm 0.25_x$	$0.34 \pm 0.09_x$	$1.35 \pm 0.17_y$
	exclusion	0.45 ± 0.13	0.28 ± 0.07	0.71 ± 0.15*
CO_2 emission (μmol/m^2/s)	control	$6.71 \pm 0.44_x$	$5.89 \pm 0.43_x$	$6.80 \pm 0.43_y$
	exclusion	4.41 ± 0.32*	4.26 ± 0.18*	6.05 ± 0.23
CH_4 flux (ng C/cm^2/hr)	control	$-3.58 \pm 0.85_x$	$-1.57 \pm 1.15_x$	$-0.46 \pm 0.20_x$
	exclusion	-2.94 ± 1.43	-2.24 ± 1.11	-2.52 ± 0.63*
N_2O flux (ng N/cm^2/hr)	control	$0.03 \pm 0.12_x$	$-0.10 \pm 0.23_x$	$3.08 \pm 0.91_y$
	exclusion	-1.19 ± 0.50*	-1.16 ± 0.58	-1.28 ± 0.62*

[a] Subscript letters indicate significant differences among forest sites; asterisk indicates significant differences between treatments ($P < 0.05$). Throughfall N and P were conducted on a composite sample. As such, treatment differences were not analyzed for throughfall N and P.

rainfall using the same protocol as for soil CO_2 emissions (discussed above). N_2O and CH_4 samples were collected from all 30 plots two weeks prior to shelter installation. Subsequent gas samples were collected every two weeks. We repeated this collection regime for the three-month duration of the drought treatment as well as for three months post-treatment for a total of 12 collection dates. For each collection date five 30 mL air samples per plot were collected with an air-tight syringe over a 40 min period (t = 0, 5, 15, 25, 40 min) and were injected into pre-evacuated 20 mL glass vials fitted with Geo-Microbial septa (GMT, Ochelata, OK, USA). Three replicates for each standard gas (CH_4, N_2O and CO_2) were also injected into evacuated vials on each collection date to test for effects of storage and shipping on sample quality. Vials were shipped to University of California-Berkeley where they were analyzed within six months of sample collection by gas chromatography (GC) on a Shimadzu GC-14A (Shimadzu Scientific Inc., Columbia, MD, USA), equipped with a Porpak-Q column, using a flame ionization detector (FID) for CH_4 detection, and an electron capture detector (ECD) for N_2O detection. Methane and N_2O fluxes were calculated from the concentration change over time, and were determined using an exponential curve-fitting procedure (iterative model) described by *Matthias et al.* [1978]). Fluxes were considered to be zero when the relationship between time and concentration was not significant at p = 0.05.

2.6. Statistical Analyses

[15] We analyzed soil moisture, temperature, trace gas fluxes (CO_2, CH_4 and N_2O), soil pH, and soil nutrient concentrations for a response to soil drying using repeated measures analysis of variance (ANOVA; Proc Mixed Repeated in SAS; SAS for Windows V8.0, 2002, SAS Institute [*Littell et al.*, 1998]). We used this analysis to determine whether there were significant differences among the three topographic positions and if there was a broad treatment effect across all sites. We used a post-hoc test (Tukey-Duncan) to determine where significant differences occurred. A repeated measures ANOVA blocked by topographic zone (ridge, slope, valley) was used to determine whether there was a significant treatment effect within each of the study sites. If the homogeneity of variance assumption was not met, we log transformed the data, which successfully corrected this problem in all instances. We used regression analyses to determine relationships between mean trace gas fluxes (averaged by plot over exclusion period, n = 30) and mean soil characteristics (e.g., gravimetric soil moisture, temperature, pH, as well as soil N and P; averaged by plot over exclusion period, n = 30). All regressions were performed using SigmaPlot 10 (SigmaPlot for Windows, v. 7.101, 2001, SPSS Inc.).

[16] We calculated the mean treatment effect for trace gas fluxes as the percent difference between the treatment and control throughout the entire study period (exclusion and non-exclusion). The total trace gas fluxes were calculated by interpolating data from each plot over the study period and then averaging by treatment and topographic zone. We converted the total CH_4 and N_2O emissions to CO_2 equivalents by multiplying total CH_4 and N_2O emissions by their respective 100-year warming potentials (25 and 298, respectively [*Forster et al.*, 2007]). Statistical significance was determined as $P < 0.05$ unless otherwise noted. Values reported in the text are means ± 1 standard error.

