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Effects of an experimental drought and recovery on soil emissions of carbon dioxide, methane, nitrous oxide, and nitric oxide in a moist tropical forest

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Abstract

Changes in precipitation in the Amazon Basin resulting from regional deforestation, global warming, and El Niño events may affect emissions of carbon dioxide (CO_2), methane (CH_4), nitrous oxide (N_2O), and nitric oxide (NO) from soils. Changes in soil emissions of radiatively important gases could have feedback implications for regional and global climate. Here, we report the final results of a 5-year, large-scale (1 ha) throughfall exclusion experiment, followed by 1 year of recovery with natural throughfall, conducted in a mature evergreen forest near Santarém, Brazil. The exclusion manipulation lowered annual N_2O emissions in four out of five treatment years (a natural drought year being the exception), and then recovered during the first year after the drought treatment stopped. Similarly, consumption of atmospheric CH_4 increased under drought treatment, except during a natural drought year, and it also recovered to pretreatment values during the first year that natural throughfall was permitted back on the plot. No treatment effect was detected for NO emissions during the first 3 treatment years, but NO emissions increased in the fourth year under the extremely dry conditions of the exclusion plot during a natural drought. Surprisingly, there was no treatment effect on soil CO_2 efflux in any year. The drought treatment provoked significant tree mortality and reduced the allocation of C to stems, but allocation of C to foliage and roots were less affected. Taken together, these results suggest that the dominant effect of throughfall exclusion on soil processes during this 6-year period was on soil aeration conditions that transiently affected CH_4, N_2O, and NO production and consumption.

Keywords: Amazon Basin, Brazil, climate change, CH_4, CO_2, N_2O, nitrogen, NO, soil carbon

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Introduction

Some climate models predict that the drought episodes and seasonal water deficits in the eastern and southern Amazon Basin may be more common and more severe as global climatic change proceeds during the 21st century (Cox *et al*., 2004; Li *et al*., 2006; Malhi *et al*., 2008). Global warming may also increase the intensity of El Niño Southern Oscillation (ENSO) events (Hansen *et al*., 2006), which cause severe drought in the eastern Amazon Basin (Nepstad *et al*., 1999). In 1998, a particularly severe El Niño episode was associated with prolonged drought in eastern and northern Amazonia (Nepstad *et al*., 1999, 2004; Alencar *et al*., 2006). In 2005, warming of the tropical North Atlantic triggered the worst drought in 40 years across the southern Amazon Basin (Brown *et al*., 2006; Aragão *et al*., 2007). Tropical rainfall inhibition by smoke (Rosenfeld, 1999; Andreae *et al*., 2004) may exacerbate this general drying trend in this moist tropical forest region.

Reduced precipitation may have important feedback effects on climate change by altering soil emissions of radiatively important gases, such as CO_2, CH_4, N_2O

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(Forster *et al*., 2007), and NO (NO is not, itself, a greenhouse gas, but it is a precursor to the formation of tropospheric ozone, which is a greenhouse gas; Lammel & Graßl, 1995). Upland forest soils of the tropics are known to be important sources of N_2O (Matson & Vitousek, 1990) and NO (Davidson & Kingerlee, 1997) and sinks for CH_4 (Potter *et al*., 1996). Both primary productivity and respiration are high in many tropical ecosystems, resulting in large emissions of CO_2 from soils (Davidson *et al*., 2000b).

Variation in precipitation influences trace gas emissions by affecting soil water content and soil aeration, which, in turn, affects microbial processes of production and consumption of these trace gases (Davidson & Schimel, 1995; Davidson *et al*., 2000a). Climate change can also alter root turnover, litterfall, decomposition, and mineralization, which would, in turn, affect the availability of carbon and nitrogen substrates for trace gas production.

We previously reported on the first 3 treatment years and 2 pretreatment years of trace gas flux measurements in a large-scale (1 ha) throughfall experiment manipulation conducted in the Tapajós National Forest, near Santarém, Pará, Brazil (Davidson *et al*., 2004). Here, we report the final results of the entire throughfall exclusion manipulation experiment, including pretreatment, 5 years of throughfall exclusion, and 1 year of posttreatment recovery. The previously reported results for effects on NO, N_2O, CH_4, and CO_2 are generally reconfirmed, although a natural drought that occurred during the fourth year of the treatment yielded novel results. Finally, we report on the first year of recovery after permitting throughfall to return at natural rates in the exclusion plot.

