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Fluxes of greenhouse gases between soils and the atmosphere in a temperate forest following a simulated hurricane blowdown

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Abstract. Fluxes of nitrous oxide (N_2O), carbon dioxide (CO_2), and methane (CH_4) between soils and the atmosphere were measured monthly for one year in a 77-year-old temperate hardwood forest following a simulated hurricane blowdown. Emissions of CO_2 and uptake of CH_4 for the control plot were 4.92 MT C ha^{-1} y^{-1} and 3.87 kg C ha^{-1} y^{-1}, respectively, and were not significantly different from the blowdown plot. Annual N_2O emissions in the control plot (0.23 kg N ha^{-1} y^{-1}) were low and were reduced 78% by the blowdown. Net N mineralization was not affected by the blowdown. Net nitrification was greater in the blowdown than in the control, however, the absolute rate of net nitrification, as well as the proportion of mineralized N that was nitrified, remained low. Fluxes of CO_2 and CH_4 were correlated positively to soil temperature, and CH_4 uptake showed a negative relationship to soil moisture. Substantial resprouting and leafing out of downed or damaged trees, and increased growth of understory vegetation following the blowdown, were probably responsible for the relatively small differences in soil temperature, moisture, N availability, and net N mineralization and net nitrification between the control and blowdown plots, thus resulting in no change in CO_2 or CH_4 fluxes, and no increase in N_2O emissions.

Introduction

Nitrous oxide (N_2O), carbon dioxide (CO_2), and methane (CH_4) are greenhouse gases that absorb long-wave radiation and thus influence the global heat budget (Donner & Ramanathan 1980; Lashof & Ahuja 1990). Atmospheric concentrations of these gases are increasing (Watson et al. 1990), however the global budgets for these gases are incomplete. An important but inadequately quantified component of global trace gas budgets are fluxes between soils and the atmosphere. In temperate forests, physical or chemical disturbances that alter soil conditions and nitrogen (N) cyclng can change rates of greenhouse gas fluxes between soils and the atmosphere. For example, both forest cutting (Bowden & Bormann 1986) and N fertilization (Aber et al. 1993; Matson et al. 1992) can increase nitrification and alter soil N_2O emissions and CH_4 uptake.

Hurricane disturbances may also change trace gas flux rates between soils and the atmosphere. In a wet subtropical forest in Puerto Rico, a natural hurricane that damaged most vegetation caused large increases in N_2O emissions and decreases in CH_4 uptake (Steudler et al. 1991). In New England, catastrophic hurricanes are historically responsible for much of the structural pattern and dynamics of upland forests (Foster 1988) and occur approximately once every 70—100 years (Neumann et al. 1978). At the Harvard Forest in north-central Massachusetts, a 1938 hurricane destroyed approximately 70% of standing timber (Gould 1960).

The influence of hurricanes on vegetation dynamics, nutrient cycling, and trace gas fluxes is being examined on a 0.8-ha plot at the Harvard Forest Long-Term Ecological Research site, where trees were pulled over to mimic a hurricane-induced forest blowdown. The purpose of this study was to examine the influence of the simulated hurricane blowdown on N_2O, CO_2, and CH_4 fluxes between soils and the atmosphere in a mixed temperate hardwood forest. Changes in soil N availability and cycling, as well as soil temperature and moisture, were examined to understand factors and processes important in controlling trace gas exchanges.

Site description

The 77-year-old mixed hardwood study site in north-central Massachusetts, USA (42°30′N, 72°12′W), has a gentle slope (5—11%), a north-westerly aspect, and an elevation of 309—320 m. Prior to the simulated hurricane (referred to as the blowdown), predominant woody species (>5.0 cm) were northern red oak (*Quercus borealis* Michx. f.) and red maple (*Acer rubrum* L.), with minor contributions from paper birch (*Betula papyrifera* Marsh), white ash (*Fraxinus americana* L.), black birch (*B. lenta* L.), and white pine (*Pinus strobus* L.). Basal area of live stems was 29.1 m^2 ha^{-1} in the control plot (70% red oak, 17% red maple), and 26.9 m^2 ha^{-1} in the blowdown plot (63% red oak, 19% red maple) (Lezberg & Foster 1991a). The current forest developed on the site following clearcutting of an old-field white pine stand in 1915. The stand was thinned several times from 1919 until 1948; little damage was sustained during the 1938 hurricane. Soil at the site averages 3 m thick and is a moderately well-drained stony loam of the Charlton series (Inceptisol) derived from glacial till. The forest floor ranges from 3—8 cm thick and is a moder to mor type with a thin Oa horizon (1—3 cm thick).