3. Results

3.1. Throughfall and Throughfall Nutrients

[17] There was no significant difference in the amount of throughfall among the three topographic zones (df = 2, 27,

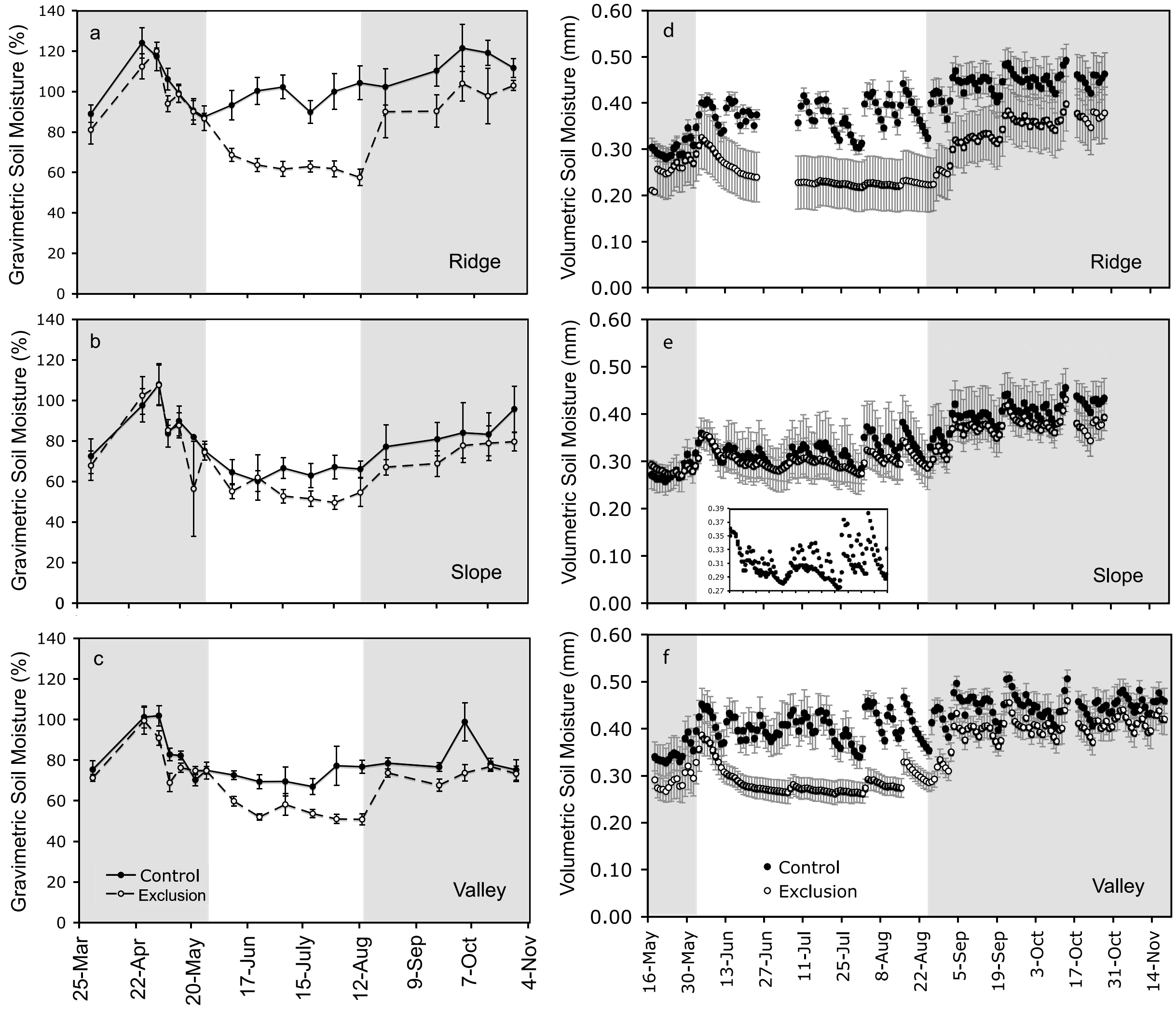

Figure 1. Mean gravimetric soil moisture (±S.E., 0–10 cm, n = 5) of the control and exclusion plots for the (a) ridge, (b) slope and (c) valley sites and (d–f) mean volumetric soil moisture (±S.E., 0–30 cm, n = 3) for same sites and periods. Throughfall exclusion significantly reduced gravimetric soil moisture (16–36%) and volumetric soil moisture (5–36%) in all forest sites ($P < 0.001$). The additional inset in Figure 1e (slope volumetric soil moisture) shows the same data on a smaller scale. The un-shaded areas represent when the shelters were in place.

$F = 1.02$, $P > 0.05$); however, the concentrations of total dissolved N and P in throughfall were 4 and 11 times higher, respectively, in the valley than in the slope and ridge sites (Table 2; df = 2, 27, $F = 15.43$, $P < 0.0001$ [N]; df = 2, 27, $F = 19.5$, $P < 0.001$ [P]). During the treatment period, we excluded a total of 577 ± 81, 393 ± 65 mm and 453 ± 65, of throughfall from the ridge, slope and valley sites, respectively (Table 1). This was the equivalent of excluding 22 - 32% of the annual throughfall, which is within the range of rainfall reductions predicted for this region [*Meehl et al.*, 2006].

3.2. Soil Moisture

[18] Gravimetric soil moisture (0–10 cm depth) varied significantly with topography, and was significantly higher in ridge sites than in valley or slope sites (Mean of 102 ± 3%, 83 ± 2%, 89 ± 3%, respectively; df = 2, 161; $F = 37.55$; $P < 0.0001$). These site differences persisted throughout the duration of the study. In contrast the valley site had significantly higher volumetric soil moisture (0–30 cm depth) than either the ridge or slope sites (df = 2, 1328, $F = 62$, $P < 0.0001$).