Materials and methods

The study area and methods employed here are the same as those described by Davidson *et al*. (2004). We present an abbreviated description here.

Study area

The Tapajós National Forest, located in east central Amazonia (2.8968°S, 54.9519°W), receives 600–3000 mm of rain each year, with a mean of 2000 mm, most of which falls during the wet season from January to June (Fig. 1a). The forest is situated on a terrace of Tertiary sediments capped by the Belterra Clay Formation (Clapperton, 1993). The Oxisol soil (Haplustox) is acidic (pH 4–5), is dominated by kaolinite clay minerals (60–80% clay), and is free of hardpan or iron oxide concretions in the upper 12 m; the water table is more than 100 m deep. The forest has emergent trees up to 55 m in height, with a continuous canopy at approximately 30 m (Nepstad *et al*., 2002).

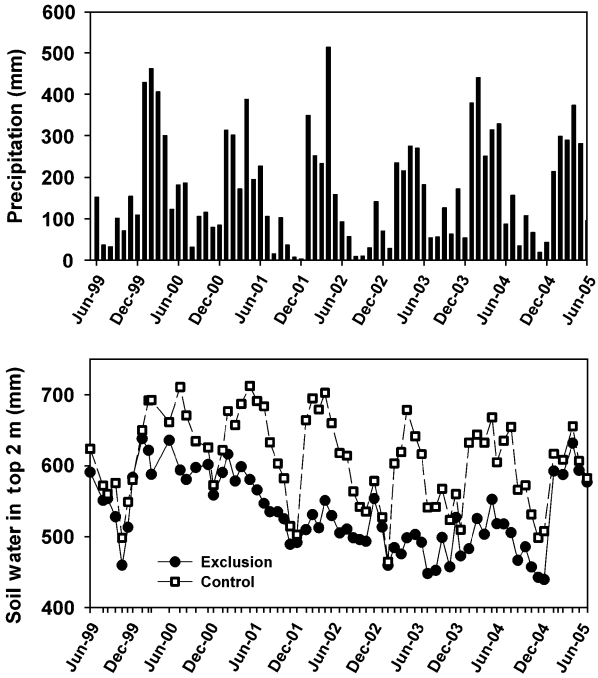

Fig. 1 Monthy precipitation (a) and volumetric water content of the top 2 m of soil (b). The throughfall exclusion treatment was applied during the rainy seasons of 2000–2004.

Experimental design

Two 1 ha plots were identified from an initial survey of 20 ha of forest. Details of site selection, research infrastructure, and the broad array of ecological measurements are available in other project publications (Nepstad *et al*., 2002, 2007; Oliveira *et al*., 2005; Brando *et al*., 2006).

A 1.5 m deep trench was excavated around the perimeter of the treatment plot to reduce the potential for lateral movement of soil water from the surrounding forest into the plot. A similar trench was excavated around the control plot to avoid the confounding of treatment and trenching effects. All measurements reported here were taken at least 20 m from the trench edge to guard against edge effects.

As with many large-scale ecosystem manipulations, such as the well-known watershed manipulations at Hubbard Brook, this experiment is prohibitively large and expensive to permit replication. Hence, the treatment design follows the methodology for unreplicated large-scale ecosystem manipulation experiments (Hurlbert, 1984). Before imposing the throughfall exclusion treatment, we first intercalibrated the two plots by

making measurements in each plot during an 18-month intercalibration period, beginning in September 1998. By determining differences between the two plots before and after rainfall exclusion, treatment effects are clearly identified when pretreatment similarities and differences between plots begin to diverge after the treatment begins.

