Methane flux response to nitrogen amendment in an upland pine forest soil and riparian zone

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[1] Methane (CH_4) is an important anthropogenic greenhouse gas, up to 15% of which is consumed by terrestrial soils. In this field study of the CH_4 cycle of a pine forest, 18 plots were established at each of two sites, located 40 m apart. The upper site was well-drained and the lower site was poorly drained, but they shared similar overstory tree composition. Nitrogen was added as NH_4NO_3 incrementally across the 2009 growing season in a high (67 kg NH_4NO_3 ha^{-1} yr^{-1}) and a low (5 kg NH_4NO_3 ha^{-1} yr^{-1}) concentration. The sites were monitored for soil and air temperature, soil moisture, precipitation, air pressure, and NH_4 and NO_2+NO_3 concentrations throughout the growing season. Across all treatments for the duration of the field season, average CH_4 flux showed consumption of −0.84 kg CH_4 ha^{-1} yr^{-1}, but CH_4 flux differed between the upper and lower sites. Across all treatments, upper site CH_4 flux averaged −5.38 kg CH_4 ha^{-1} yr^{-1}, while lower site flux averaged 3.72 kg CH_4 ha^{-1} yr^{-1}, with greater variance than was observed at the upper site. High N treatments caused greater CH_4 release than the control in the lower, but not the upper, site. The main correlated variable with CH_4 flux was soil moisture; however, it accounted for <14% of the variation. Statistics were run several different ways, resulting in multiple environmental factors contributing up to 84% of the variation in CH_4 flux. Long-term drainage differences between the sites likely drove the differences in CH_4 flux.

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1. Introduction

[2] Methane (CH_4) is considered the third most potent greenhouse gas in terms of atmospheric heat-holding capacity [*Intergovernmental Panel on Climate Change* (*IPCC*), 2007]. Over the past 150 years, atmospheric CH_4 has increased monotonically due to anthropogenic inputs to the atmosphere. The increase in atmospheric CH_4 is believed to have been steady for much of that time period, but it became erratic in the 1990s and did not increase overall from around 1999 until 2008, when it began increasing again [*Rigby et al.*, 2008]. The causes of these dramatic shifts are still hotly debated [*Aydin et al.*, 2011; *Kai et al.*, 2011].

[3] Drivers of variation in atmospheric CH_4 concentrations, in particular the controls on interannual changes in CH_4 flux into and out of soils, are only recently coming into focus. Field research in CH_4 flux has given detailed but somewhat conflicting views on the driving factors [*McLain et al.*, 2002; *Phillips et al.*, 2001]. The study of the microbial mechanisms involved is needed to address this uncertainty [*Aronson and Helliker*, 2010]. As soil microorganisms are the most important biological sources and sinks for CH_4, the study of highly complex in situ CH_4 flux responses to environmental stimuli can greatly improve our understanding of past, current and future fluctuations in atmospheric CH_4.

[4] Soil exchange of CH_4 with the atmosphere is regulated by two main groups of microorganisms, methanogens and methanotrophs. The different environmental requirements of these two groups, particularly oxygen level, water content, nutrient availability, and temperature, determine the CH_4 flux of a given ecosystem [*Silver et al.*, 1999]. Methanogenic archaea, active in anaerobic conditions, produce CH_4 as a byproduct of metabolism and are the main biological source of CH_4 in natural systems, landfills and agriculture [*Bartlett and Harriss*, 1993]. Methanotrophic bacteria are active in aerobic conditions and derive energy and carbon from the oxidation of CH_4 [*Hanson and Hanson*, 1996]. The balance between production and consumption by these groups determines the direction and magnitude of flux of CH_4 across the soil surface. Variation in temperature, precipitation, nitrogen status and other environmental parameters controls the balance of activity between methanogens and methanotrophs—and hence net CH_4 flux—in any soil [*Conrad*, 2007]. In particular, forest soil

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pH, forest type and temperature have been found to shape methanotrophic communities, while specific effects on individual microbial species are largely unknown [*Kolb*, 2009].