[19] There were no significant differences in either volumetric or gravimetric soil moisture among the control and treatment plots within topographic zones prior to shelter installation. Over the 3-month exclusion period, gravimetric soil moisture declined by 16 to 36% in the treatment plots (df = 1, 161; $F = 151.09$; $P < 0.0001$, Figures 1a–1c), and volumetric soil moisture decreased by 5 to 36% (df = 1, 1328, $F = 819.11$; $P < 0.0001$, Figures 1d–1f). Gravimetric soil moisture quickly recovered in the valley when the shelters were removed, but remained 12 to 14% lower than controls in the slope and ridge sites, respectively, three months later (df = 2, 140, $t = 2.04$, $P < 0.05$ [slope]; df = 2, 140, $t = 3.31$, $P < 0.01$ [ridge]). Volumetric soil moisture also remained suppressed in ridge sites during this period

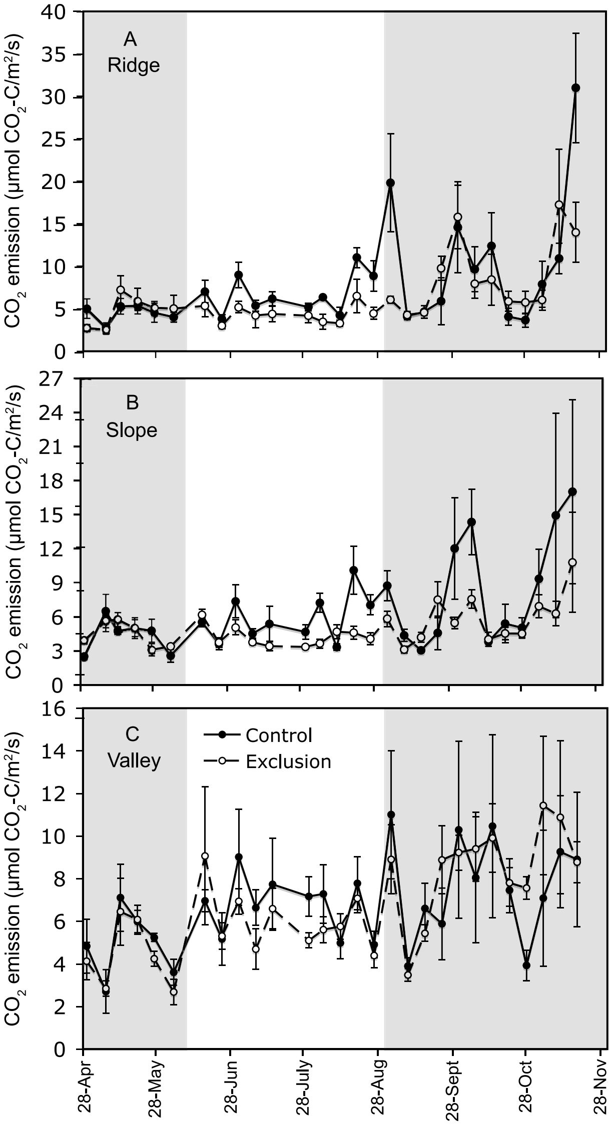

Figure 2. Mean weekly CO_2 efflux (±S.E.) from control and exclusion plots for the (a) ridge, (b) slope and (c) valley sites. The un-shaded areas represent when the shelters were in place. There was no significant difference between the control and exclusion sites in the valley forest; however, total CO_2 emissions from the exclusion plots was 19% and 26% lower than the controls in the ridge and slope forest sites, respectively.

(df = 2, 780, F = 12.54, P < 0.0001 [ridge]), but recovered in both the valley and slope sites.

3.3. Soil Temperature

[20] There were no significant differences in soil temperature among the three topographic zones, nor were there significant pre-treatment differences in soil temperature between the control and treatment plots prior to shelter installation. Mean daily soil temperature ranged from 21 to 27°C throughout the study. Soil temperature was slightly higher (0.1°C) in the ridge (df = 1, 71; t = 4.88; P < 0.05) and valley control plots (df = 1,67; t = 5.16; P < 0.05) during the exclusion period and up to three months after they were removed, suggesting it was not a shading effect.

3.4. Soil Chemical Properties

[21] Soil pH and exchangeable Fe and P differed significantly by topography (df = 2, 140, F = 87.35, P < 0.0001 [pH]; df = 2, 169, F = 587.66, P < 0.0001 [Fe]; df = 2, 169, F = 68.84, P < 0.0001 [P]). Soils became more basic and exchangeable Fe declined from ridge to valley (Table 2). Exchangeable P was highest in the valley followed by the ridge and the slope sites (Table 2). Inorganic N was significantly higher in the valley than both the ridge and slope sites (df = 2, 140, F = 61.95 P < 0.0001[NO_3^-]; df = 2, 140, F = 13.25, P < 0.0001 [NH_4^+]). The same was true of the NO_3^-:NH_4^+ ratio, with significantly higher NO_3^-:NH_4^+ in the valley than in the ridge and slope forest sites (df = 2, 140, F = 11.46, P < 0.0001).