Throughfall was partially excluded from the treatment plot during the rainy seasons of 2000 through 2004, using 5660 panels made of clear, PAR-transmitting greenhouse plastic mounted on wooden frames. The panels were removed during the dry season to reduce their influence on the forest floor. Only $\sim 1\%$ of solar radiation penetrates the forest canopy (Nepstad *et al.*, 1996), and panels change forest floor temperature by $< 0.2\,^{\circ}C$. The panels were flipped on their sides every 2 days to transfer accumulated litter onto the forest floor beneath. Each $3\,m \times 0.5\,m$ panel drained into a plastic-lined, wooden gutter that carried the water into the trench, which was also lined with plastic; the gutters served as catwalks for various measurements and panel maintenance. Water flowed by gravity from the trenches into a deeper drainage ditch, and into a small valley 250 m away from the plot. The panels and gutters covered only 78% of the forest floor; openings were left around tree stems. Stemflow was not excluded from the plot, given its small contribution to forest floor soil water input (1–2%; P. Jipp *et al.*, unpublished manuscript), and its disproportionately high contribution to nutrient inputs to the soil. Water yield from the gutters that drain the plot was 72–75% of throughfall, and 34–40% of total annual rainfall (Brando *et al.*, 2008).

Volumetric water content

Volumetric soil water content (VWC; cm^3 water cm^{-3} soil) was measured to 11 m depth in each of the soil shafts using Time Domain Reflectrometry (TDR) as described by Nepstad *et al.* (2002). Each of the six shafts (three per plot) had duplicate vertical sensors at the soil surface and duplicate horizontal sensors in opposite walls at 50, 100, 200, 300 cm, and at 100 cm intervals to 1100 cm depth. The dielectric constant of the TDR probes was measured with a cable tester, and VWC was estimated from the calibration equation developed in a similar Belterra clay formation, in eastern Amazonia (Jipp *et al.*, 1998). The mean VWC was calculated from the duplicate TDR probes at each depth in each shaft.

Gas flux measurements

Fluxes of gases at the soil surface were made using chambers consisting of a polyvinyl chloride (PVC) ring (20 cm diameter $\times$ 10 cm height) and a vented PVC cover made from an end-cap of a 20 cm diameter PVC pipe. In September 1998, PVC rings were pushed into the soil to a depth of 2–3 cm to make the base of the chamber and have been left in place for the duration of the study. Six rings were placed in each of the three subplots within the rainfall exclusion plot and the control plots, yielding a sample size of 18 for each treatment.

A dynamic chamber method was used for measuring the fluxes of NO (Verchot *et al.*, 1999) and CO_2 (Davidson *et al.*, 2002). Air drawn from the chamber was circulated through a nafion gas sample dryer, a Scintrex LMA-3 NO_2 analyzer (Scintrex Limited, Concord, ON, Canada), and a LiCor infrared gas analyzer (LiCor, Lincoln, NE, USA), and then back to the chamber, using teflon tubing and a battery-operated pump, at a flow rate of $0.5\,L\,min^{-1}$. Fluxes were calculated from the rate of increase of NO and CO_2 concentrations, recorded by a datalogger at 12 s intervals between 1 and 3 min after placing the cover over the ring. The instruments were calibrated twice daily in the field. Fluxes of N_2O and CH_4 were measured using a static chamber technique (Matson *et al.*, 1990; Verchot *et al.*, 1999, 2000) and using the same chamber bases as those described above. Syringe samples removed from the chamber headspace at 30 s, 10 min, 20 min, and 30 min were analyzed in the laboratory by gas chromatography within 48 h, using an electron capture detector (ECD) for N_2O analysis and a flame ionization detector (FID) for CH_4 analysis (Verchot *et al.*, 1999, 2000). Fluxes were calculated from the rate of concentration change, determined by linear regression. Both dynamic and static chamber flux measurements were made on the same day and, in most cases, within 90 min of each other. Detailed discussion of spatial and temporal variation using this sampling scheme have been addressed in other publications (Verchot *et al.*, 1999, 2000; Davidson *et al.*, 2000b).

Statistical analyses

The surface gas flux measurements were not normally distributed, so the data were logarithmically transformed before analysis of variance. In the case of CH_4 and N_2O and NO, where negative fluxes were observed, a constant (5 CH_4, 2 for N_2O, and 0.1 for NO) was added to all fluxes to make the values positive before logarithmic transformations.