Methods

The 160 × 50 m blowdown plot was created during autumn (October 1—5 of 1990), the hurricane season for New England forests (Foster & Boose 1992). Overstory trees were pulled over in a northwesterly direction with a cable and winch attached to a logging skidder outside the treatment plot; fallen trees were left in place. The direction and proportion of trees chosen to be pulled over was determined from empirical data on hardwood stands destroyed at the Harvard Forest during the 1938 hurricane (Lezberg & Foster 1991b). The simulated hurricane resulted in major damage to 68% of the originally standing trees (live plus dead): 36% were uprooted, 15% were bent or leaning, and 17% were snapped (Lezberg & Foster 1991b). Damage to the forest floor caused by falling trees was minimal, with 3.9% of the area covered by mounds from uprooted trees, and 4.4% covered by pits (Ann Lezberg, Harvard Forest, personal communication). A 120 × 50 m (0.6 ha) control plot was established 30 m from the blowdown plot.

Gas exchanges were measured *in situ* using two-piece, 28.7 cm-dia. plastic chambers (for detailed descriptions, see Steudler et al. 1989; Bowden et al. 1990, 1991). The lower half (anchor) of the chamber was attached to the forest floor and left in place so fluxes would be measured at the same location during each sampling. During each 30-min flux measurement, the upper half of the chamber was placed upon the anchor and air samples were withdrawn with 20-mL nylon syringes at 0, 10, 20, and 30 min. Carbon dioxide and N_2O were measured using electron-capture gas chromatography and CH_4 concentrations were measured using flame-ionization gas chromatography. Fluxes were calculated using the linear portion of the gas concentration change during the incubation.

The pre-treatment similarity of the control and blowdown plots was assessed by measuring gas fluxes three times (April, July, September, 1990) prior to the treatment. After treatment, fluxes were measured 1—2 times/mo for one year (except for January and February when soils were frozen and snow-covered). During the preblowdown period, six chambers were used in each plot. Following the blowdown, three chambers were located in the control plot and six chambers were used in the blowdown plot. In each plot, chambers were placed about 20 m apart in locations where the forest floor had not been disrupted by uprooted or fallen trees.

On each sampling date, flux measurements were made 4—5 times (0500—0700 hrs, 1000 hrs, 1400 hrs, 1800—2200 hrs) in a 24-hr period and timed to provide sampling at approximate minimum and maximum soil temperatures. Annual gas fluxes were calculated by considering each sampling date as the midpoint of a sampling period, and then summing the gas fluxes over all sampling periods (Bowden et al. 1990; Matson et al. 1992). Annual flux estimates for each gas were thus based on 144 individual flux measurements for the control plot and 288 flux measurements for the blowdown plot.

Ambient air (1 m), chamber air, and soil temperatures (0—2.5 cm and 2.5—5.0 cm) were measured during each incubation. Temperatures were measured at one chamber in each plot prior to the blowdown. After the blowdown, temperatures were measured at one chamber in the control and at each chamber in the blowdown plot. Soil samples collected near each chamber on each sampling date were analyzed gravimetrically for moisture.

Net N mineralization and net nitrification in the forest floor (O-horizon) and top 5 cm of mineral soil (A-horizon) of the control and blowdown plots were measured using *in-situ* buried bag incubations of one-month duration (Aber et al. 1983) from mid-July to mid-October following the blowdown.

Statistical differences in soil temperatures, moisture, and N cycling were analyzed using a one-way analysis of variance (ANOVA). Differences in trace gas fluxes between plots were analyzed using a repeated measures ANOVA (RMANOVA).

Results

Prior to the blowdown, mean gas fluxes (n = 6 chambers) in the control and blowdown locations (Fig. 1) were not significantly different. In the year following the blowdown, N_2O emissions were significantly lower in the blowdown than in the control (RMANOVA, $P < 0.05$, $F = 5.79$, df = 1,8), with the annual blowdown flux only 22% of the control flux (Table 1). Methane uptake showed no overall treatment effect, however there was a significant treatment × sampling time interaction effect (RMANOVA; $P < 0.01$, $F = 11.77$, df = 11,77). No treatment effects were detected for CO_2 emissions.