[22] There were no pre-treatment differences between the control and treatment plots for any of the soil nutrients measured (N, P, Fe) or pH (P > 0.05). Soil pH was significantly lower in the treatment plots during throughfall exclusion relative to the controls in all forest sites (Table 2; average reduction of 0.1; df = 1, 140; F = 12.75; P < 0.001). Exchangeable Fe concentrations were significantly lower in the exclusion plots in the valley and the ridge forest sites, while exchangeable P decreased significantly in ridge and slope sites (df = 2, 169, F = 13.78, P < 0.001 [Fe]; df = 2, 169, F = 10.87, P < 0.01 [P]; Table 2). There was a strong positive correlation between exchangeable Fe and P concentrations for both the valley (r^2 = 0.62, P < 0.01) and slope sites (r^2 = 0.57, P < 0.01), but not the ridge. There was no significant difference in either NO_3^- or NH_4^+ between the control and exclusion plots of the ridge and slope forest sites; however, NH_4^+ was significantly higher in the exclusion plots than in the controls for the valley forest (df = 1, 120, t = −3.66, P = 0.004) resulting in a significantly lower NO_3^-:NH_4^+ in the exclusion plots relative to the controls in this forest (df = 1, 120, t = 2.93, P = 0.004).

3.5. Trace Gases

[23] Topography had a significant effect on soil CO_2 emissions with higher CO_2 effluxes in the valley than in the other zones (Figure 2; df = 2, 284; F = 11.02; P < 0.0001). There were no statistically significant differences in CO_2 emissions between treatment and control plots within topographic zones prior to shelter installation. During the exclusion period, soil CO_2 efflux was on average 28% lower in the exclusion plots relative to the controls in the slope sites (df = 1, 80, F = 19.04, P < 0.0001) and 30% lower on the ridge (df = 1, 80, F = 24.01, P < 0.0001; Figure 2). Over the course of the study, total CO_2 efflux was reduced by 19% and 26% in the slope and ridge sites, respectively. A similar but non-significant trend was seen in the valley forest. Soil CO_2 emissions in the exclusion plots recovered quickly to control levels when the shelters were removed.

[24] Methane emissions did not differ significantly with topography (df = 2, 169, F = 1.87, P > 0.05). We measured average net CH_4 consumption throughout the study (Figure 3). There were no pre-treatment differences in CH_4 fluxes between treatment and controls. During the experimental drought, CH_4 consumption was higher in the exclusion plots than the controls in the valley (Figure 3; df = 1,

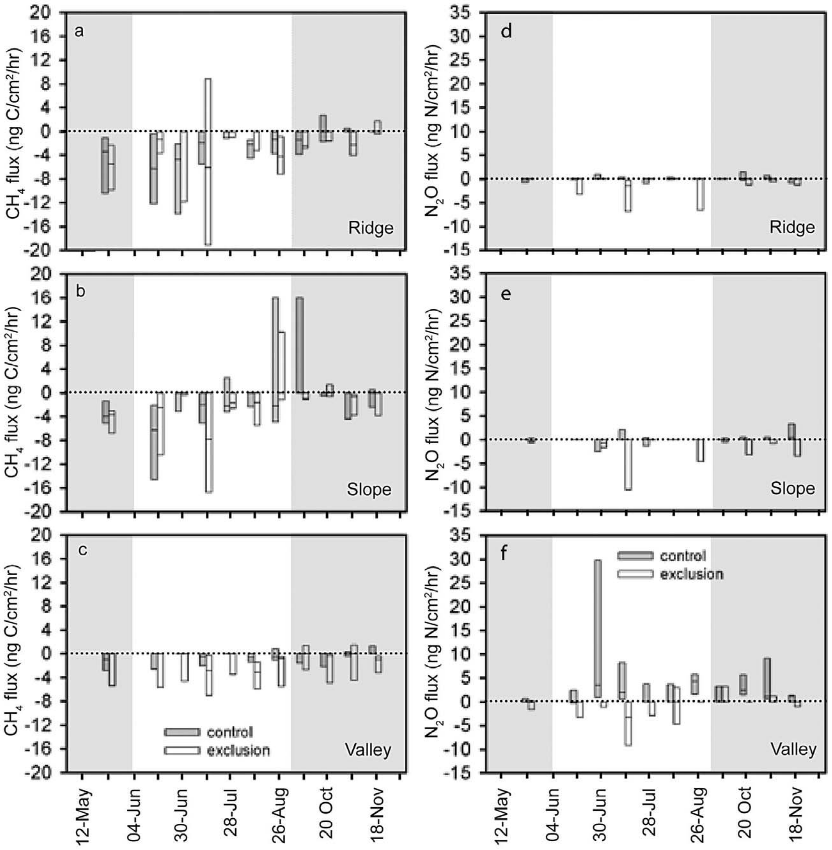

Figure 3. Box plots of bi-weekly (a–c) CH_4 and (d–f) N_2O fluxes from the control and exclusion plots of the ridge (Figures 3a and 3d), slope (Figures 3b and 3e) and valley (Figures 3c and 3f) sites (line = mean). The CH_4 fluxes from the exclusion plots were 480% lower than that of the controls in the valley forest site. The experimental drought had no effect on CH_4 fluxes in the slope and ridge sites. The N_2O fluxes were reduced by 108% in the valley and by 1788% in the ridge. There was no effect of drought on N_2O fluxes from the slope forest site. The un-shaded areas represent when the shelters were in place.