A repeated measures design was used to test the effects of plot, year, season, and their interactions. The data were aggregated to a seasonal mean (wet and dry seasons) for each year, from the dry season of 1998 to the wet season of 2005. Plot was a grouping variable; year and season were considered as two repeated trial factors. Because there were pretreatment differences in

CO_2 and NO fluxes between the two plots (Davidson *et al*., 2004), the between-subjects test of plot effects is not an adequate test of the throughfall exclusion treatment. Rather, we examined the within-subjects interactions of plot, year, and season across the pretreatment (1998–1999), treatment (2000–2004), and posttreatment (2004–2005) periods to analyze the response to the throughfall exclusion manipulation.

Data were aggregated across treatment years (2000–2004) to derive average annual flux estimates for each individual flux chamber. During this period, 13 wet season measurements and 10 dry season measurements were averaged to derive a seasonal mean. Each season is about 6 months long, so the seasonal means were weighted equally to derive an average annual flux estimate. After calculating an annual flux for each chamber, the mean and 95% confidence interval was calculated for the 18 chambers within each treatment plot. Hence, temporal variation was addressed in the repeated measures analysis, while the error terms of the annual estimates reflect only spatial heterogeneity.

Results

Nitrous oxide

Fluxes of N_2O were marginally significantly higher ($P = 0.04$) in the exclusion plot before the start of the exclusion treatment (Davidson *et al*., 2004). Fluxes of N_2O increased during the wet season in the control plot in every year except the drought year of 2003, but the throughfall exclusion treatment effectively inhibited this wet season increase (Fig. 2a). This season-by-year-by-treatment effect was significant in the repeated measures analysis of all data, where the within-subjects effects of year, season, and all two-way and three-way interactions were significant (Table 1). After the exclusion treatment ended and the natural throughfall was permitted back in the treatment plot in the wet season of 2005, there was no significant difference in N_2O emissions between plots.

Nitric oxide

Fluxes of NO were slightly higher in the treatment plot than in the control plot in 1998 and 1999, before initiation of the throughfall exclusion treatment (Fig. 2b). Although the difference was modest, the effect was statistically significant ($P < 0.01$), and we attributed it to pre-existing differences between the plots of unknown origin (Davidson *et al*., 2004). This same pattern was maintained through the first three wet seasons of the exclusion experiment, which initially led us to conclude that the exclusion treatment had had no significant effect on NO emissions. However, the NO emissions in the exclusion plot began to increase relative to the control plot in December 2002 and continued to remain elevated through 2004 (Fig. 2b). This year-by-treatment effect was significant, as were all but one of the interaction terms (Table 1). After the exclusion treatment ended and the natural throughfall was permitted back in the treatment plot in the wet season of 2005, there was no significant difference in NO emissions between plots.