Nitrous oxide fluxes ranged from net emissions to net uptake, with no seasonal trend (Fig. 1). Carbon dioxide effluxes and CH_4 uptake were strongly seasonal, with the greatest fluxes in midsummer. Small but

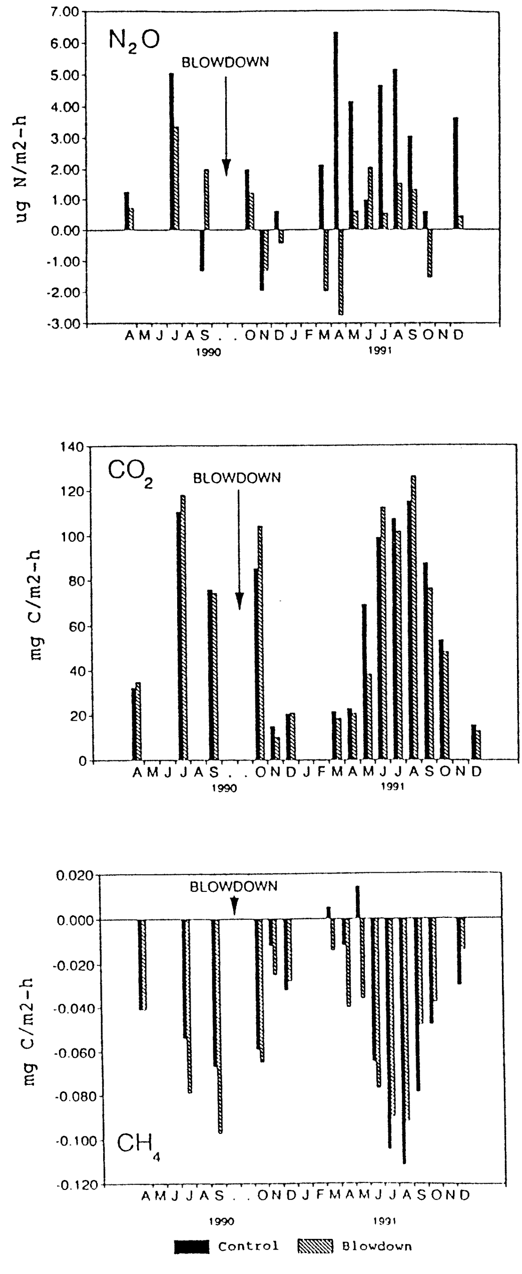

Fig. 1. Fluxes of N_2O, CO_2, and CH_4 between soils and the atmosphere during the pre-blowdown and post-blowdown periods in the control and blowdown plots at the Harvard Forest. Negative fluxes indicate uptake.

Table 1. Mean flux rates of N_2O, CO_2, and CH_4 between soils and the atmosphere at the Harvard Forest control and simulated hurricane blowdown plots (October 5, 1990—September 23, 1991) sampling periods. Negative fluxes indicate uptake.

	N_2O-N		CO_2-C		CH_4-C	
	ug m^{-2} h^{-1}	kg ha^{-1} y^{-1}	mg m^{-2} h^{-1}	MT ha^{-1} y^{-1}	mg m^{-2} h^{-1}	kg ha^{-1} y^{-1}
Control						
mean	2.86	0.23	63.8	5.04	−0.049	−3.87
SE[#]	0.45	0.04	4.5	0.36	0.003	0.24
Blowdown						
mean	0.64*	0.05	62.3	4.92	−0.052	−4.11
SE	0.53	0.04	1.9	0.15	0.005	0.40

[#] Standard error ($n = 3$ chambers for control; $n = 6$ chambers for blowdown).
* Significantly different from control (RMANOVA; $P < 0.05$, F = 5.79, df = 1,8).

measurable CH_4 emissions were observed in early spring in the control plots. No strong diel trends were noted for any of the gases.

Temperature had a positive influence on both CO_2 and CH_4 fluxes. Carbon dioxide effluxes were related exponentially to soil temperature (CO_2-C efflux = $e^{(0.11228 \text{ Soil °C} + 2.9006)}$; $r^2 = 0.88$) and CH_4 uptake was linearly related to soil temperature (CH_4-C uptake = 0.00340(Soil °C) + 0.020; $r^2 = 0.60$). The relationship was strongest for soil temperatures at the 0—2.5 cm depth for CO_2 and at the 2.5—5.0 cm depth for CH_4. Methane uptake was also negatively related to O-horizon soil moisture (CH_4 uptake = 0.098 − 0.00025 (% soil moisture), $r^2 = 0.52$). A multiple regression of CH_4 fluxes versus both temperature and moisture showed that these two factors together strongly predicted CH_4 uptake ($r^2 = 0.80$, uptake = 0.003027(soil °C) − 0.00014(% soil moisture) + 0.0459).