48; F = 8.65, $P < 0.01$), increasing CH_4 uptake by a total of 480% relative to controls over the course of the study. There was no significant effect of throughfall exclusion on CH_4 emissions on ridge (df = 1, 48, F = 0.14, $P > 0.05$) or slope forest (df = 1, 49, F = 0.22, $P > 0.05$). Net CH_4 consumption in the exclusion plots of the valley forest quickly re-equilibrated to values similar to the controls when the shelters were removed (df = 1, 26, F = 3.03, $P > 0.05$). Overall, 6% of measured fluxes across all time points and plots were positive, 46% had no significant flux and 48% were negative.

[25] As with CO_2, the N_2O fluxes from the valley were significantly higher than both the ridge and slope sites (Figure 3; df = 2, 169; F = 2.87; P = 0.05). There were no pre-treatment differences in N_2O fluxes between treatment and control plots for any topographic zone. The experimental drought significantly lowered N_2O fluxes in the valley and ridge sites, but not the slope sites (df = 1, 48; F = 4.42; $P < 0.05$ [valley]; df = 1, 48; F = 5.97; $P < 0.05$ [ridge]; df = 1, 48; F = 3.05, $P > 0.05$ [slope]). The total N_2O fluxes from the sheltered valley plots were 108% lower than the controls and 1788% lower in the ridge over the course of the study, and in both sites the throughfall exclusion plots were net sinks of N_2O. The N_2O fluxes in the valley site remained suppressed up to three months after the shelters were removed (df = 1, 35; F = 6.40; $P < 0.05$). Overall, a total of 15% of the measured N_2O fluxes across all plots and time points were negative, 67% had no significant fluxes, and 18% of the values were positive. Of the negative values observed, 82% were from the exclusion plots.

3.6. Relationships Between Mean Trace Gas Emissions and Soil Characteristics

[26] Mean soil CO_2 and N_2O emissions from all sites (n = 30) were positively related to both exchangeable P (Table 3) and the NO_3^-:NH_4^+ ratio of the soil during the three-month treatment period. Mean CH_4 fluxes were not explained by any of the variables measured; however, when we restricted the analysis to plots with net CH_4 consumption (n = 26 of 30), mean CH_4 uptake was positively related to exchangeable P, NO_3^-, and NO_3^-:NH_4^+ and were negatively related to exchangeable Fe (Table 3). We found a nonlinear relationship between volumetric soil moisture and mean N_2O efflux (Table 3), but no relationship between volumetric soil moisture and CO_2 and CH_4 emissions. There was no significant relationship between mean trace gas emissions

Table 3. Regressions Between Soil Variables and Mean Trace Gas Fluxes (Values = R^2)[a]

Variable	Mean CO_2 Emission (μmol/m^2/s)	Mean CH_4 Emission (ng C/cm^2/hr)	Mean CH_4 Consumption[b] (ng C/cm^2/hr)	Mean N_2O Flux[c] (ng N/cm^2/hr)
Exchangeable P (mg P/g)	0.25**	N.S.	0.18*	0.26**
NO_3^- (mg N/g)	N.S.	N.S.	0.33**	0.26**
NH_4^+ (mg N/g)	N.S.	N.S.	N.S.	N.S.
NO_3:NH_4	0.22**	N.S.	0.34**	0.36***
Fe (mg Fe/g)	N.S.	N.S.	−0.25**	N.S.
Soil pH (in KCl)	N.S.	N.S.	N.S.	N.S.
Volumetric soil moisture[d]	N.S.	N.S.	N.S.	0.68***[e]
Gravimetric soil moisture (%)	N.S.	N.S.	N.S.	0.53* (ridge), 0.53* (valley)

[a] Asterisk indicates $P < 0.05$, two asterisks indicate $P < 0.01$, and three asterisks indicate $P < 0.001$. Means calculated as the average for each plot over the exclusion period (n = 30). Negative R^2 values indicate a negative relationship.

[b] Positive CH_4 fluxes were excluded from the analysis (n = 26).

[c] Includes net N_2O emissions and consumption.

[d] Volumetric soil moisture was measured in a subset of plots (n = 18).

[e] U-shape curvilinear relationship ($f = y0 + a*x + b*x^2$; y0 = 22, a = −166, b = 92).

and gravimetric soil moisture, soil pH, or NH_4^+ concentrations (Table 3).

4. Discussion

4.1. Effects of Drought on Soil Moisture and Temperature

[27] Although initial gravimetric soil moisture differed among topographic zones, throughfall exclusion reduced gravimetric soil moisture to a similar level regardless of topographic position (~60% gravimetric soil moisture, 0–10 cm). Hence, physical factors such as soil mineralogy that are likely to be consistent at ecosystem or landscape scales may outweigh differences derived from topography and plant community composition as determinants of soil drying potential. The ridge sites had the highest initial and background gravimetric soil moisture content and experienced the greatest decline in soil moisture during the experiment. Ridge tops tend to have higher concentrations of soil organic matter than slopes and valleys (Table 1), which increases water holding capacity [*Hudson*, 1994]. Throughfall exclusion also reduced volumetric soil moisture in all three topographic zones. Volumetric soil moisture (0–30 cm depth) was less sensitive to throughfall exclusion than gravimetric soil moisture (0–10 cm depth). This may be related to subsurface lateral movement of water along slopes. Gravimetric and volumetric soil moisture returned to control levels in the valley sites when the shelters were removed. In contrast, gravimetric soil moisture remained depressed in the slope sites and both volumetric and gravimetric soil moisture remained depressed in the ridge sites. The reduction of soil water content could have increased soil water repellency in these soils. Subsequent uneven penetration of rainwater may cause a long-term reduction of soil water availability in these sites [*Goebel et al.*, 2011].