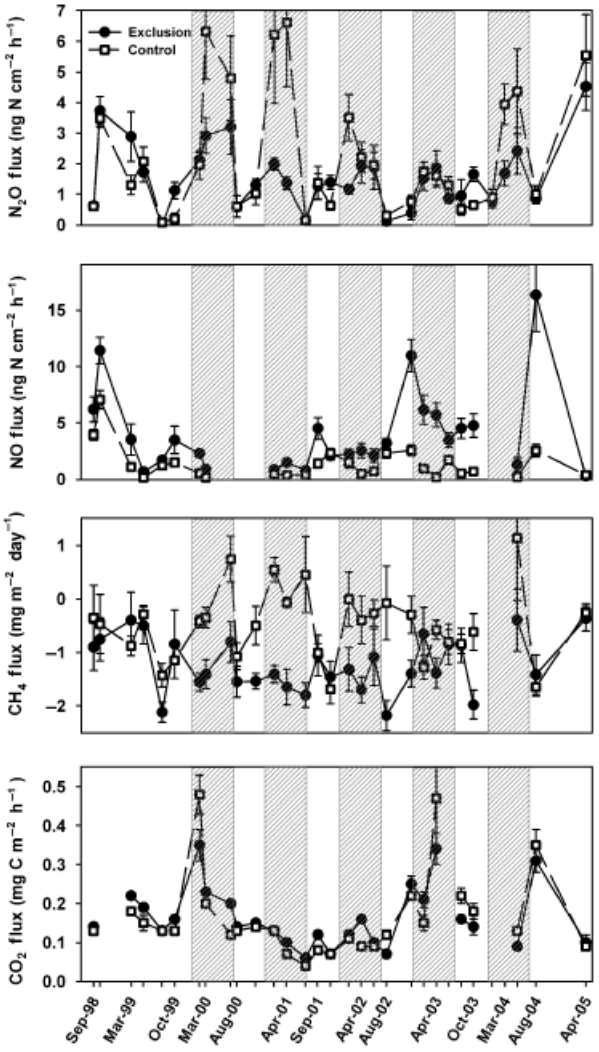

Fig. 2 Mean surface fluxes ($N = 18$) of nitrous oxide, nitric oxide, methane, and carbon dioxide in the throughfall exclusion plot (closed circles) and control plot (open squares). For CH_4, negative fluxes indicate net consumption by the soil of atmospheric CH_4, whereas positive values indicate net emission from the soil. The error bars (a few of which are smaller than the plotting symbols) represent standard errors of the mean for each sampling date. Missing data are due to equipment failure. The shaded regions show the periods when the throughfall exclusion panels were in place.

Table 1 *P*-values for repeated measures analysis of flux data from 1998 to 2004

Effect	N_2O	NO	CH_4	CO_2
Plot	0.516	**<0.001**	**<0.001**	0.229
Year	**<0.001**	**<0.001**	**0.039**	**<0.001**
Year × Plot	**0.040**	**<0.001**	**0.013**	**<0.001**
Season	**<0.001**	**<0.001**	**<0.001**	0.878
Season × Plot	**<0.001**	0.331	0.507	0.060
Year × Season	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Year × Season × Plot	**<0.001**	**<0.001**	**0.012**	0.650

The 'plot' effect is the between-subject effect of the throughfall exclusion treatment, which was initiated in 2000. The others are within-subject effects. Values <0.05 are highlighted in bold.

Methane

Fluxes of CH_4 were not significantly different ($P > 0.05$) in exclusion and treatment plots before the start of the exclusion treatment, but diverged after the throughfall exclusion began (Fig. 2c). The control plot was a net source of CH_4 to the atmosphere in all wet seasons except the drought year of 2003. In contrast, the exclusion plot remained a net sink for atmospheric CH_4 throughout the years of the exclusion treatment. The differences between treatments were generally larger during the wet season. This season-by-year-by-treatment effect was significant in the repeated measures analysis of all data, where the within-subjects effects of year, season, and all interaction terms but one were significant (Table 1). After the exclusion treatment ended and the natural throughfall was permitted back in the treatment plot in the wet season of 2005, there was no significant difference in CH_4 emissions between plots, both being a net source of atmospheric CH_4 in that wet season (Fig. 2c).

Carbon dioxide

Fluxes of CO_2 were slightly higher in the treatment plot than in the control plot in 1998 and 1999, before initiation of the throughfall exclusion treatment (Fig. 2d), and the effect was statistically significant ($P < 0.01$; Davidson *et al*., 2004). Although there was subsequently a significant treatment-by-year interaction, the effect of the exclusion treatment was not consistent among years or seasons, and the treatment-by-year-by-season interaction was not significant (Table 1). When large pulses were measured, as in February 2000, April 2003, and August 2004, which were probably related with recent wetting events, they tended to be higher in the control plots (Fig. 2d). On the other hand, the exclusion plot had somewhat higher CO_2 efflux rates on most of the other dates during the exclusion treatment years. These differences in apparent treatment effects across time nearly completely cancelled, resulting in nearly identical estimates of annual CO_2 efflux from the two plots (Table 2). After the exclusion treatment ended and the natural throughfall was permitted back in the treatment plot in the wet season of 2005, there was no significant difference in CO_2 fluxes between plots.