[5] Patterns of temperature and rainfall are shifting [*IPCC*, 2007], and changes in both can have dramatic impacts on CH_4 uptake by soils [*Le Mer and Roger*, 2001]. Soil moisture, which is correlated both with precipitation and water table height, is generally regarded as the greatest predictor of CH_4 flux. Precipitation exclusion has been shown to result in increased uptake of CH_4 in seasonal tropical forest [*Davidson et al.*, 2008], and heavy precipitation leads to decreased uptake or even release from terrestrial ecosystems [*Singh et al.*, 1997]. In general, high and low temperatures inhibit CH_4 consumption, while CH_4 production correlates positively with increasing temperatures [*Conrad*, 2007; *Castro et al.*, 1995]. Increased CO_2 concentrations at forest Free Air CO_2 Experiment (FACE) sites have been shown to decrease net methane consumption [*Phillips et al.*, 2001], possibly due to increased soil moisture effects on methanogenesis in the lower soil layers [*McLain et al.*, 2002; *McLain and Ahmann*, 2008; *Dubbs and Whalen*, 2010].

[6] Overall, nitrogen (N) input from atmospheric deposition and fertilizer use is projected to double from 1990 levels by the year 2050 [*Kroeze and Seitzinger*, 1998]. It has been established that cropland and pasture where N fertilizer is routinely applied tend to consume less CH_4 than natural forest and grassland [*Ojima et al.*, 1993; *Willison et al.*, 1995]. In general this is thought to occur because added ammonium to the soil can lead to increased concentrations of ammonia, which many methanotrophs can oxidize in place of CH_4 [*Hanson and Hanson*, 1996]. The genetics and enzyme kinetics behind CH_4 oxidation show tight evolutionary and functional linkages between the enzymes that enable CH_4 and ammonia oxidation [*Dunfield and Knowles*, 1995]. However, wetland research has shown that small amounts of N addition to nutrient-poor wetlands can result in increased CH_4 oxidation, which may lower the net release of CH_4 from the soil [*Bodelier et al.*, 2000]. A recent meta-analysis on the impact of N addition on methane consumption in non-wetland ecosystems found that larger N additions led to decreased CH_4 consumption from the atmosphere, and that previous fertilizer application to soil led to a greater decrease in CH_4 consumption with new fertilization [*Aronson and Helliker*, 2010].

[7] In recent years there has been increasing interest in the study of the effects of environmental and climatic variables on CH_4 consumption in forested ecosystems, which is one of the greatest but most variable biological sinks for CH_4 [*Dutaur and Verchot*, 2007]. In particular, the Pinelands in New Jersey constitute the largest contiguous region of pine forest, a common vegetation type in the northeast USA, in the country [*McCormick and Forman*, 1979]. In the present study we characterize the effects of N addition, and the interactive effects of N addition with season, drainage, temperature and moisture, on the CH_4 uptake and release of a sandy pine forest soil.

2. Materials and Methods

2.1. Site Description

[8] Measurements were made in a sandy pine forest soil in New Jersey, USA (39°55′N, 74°35′W) during the summer and early fall of 2009. The average annual temperature is 12.3°C and precipitation is 1143 mm. The sites were located roughly 1 mi from the Rutgers Pinelands Field Station, part of the greater New Jersey Pinelands Preserve, which includes approximately 304,000 ha of land with heavily restricted development in south-central New Jersey [*Krumins et al.*, 2009]. The study location consisted of two sites separated by 30–40 m: one well-drained at an elevation of 30 m asl and 7 m above the water table. The other, poorly drained at an elevation of 23 m asl and located at the water table ±5 cm. The well-drained site was considered an "excessively drained" sand of the Evesboro series, which consists of Mesic, coated Lamellic Quartzipsamments covered by an organic (O) horizon [*Krumins et al.*, 2009]. The poorly drained site was considered a Fluvaquent or "frequently flooded sediment" by the Web Soil Survey available from the U.S. Department of Agriculture (http://websoilsurvey.nrcs.usda.gov/app/), which in this case has a large O horizon of variable depth, sometimes topped with peat.

[9] The sites, though very different in soil and drainage characteristics, shared overstory species of trees. These included bear oak (*Quercus ilicifolia*), chestnut oak (*Q. prinus*), eastern black oak (*Q. velutina*), shortleaf pine (*Pinus echinata*) and pitch pine (*P. rigida)*. The understory was more variable, and included lowbush blueberries (*Vaccinium angustifolium*), wintergreen (*Gaultheria procumbens*) and peat moss (*Sphagnum* spp.) among sparse grasses. Further information on vegetation in the New Jersey Pinelands has been published by *Krumins et al.* [2009].