Soil temperatures (0—2.5 cm) were highest in July (19 °C) and lowest in December (−3.5 °C). Soil temperature showed little difference between the control and blowdown plots; average 0—2.5 cm soil temperatures in June were greater in the blowdown plot (18 °C) than in the control plot (14 °C) (ANOVA, F = 16.35, df = 1,7, $P < 0.005$), but no other significant differences were detected. Soil moisture showed no consistent difference between the plots.

Available soil NH_4^+, concentrations in the O-horizon, averaged over the year, were significantly higher in the blowdown (42.7 ± 6.1 mg N kg $soil^{-1}$) than in the control (24.1 ± 4.1 mg N kg $soil^{-1}$) (ANOVA, F = 4.00, df = 1,7, $P < 0.10$). Concentrations were much lower in the mineral soil, but were not significantly different between plots (blowdown:

10.6 ± 1.5 mg N kg $soil^{-1}$; control: 6.6 ± 0.5 mg N kg $soil^{-1}$; ANOVA, F = 3.08, df = 1,7). Forest floor and mineral soil available NO_3^- concentrations were below detection limits (0.30 mg N kg $soil^{-1}$) in all but one sample over the year.

Net N mineralization showed very little difference between the control and blowdown plots (Table 2). Over the 3-month buried bag study period, 28.3 kg N ha^{-1} were mineralized in the control, compared to 32.8 kg N ha^{-1} in the blowdown. Net nitrification, however, increased from negligible amounts in the control (0.2 kg N ha^{-1}) to larger rates in the blowdown (7.2 kg N ha^{-1}).

Table 2. Net N mineralization and net nitrification rates (kg N/ha/mo, mean ± SE) for forest floor and mineral soil (0—10 cm) in control and blowdown plots at Harvard Forest (*n* in parentheses).

Incubation period		Net N mineralization		Net nitrification	
		Forest floor	Mineral soil	Forest floor	Mineral soil
Jul-Aug	Control	3.4 ± 1.5 (6)	1.2 ± 0.2 (6)	0.0 ± 0.0 (6)	0.2 ± 0.2 (6)
	Blowdown	9.2 ± 3.0 (10)	6.7 ± 1.4 (10)[#]	0.0 ± 0.0 (10)	2.9 ± 1.0 (11)*
Aug—Sept	Control	8.8 ± 3.4 (6)	11.2 ± 9.3 (6)	0.0 ± 0.0 (6)	0.0 ± 0.0 (6)
	Blowdown	7.0 ± 1.6 (10)	7.1 ± 1.3 (11)	0.0 ± 0.0 (10)	3.0 ± 1.6 (11)
Sept—Oct	Control	1.1 ± 2.5 (3)	2.6 ± 1.4 (6)	0.0 ± 0.0 (3)	0.0 ± 0.0 (6)
	Blowdown	0.1 ± 0.6 (10)	2.7 ± 0.8 (11)	0.1 ± 0.1 (10)	1.2 ± 0.8 (11)

[#] Significantly greater than control, F = 14.83 (df = 1,15), $p < 0.05$.
* Significantly greater than control, F = 4.76 (df = 1,15), $p < 0.05$.

Discussion

Trace gas flux rates at the control plot are generally similar to flux rates in other temperate forests. The mean N_2O efflux rate (2.86 ugN m^{-2} h^{-1}) is within the range of rates reported for other temperate hardwood forests (Bowden et al. 1991), but is higher than fluxes at a nearby, less productive mixed hardwood stand at the Harvard Forest (0.27—0.29 ugN m^{-2} h^{-1}, Bowden et al. 1991). Soil respiration (CO_2 emissions) and CH_4 uptake rates were also within the ranges for a wide variety of temperate deciduous forests (Raich & Schlesinger 1992; Crill 1991; Yavitt et al. 1990; Steudler et al. 1989).