Table 2 Mean annual trace gas emissions based on 5 years of sampling after initiation of the throughfall exclusion treatment (see text)

	Exclusion	Control
CO_2 ($Mg\,C\,ha^{-1}$)	12.8 ± 1.0	12.8 ± 1.3
NO ($kg\,N\,ha^{-1}$)	2.8 ± 0.7	0.8 ± 0.2
N_2O ($kg\,N\,ha^{-1}$)	1.4 ± 0.2	2.1 ± 0.7
CH_4 ($kg\,CH_4\,ha^{-1}$)	−4.9 ± 1.0	−1.6 ± 0.9

The error terms represent the 95% confidence interval derived from analysis of spatial heterogeneity among the 18 flux chambers per study plot.

Correlations with VWC

Qualitatively, the observed responses to variation in VWC did not change from those reported by Davidson *et al*. (2004), but an additional 3 years of measurements permits some distinction between responses in treatment and control plots. As previously reported, there remained no relationship between VWC of the top 30 cm soil and CO_2 (Fig. 3a), except perhaps a weak indication of the highest fluxes at intermediate water contents. In contrast to CO_2, NO fluxes were negatively correlated with VWC (Fig. 3b), N_2O and CH_4 fluxes were positively correlated with VWC (Fig. 3c and d), and the ratio of N_2O:NO fluxes was positively correlated with VWC (Fig. 3e). The slope for the VWC–NO regression is steeper in the exclusion plot than in the control plot (Fig. 3b) and is steeper that we previously reported for the earlier combined dataset (Davidson *et al*., 2004). We speculate that there may have been a change in substrate availability to nitrifying bacteria, thus enhancing NO emissions at low water content. Similarly, the VWC–N_2O regression slope is less steep for the exclusion plot than the control plot. Although N_2O emissions were generally lower in the exclusion plot compared with the control plot on most dates (Fig. 2a), comparing N_2O emissions at common VWC values reveals that N_2O emissions were somewhat higher in the exclusion plot compared with the control plot when VWC was $<0.30\,cm^3\,cm^{-3}$ (Fig. 3c). This result

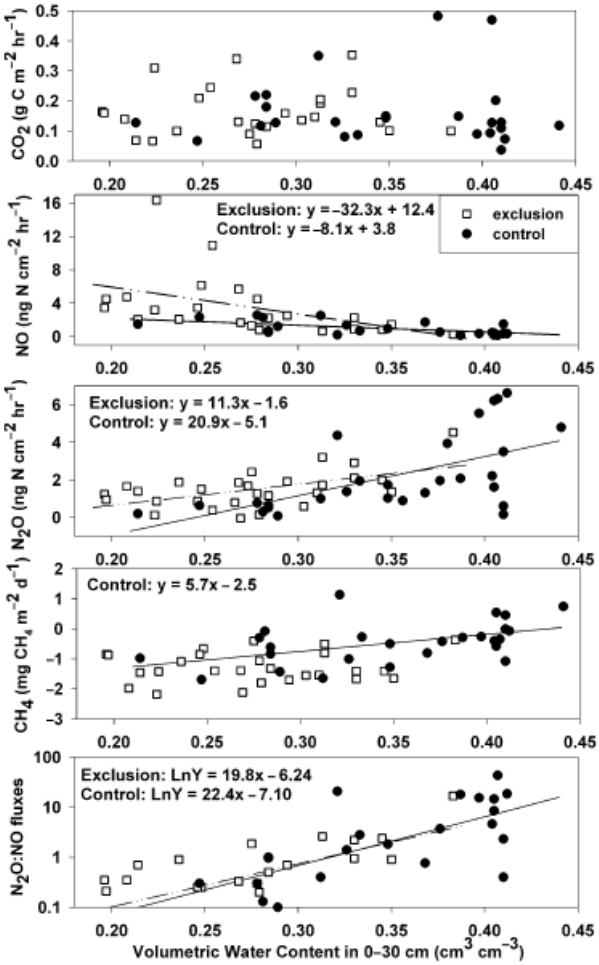

Fig. 3 The relationship between volumetric water content of the top 30 cm soil with surface fluxes of carbon dioxide, nitric oxide, nitrous oxide, methane, and the ratio of nitrous oxide/nitric oxide in the throughfall exclusion plot (open symbols) and control plot (solid symbols). The R^2 values for the regression lines are 0.31, 0.21, 0.01, and 0.38 for NO, N_2O, CH_4, and ln(N_2O/NO), respectively, in the exclusion plot (broken lines) and 0.36, 0.37, 0.24, and 0.53 for NO, N_2O, CH_4, and ln(N_2O/NO), respectively, in the control plot (solid lines). The regression for NO in the exclusion plot is significant at $P < 0.03$, the regression for CH_4 in the exclusion plot is not significant ($P > 0.05$), and the others are significant at $P \leq 0.01$.