[28] We observed a small difference in soil temperature of ~0.1°C in the treatment plots of all three sites, possibly driven by changes in evaporative cooling. However, the effect persisted for three months after the shelters were removed, which could indicate that the temperature differences are unrelated to the shelters. Nevertheless, the temperature difference we observed between the exclusion and control plots are similar to that observed in a drought experiment in a Brazilian tropical forest [*Davidson et al.*, 2004].

4.2. Effects of Drought on Soil Chemical Properties

[29] Nutrient cycling can be very dynamic in humid tropical forests and is likely to be sensitive to precipitation changes [*Silver et al.*, 1996, 2000]. One of the important drivers of tropical forest biogeochemistry is redox potential [*Silver et al.*, 1999; *Schuur and Matson*, 2001]. Drought is likely to increase soil redox potential, and thus favor aerobic processes such as nitrification and Fe oxidation. In this study we found a positive correlation between exchangeable Fe and P across all treatments. In Fe-rich highly weathered soils, Fe oxide and hydroxide minerals readily bind with P, removing it from the soil exchange complex and contributing to P limitation of plants and microbes [*Vitousek and Sanford*, 1986]. The affinity of reduced Fe for P is lower than more oxidized forms, which can lead to higher soil P availability under low or fluctuating redox conditions [*Chacon et al.*, 2006; *Liptzin and Silver*, 2009]. In this study, soil drying led to a significant reduction in exchangeable P in both the ridge and slope sites; however, there was no significant effect of soil drying on exchangeable P in the valley site. The valley site was characterized by lower exchangeable Fe concentration, likely due to enhanced leaching of reduced forms associated with frequent low redox events [*Silver et al.*, 1994, 1999]. The lower concentrations of exchangeable Fe in the valley site relative to the ridge and slope sites may have minimized the effect of drought on soil P availability [*Chacon et al.*, 2006; *Liptzin and Silver*, 2009]. Evaluating the specific forms of Fe and their response to drought may enable further insight into Fe-P dynamics in tropical soils.

[30] The experimental drought significantly increased NH_4^+ concentrations in the exclusion plots of the valley, decreasing the ratio of NO_3^-:NH_4^+. Changes in the proportion of different soil N pools has been shown to affect a variety of ecosystem processes, such as decomposition rates, plant cover and ultimately C cycling [*Austin et al.*, 2006]. That the drought effect on NH_4^+ concentrations was limited to the valley soils may be the result of increased N mineralization rates as redox increased with drying. Low redox potential, which frequently occurs in valleys within the LEF [*Liptzin et al.*, 2010; *Silver et al.*, 1999], can decrease decomposition and associated N mineralization rates [*Day and Megonigal*, 1993].

[31] Soil acidity plays an important role in tropical forest soils that are dominated by variable charge clays. In these

soils, increasing acidity can decrease cation exchange capacity and lead to nutrient losses [*Sollins and Radulovich*, 1988]. Despite strong initial differences in pH among the three sites, drought led to a small, yet similar increase in the acidity of the soil in all topographic zones (Table 2). Increased Fe oxidation with drying is one potential mechanism for the lower pH observed. In addition to potential nutrient cycling effects, soil pH is known to influence enzyme activation energies, the binding of organic matter to soil, and consequently decomposition of soil organic C and nutrient mineralization [*Focht*, 1974; *Kleber*, 2010; *Sollins and Radulovich*, 1988; *Tietema et al.*, 1992].

4.3. Effects of Drought on Trace Gas Emissions

[32] One of the primary goals of this research was to determine if seasonal drought would result in feedbacks to climate change in humid tropical forests. In this study, soil CO_2 emissions were lower in the exclusion plots of both the ridge and slope sites (30% and 28% reduction, respectively). Ridges and slopes are the dominant landforms of this region and account for over 80% of the land area [*Scatena et al.*, 1993]. Mean soil CO_2 emissions were significantly positively related to both exchangeable P and NO_3^-:NH_4^+. Lower CO_2 efflux in the exclusion plots may result from lower soil P availability in the upper topographic zones. Previous research linking P availability and CO_2 emissions in tropical forests further supports this theory [*Cleveland and Townsend*, 2006].