Despite the large disturbance to vegetation caused by the simulated hurricane, CO_2 flux rates were unaltered. Responses of soil respiration to disturbance are variable, and both increased and decreased CO_2 emissions following forest cutting have been observed across a wide range of forests (Raich & Schlesinger 1992). For CH_4, even though there was no overall treatment effect, the significant interaction effect indicates that CH_4 uptake may have had a small, delayed response to the blowdown. Methane fluxes during the preblowdown period and first few months following the blowdown were generally lower in the control than the blowdown plot (Fig. 1). By the summer following the blowdown, however, uptake rates were routinely greater in the control than the blowdown. The lack of a strong CH_4 response in this study differs from decreased uptake by tropical forest soils subjected to a catastrophic hurricane or to forest clearcutting (Keller et al. 1986; Steudler et al. 1991).

The annual N_2O efflux (Table 1) was nearly five-fold lower in the blowdown plot than the control plot, however, two points should be noted. First, pre-treatment N_2O fluxes were somewhat lower in the blowdown plot than the control plot. Secondly, and more importantly, the efflux rates from the control plot are among the lower estimates for temperate forests. Thus, even though the relative difference between the control and blowdown plots is large, the absolute difference is rather small. We are unaware of other published results on responses of trace gas fluxes to natural disturbances in temperate forests.

Sampling constraints prevented us from measuring gas fluxes in pits and on mounds in the blowdown plot. Recent measurements, however, indicate that soil respiration rates in pits and on mounds are 20% and 55% lower, respectively, than rates from undisturbed areas (Millikin & Bowden, unpublished data).

We believe that the relatively small responses of trace gas fluxes to the simulated hurricane are due to important physical factors and biological processes that underwent little or no change. The forest floor remained relatively unaffected, and even though most trees in the blowdown had been damaged, the majority of stems (65%) leafed out or resprouted in the summer following the blowdown (Ann Lezburg, Harvard Forest, personal communication).

Nitrogen cycling also showed relatively small changes. Nitrification is a key process in N_2O production (Firestone & Davidson 1989) and it is probably the most important N_2O-producing process in aerobic soils (Keller et al. 1986; Robertson & Tiedje 1987). Although we did observe increases in net nitrification from negligible rates to 7.2 kg N ha^{-1} over the 3-month buried bag study, the absolute amount of net nitrification, as well as the proportion of mineralized N that was nitrified, is very low compared to rates in other temperate forests (e.g. Pastor et al. 1984) especially forests showing high rates of N_2O efflux (Brumme & Beese 1992). The reason for the small but absolute decrease in N_2O effluxes is not clear. Our buried bag data suggest that net nitrification increased, however we do know what gross nitrification rates were.

Nitrogen cycling is also important in controlling CH_4 uptake. Nitrogen fertilization studies in temperate forests (Steudler et al. 1989) and grasslands (Mosier et al. 1991) have shown that CH_4 uptake is sensitive to rates of net mineralization and net nitrification. Reduction of CH_4 uptake can be caused by an inhibitory effect of nitrogen, particularly NH_4^+, on CH_4-oxidizing bacteria, as well as by decreased oxidation by nitrifying bacteria when soil NH_4^+ concentrations are increased (e.g. Whittenbury et al. 1970; O'Neill & Wilkinson 1977). Although we did find an increase in available soil NH_4^+ in the forest floor, the absolute changes in net nitrification were not large; the significant interaction effect suggests a measurable but small decrease in uptake in the year following the blowdown. We also found that soil moisture and temperature strongly controlled CO_2 and CH_4 fluxes, but the relatively small differences in temperatures and moisture between the control and blowdown plots are probably additional factors contributing to the similarity of flux rates between the plots. Shading by new growth and resprouted trees may have prevented soils from reaching greatly elevated temperatures, and moisture showed little change because evapotranspiration was probably not greatly different between the blowdown and control plots.

Our study is limited, somewhat, by having only one large simulated blowdown plot rather than a replicated set of treatment plots; in addition there are statistical limitations created by repeated measures from the same locations in each plot. Despite these limitations, our results suggest that temperate forests in general may be resistant to large changes in CO_2, N_2O, and CH_4 flux rates caused by natural physical disturbances. The response of trace gas fluxes to disturbances in temperate forests depends on the extent to which key soil processes and factors are altered. We suggest that rapid reestablishment of vegetation in the blowdown plot tempered potentially important changes in soil temperature and moisture, as well as changes in soil N cycling, thus preventing changes in trace gas fluxes that would have increased trace gas concentrations in the atmosphere.

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