is consistent with increased NO and N_2O production by nitrifying bacteria under relatively dry conditions in the exclusion plot. The positive correlation between VWC and CH_4 fluxes is significant only for the control plot, because the range of VWC in the exclusion plot was too narrow to include many periods of high VWC and net CH_4 emissions. The graphs in Fig. 3 demonstrate that the exclusion treatments shifted the VWC toward the drier end of the gradient, thus increasing CH_4 consumption, decreasing production of N_2O and CH_4, and increasing the production of NO.

Annual fluxes

The addition of data from 2003 and 2004 has not changed the direction of the throughfall exclusion effect on annual flux estimates compared with our previous estimates (Davidson *et al*., 2004), although the magnitudes differ slightly. The differences in N_2O and CH_4 fluxes between plots were diminished during the drought year of 2003, which lowered slightly the differences in average annual emissions between treatments. The exclusion plot had 33% lower average annual N_2O emissions and three times higher average annual CH_4 uptake rates compared with the control plot (Table 2). The appearance of a treatment effect on NO emissions in 2003 and 2004 increased the difference between treatment plots to a factor of 3.5. The average annual CO_2 efflux rates are somewhat higher than previously reported, but there continues to be no difference between treatments.

Discussion

Extending our measurements into 2005 revealed four new results. First, a treatment effect on NO emissions emerged during the third year of the throughfall exclusion treatment, coinciding with a natural drought year. An increase in NO emissions with drought was initially hypothesized, because dry soil conditions tend to favor NO emissions over N_2O emissions (Firestone & Davidson, 1989; Davidson *et al*., 2000a), but it apparently required very dry conditions resulting from 3 years of exclusion and a natural drought (Fig. 1a and b), before that effect was observed. It is possible that an increase in N availability to nitrifying bacteria may have occurred by the third year of drought treatment, increasing NO, and to a lesser extent, N_2O emissions under dry soil conditions. The fine texture of this soil also favors N_2O emissions, so the drought conditions may need to be severe before NO emissions are favored in this soil.

Second, a natural drought in 2003 nearly eliminated the usual wet season increase in N_2O emissions and net CH_4 production in the control plot, so that the exclusion treatment effect was not observed in that year. This result emphasizes the need for multi-year observations to understand both natural interannual variability and how that natural variation affects manipulation experiments.

Third, the recovery of N_2O and CH_4 fluxes in the exclusion treatment plot to rates similar to the control plot in 2005 is striking. Once natural throughfall was allowed back into the exclusion treatment plot, the N_2O and CH_4 fluxes increased during the wet season to

about the same magnitude as observed in the control plots. This result reinforces our earlier conclusion, that the dominant effect of the drought manipulation on trace gas emissions was mediated by its short-term effects on soil aeration rather than longer-term effects on carbon and nitrogen substrate supply. Once the soil was adequately rewetted (Fig. 1b), the anaerobic processes of denitrification and methanogenesis in soil microsites resumed in the treatment plot in 2005, demonstrating that the effect of throughfall exclusion was quickly reversible. This result does not preclude the possibility of more profound changes in nutrient cycling processes that could affect substrate supply in a longer experiment or under a sustained change in climate, but they were not observed during this 5-year manipulation. In contrast, significant changes in plant phenology (Brando *et al*., 2006), hydraulic redistribution of soil water (Oliveira *et al*., 2005), and tree mortality (Nepstad *et al*., 2007) were observed.

Fourth, the curious lack of a consistent exclusion treatment effect on soil CO_2 efflux can now be interpreted in the light of other carbon cycling responses of the forest. Throughfall exclusion could be hypothesized to provoke numerous changes in C cycling processes, such as reduced litterfall due to less foliar production by stressed trees, reduced heterotrophic respiration in the litter layer and mineral soil due to drought stress or substrate limitation of heterotrophs (Davidson *et al*., 2000b, 2006; Saleska *et al*., 2003), increased allocation of C to fine roots to explore for deep water resources (Nepstad *et al*., 1994), and increased root mortality and subsequent decomposition due to tree mortality (Brando *et al*., 2008).