[33] Control plots in all three topographic zones were a net sink for CH_4 throughout the study, with no significant differences among sites. Drought conditions increased the CH_4 sink by 480% in the valley relative to the controls, while drought had no effect on CH_4 fluxes in the slope and ridge sites. The observed increase in net CH_4 consumption with soil drying in the valley is likely to result from decreased CH_4 production and/or increased CH_4 oxidation [*Teh et al.*, 2005] related to increased redox potential with throughfall exclusion. Although these forests were in general net sinks of CH_4, some of the plots demonstrated net CH_4 emissions. When we limited our analyses to plots with net CH_4 consumption we found significant positive relationships with NO_3^- and NO_3^-:NH_4^+. The positive relationship between CH_4 consumption and NO_3^- is interesting as high mineral N availability has been linked to the inhibition of CH_4 oxidation [*Steudler et al.*, 1989]. Nitrogen limitation of methanotrophy has been reported in the literature [*Bodelier and Laanbroek*, 2004], but would appear unlikely in this relatively N-rich forest. While we can't rule out autocorrelation of methane uptake with N, Fe, C and P availability these apparent relationships have not been previously explored in tropical soils and warrant further exploration.

[34] Tropical forests are the largest natural source of N_2O [*Matson and Vitousek*, 1990]. The valley had the highest N_2O fluxes of the three forest sites. The high concentrations of N and lower redox potential of this forest relative to the other two forest sites are likely drivers of the higher N_2O emissions [*Silver et al.*, 1999]. During the experimental drought, the exclusion plots of the ridge and valley sites became significant N_2O sinks. We found a similar though non-significant trend in the slope site. The mechanism driving net N_2O consumption in soils is not well understood; however, net N_2O consumption has been reported in several temperate and tropical forests [*Butterbach-Bahl et al.*, 2002; *Chapuis-Lardy et al.*, 2007; *Goldberg and Gebauer*, 2009; *Goossens et al.*, 2001; *Verchot et al.*, 1999] and has been demonstrated in laboratory experiments [*Blackmer and Bremner*, 1976]. We found a u-shaped curvilinear relationship between N_2O fluxes and volumetric soil moisture, and a linear relationship between gravimetric soil moisture and N_2O fluxes in the valley and ridge sites, but not the slope (Table 3). We also found positive relationships between N_2O emissions and NO_3^-:NH_4^+. These findings suggest that soil moisture controls on N transformations in the soil (e.g., mineralization, nitrification and denitrification) could be playing an important role in determining N_2O emissions [*Holtgrieve et al.*, 2006]. The effect of throughfall exclusion on N_2O fluxes persisted in the valley forest 3-months following re-establishment of throughfall even though soil moisture in the exclusion plots returned to control levels. The persistent effect of drought on N_2O fluxes in this valley may be due to a persisting reduction in the ratio of NO_3^-:NH_4^+, which unlike the other two forest sites, was significantly reduced in response to drought.

4.4. Comparison With Other Tropical Throughfall Exclusion Experiments

[35] Throughfall exclusion experiments have been conducted in five other tropical forests that span a wide range in natural precipitation inputs and rainfall regimes. These drought experiments have varied significantly in size, intensity and duration (Table 4). In contrast to prior throughfall exclusion experiments, we evaluated short-term, seasonal drought (3-months), which is a likely scenario in tropical forests with climate change. All rainfall manipulation experiments introduce artifacts that can affect the magnitude of results. Here, the small size of shelters and lack of trenching likely increased the probability that roots were able to access water and nutrients from outside of the exclusion treatment. As such, the drought effects we observed are likely primarily microbial in nature. Thus the overall net effect of drought may be less severe than what would be observed in "true" drought conditions when both roots and microbes experience moisture stress. The design used here, however, maintained root-microbe interactions and did not introduce anomalous C and nutrient inputs associated with trenching [*Silver et al.*, 2005]. The decrease in CO_2 efflux during the 3-month drought was equivalent to a reduction of 79 and 71 g CO_2-C m^{-2}, and a 16 and 25% overall reduction in CO_2 emissions. The responses of CO_2 emissions to throughfall exclusion have been highly variable among tropical forest sites, ranging from a reduction to a net increase in emissions (Table 4). These differences in the CO_2 response have been attributed to several factors: differences in soil texture that led to deeper rooting [*Davidson et al.*, 2004, 2008], differential response of root, litter and soil organic matter to drought [*Metcalfe et al.*, 2007; *van Straaten et al.*, 2011], increase in the concentration of dissolved organic C [*Cleveland et al.*, 2010], and soil nutrient availability [this study]. In each of these experiments, the intensity and duration of throughfall exclusion has varied. Future work should focus on both the relative importance of edaphic factors as well as temporal scale.