Brando *et al*. (2008) reported that litterfall in this throughfall exclusion experiment was initially somewhat higher in the exclusion plot ($7.3\,Mg\,ha^{-1}\,yr^{-1}$) compared with the control plot ($6.4\,Mg\,ha^{-1}\,yr^{-1}$) in 2000, which is consistent with our observation of slightly higher pretreatment CO_2 efflux in the exclusion plot. Subsequently, there was a significant year-by-treatment interaction for litterfall, with the rates in the control plot showing no consistent trend among years, but a modestly declining litterfall rate in the exclusion plot. The largest difference was observed in 2003, when litterfall had declined to $5.1\,Mg\,ha^{-1}\,yr^{-1}$ in the exclusion plot and was $6.7\,Mg\,ha^{-1}\,yr^{-1}$ in the control plot. The greatest tree mortality was mostly among large trees with diameter at breast height $>20\,cm$ in the exclusion plots in 2003 (Nepstad *et al*., 2007; Brando *et al*., 2008). Interestingly, the smaller trees in the exclusion plot appeared to be released by the mortality of the larger trees and began growing more rapidly in 2004 and 2005, which was accompanied by an increase in litterfall in the exclusion plot back up to $6.1\,Mg\,ha^{-1}\,yr^{-1}$ in 2004 and 2005 (Brando *et al*., 2008). Although the observed modest reduction in litterfall in the exclusion plot between 2000 and 2003 was statistically significant, Brando *et al*. (2008) calculated that by far the largest effect of the throughfall exclusion on aboveground net primary productivity was reduced stem increment rather than litter production. They concluded that allocation of resources to leaves had priority over woody stems under drought stress. Of course, soil CO_2 efflux is also affected by the allocation of C belowground. Brando *et al*. (2008) also found no effect of the drought treatment on the radiocarbon content of the soil surface CO_2 efflux, indicating that the mean age of the respired carbon had not changed and suggesting that belowground C allocation may not have been significantly affected by the throughfall exclusion treatment. The absence of large, persistent effects on litterfall and the unchanged radiocarbon content of soil CO_2 are consistent with our finding of no significant effect of the exclusion manipulation on annual soil CO_2 efflux.

Our results contrast with those of Sotta *et al*. (2007), who reported an average annual reduction of 22% of soil CO_2 efflux in a similar 2-year throughfall exclusion experiment located at the Caxuianã National Forest. These authors attributed the difference in the observed soil respiration response to drought treatment between our two studies to differences in soil texture and rooting depth. Whereas the Tapajos soil is 60–80% clay, the Caxuianã soil is 70–95% sand. Roots extend to 10 m or more at Tapajos, but are rare below 5 m at Caxuianã. Drought stress for both decomposers and plants may be more easily provoked in the more shallowly rooted sandy soil at Caxuianã. Soil CO_2 production at Tapajos may be more buffered from drought because of more options for trees to tolerate dry periods, including changes in rooting depths to access a larger rooting volume of soil water resources.

Conclusion

This throughfall exclusion experiment has demonstrated that emissions of NO, N_2O, and CH_4 from Amazonian forest soils are sensitive to changing climate. The exclusion manipulation, which is similar to the reduction in rainfall experienced during severe El Niño events, lowered annual N_2O emissions by about 33% and increased rates of NO production and CH_4 consumption by a factor of about 3. No consistent treatment effect was detected for soil CO_2 efflux. Once natural throughfall was permitted back into the treatment plot, differences between plots disappeared. The responses of these microbial processes after five rainy seasons of the exclusion treatment, followed by 1 year

of recovery with natural throughfall, indicate a quickly reversible effect of soil aeration on the balance of gaseous production and consumption via nitrification, denitrification, methanogenesis, and methanotrophy. Longer-term drought effects, which might include more profound changes in C and N substrate supply for these microbial processes, probably require significant change in vegetation cover, which could be a decadal process.

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