[36] The increase in CH_4 consumption over the course of the 3-month drought in the valley is equivalent to 36 mg

Table 4. Comparison of Tropical Forest Throughfall Exclusion Experiments[a]

Forest Location	Annual Rainfall (mm)	Plot Size (No. Exp. Reps)	Months of Exclusion	No. Year Repeated	CO_2 Response	CH_4 Response	N_2O Response	Citation
Fazenda Vitoria, Brazil	1800	100 m^2 (1)	12	4	−16%	171%	−25%	*Cattânio et al.* [2002]
Tapajos National Forest, Brazil	2000	1 ha (1)	6	5	no effect	−206%	−33%	*Davidson et al.* [2004, 2008]
Caxiuanã National Forest, Brazil	2300	1 ha (1)	12[b]	1	−26%	NA	NA	*Doff Sotta et al.* [2007]
Caxiuanã National Forest, Brazil	2500	0.25 ha (1)	12[b]	4	no effect[c]	NA	NA	*Metcalfe et al.* [2007]
Central Sulawesi, Indonesia	2900	0.16 ha (3)	12[b]	2	−23%[d], −48%[e]	NA	NA	*van Straaten et al.* [2011]
LEF, Puerto Rico: Ridge	3500	1.54 m^2 (5)	3	1	−19%	no effect	−1788%	this study
LEF, Puerto Rico: Slope	3500	1.54 m^2 (5)	3	1	−26%	no effect	no effect	this study
LEF, Puerto Rico: Valley	3500	1.54 m^2 (5)	3	1	no effect	−480%	−108%	this study
Osa Peninsula, Costa Rica	5000	5.76 m^2 (10)	12[b]	1	25%	NA	35%	*Cleveland et al.* [2010] and *Wieder et al.* [2011]

[a] For comparison purposes, the responses reported in this table are the mean percent difference between control and exclusion plots over the entire study period (e.g., drought and non-drought).

[b] Partial throughfall exclusion experiment (e.g., 50%).

[c] When total soil respiration was partitioned, soil organic matter and litter respiration declined in response to drought and root respiration increased.

[d] 9 months of 50% exclusion.

[e] 15 months of 80% exclusion.

CH_4-C m^{-2} or 1 mg CO_2-equiv/m^2 assuming a global warming equivalent of 25 over 100 years [*Forster et al.*, 2007]. A seasonal forest in Brazil found a net increase in CH_4 emissions in response to experimental drought [*Cattânio et al.*, 2002], while the Tapajos, Brazil found that drought increased CH_4 consumption by 200% [*Davidson et al.*, 2008]. Our results show that even within an ecosystem, patterns can vary widely, ranging from no net effect of drought on CH_4 fluxes to a 480% increase in consumption. The high variability in the response of CH_4 fluxes both within and among tropical forest sites reflects the high degree of spatial heterogeneity and complexity of biogeochemical cycling in tropical forest ecosystems. The diversity of CH_4 responses to drought could be attributed to a variety of factors, ranging from an increase in termite activity [*Cattânio et al.*, 2002] to variability in soil texture, soil redox, and the soil microbial community [*Teh et al.*, 2005], and as in our site, to variability in nutrients or C with topography. More research is needed to determine which factors are important in determining the direction of the CH_4 response to drought among tropical forest sites.

[37] The net N_2O consumed during the three-month experimental drought was equivalent to 24 and 17 mg N_2O-N m^{-2} (valley and ridge sites, respectively). The difference in N_2O fluxes between the control and exclusion plots amounted to 58 g CO_2-equiv m^{-2} (valley) and 6 g CO_2-equiv m^{-2} (ridge) assuming a global warming potential of N_2O of 298 over 100 years [*Forster et al.*, 2007]. Other throughfall exclusion experiments have also observed a negative effect of drought on N_2O emissions (Table 4). We are the first of these experiments to report net consumption of N_2O in response to drought in mature tropical forest. The net N_2O released from soils reflects both N_2O production and consumption. Typically, N_2O consumption in soils occurs in anaerobic microsites under low NO_3^- conditions [*Chapuis-Lardy et al.*, 2007]. In this experiment, throughfall exclusion dried the surface soils, but the deeper soils most likely remained saturated. Hence, we could be observing net N_2O consumption in the deeper, wet soil, facilitated by greater diffusion through the surface with drying. The positive relationship between N_2O emissions and NO_3^- demonstrates important links between N-availability and N_2O production versus consumption for this forest.

5. Conclusions

[38] Humid tropical forests are expected to experience increased frequency and intensity of drought [*Hulme and Viner*, 1998; *Meehl et al.*, 2006]. Short-term drought (3-months) decreased net trace gas emissions from three humid tropical forest sites in Puerto Rico that differed in topographic position (i.e., ridge, slope and valley). Exchangeable P was the best predictor of soil CO_2 emissions, while CH_4 consumption was predicted by NO_3^-:NH_4^+ in the soil. Both volumetric soil moisture and NO_3^-:NH_4^+ were strong predictors of N_2O fluxes. These findings suggest that site-specific factors strongly influence overall patterns in trace gasdynamics at an ecosystem scale. Our results contribute to a small but growing database on the response of tropical forest biogeochemistry to precipitation change (Table 4). These studies have been conducted at different scales and with different experimental approaches, limiting their comparability. Nevertheless, the wide range and apparently conflicting results reported thus far highlight the need to better account for the spatial variability and complexity of these ecosystems. The variability in the response of trace gas emissions to drought both within and among tropical forests sites is indicative of the high degree of heterogeneity of these systems.

[39] Our research shows that decreased rainfall in humid tropical forests could result in a negative feedback to climate via lowered CO_2 emissions and increased CH_4 and N_2O consumption by soils. Our results also highlight the complexity of biogeochemical cycling within and across tropical forests, and the need to incorporate that complexity in field, laboratory, and modeling experiments to better understand future patterns in C and nutrient cycling with climate change.

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