[10] The New Jersey coastal forest is in the center of recent and predicted urban development, and is therefore in a zone of increasing nitrogen deposition [*Holland et al.*, 2005]. The New Jersey Pinelands are broadly representative of coastal pine systems throughout the Southeastern USA. Thus, local results can be extrapolated to a large area of the United States, with analogues across the Earth. In this system, small-scale variations in water table and organic matter content lead to large variations in soil characteristics such as water holding capacity and oxygen content, which may alter the microbial composition, abundance and function. This system contains both wetland and upland forests while maintaining a mostly homogeneous overstory vegetation distribution, hence minimizing plant effects on microbial diversity, but maximizing the potential for both CH_4 production and consumption.

2.2. Field Methods

[11] The treatment areas were 1.5 × 1.5 m plots, with the central 1 × 1 m used for all analyses. Eighteen plots were located randomly in the upper and in the lower site, including six replicates of each treatment. Fertilization was performed once every three weeks in the growing season of 2009. The N was added as NH_4NO_3 dissolved in water and sprayed onto the plot soil and understory vegetation. The control plots were divided into watered and unwatered controls, with the watered control plot receiving the same amount of water as the treatment plots. The amounts of N and water added in 2009 are listed in Table 1. The low nitrogen level was intended to mimic a doubling of the Pinelands' current rate of atmospheric nitrogen deposition [*Dighton et al.*, 2004]. The high nitrogen level was intended to mimic the average level of fertilization in a cranberry bog,

Table 1. Incremental Amounts of N and H_2O Added to Field Plots[a]

Nitrogen Level	Nitrogen Simulation	NH_4NO_3 Level Annually (kg N ha^{-1} yr^{-1})	NH_4NO_3 Added Every 3 Weeks (mg m^{-2})	H_2O Added Every 3 Weeks per Plot (L)
Control	Natural deposition	0	0	1 (half of plots) or 0 (half of plots)
Low N	Double deposition	5	164.8	1
High N	Fertilization	67	2208.8	1

[a]The annual N quantities presented extrapolated to an annual rate, while N was added for a total of 144 days.

the most common form of agriculture in the New Jersey Pinelands [*Davenport and Schiffhauer*, 2007].

[12] Half of the plots had been established for a trial run of the design in May 2008, including nine upland and nine lowland plots, of which each of the three treatments had been replicated three times. In 2008, two fertilizer applications of 736.25 mg m^{-2} for high N and 1 mg m^{-2} for low N were applied within a two-month period from mid-June through mid-August. In 2008, CH_4 flux measurements were made and some environmental variables were monitored. These data were used to assess the power of the research plan to establish the larger investigation in 2009, and these data are not reported. The nine newer plots in both the upland and lowland sites were established in late April 2009, and fertilizer applications began on 8 June 2009, with each of the plots established in 2008 receiving the same N treatment (high, low or no N) as in the previous year. The variable "condition" was used in subsequent statistical analysis to connote whether the plot was established in 2008 ("old") or in 2009 ("new").

[13] Soil sampling in a given week was performed on a block of six upper and six lower randomly selected plots, on the day before, the day of, and two days after fertilization, called "pre-fertilization," "fertilization day," and "post-fertilization," respectively. The plots were then left fallow for the next two weeks, while the other two blocks of 12 plots were analyzed. Time domain reflectometry (TDR) sensors (CS616, Campbell Scientific) and thermocouples were implanted randomly across the upper and lower sites and connected to a CR-1000 data logger (Campbell Scientific) for constant measurement of environmental variables between plots in the two sites. In July 2009, three soil oxygen probes (SO-110, Apogee Instruments) were implanted randomly in each of the upper and lower sites.

2.3. Gas Flux Measurements

[14] Gas was collected for CH_4 flux analysis in situ using opaque, nonreflective PVC chamber bases, with an internal diameter of 30 cm and a height of 20 cm. These were implanted randomly in the central 1 × 1 m of each plot, approximately 5 cm into the soil, resulting in an internal volume above the soil surface of approximately 10.5 L, as described by *Neff et al.* [1994]. The chamber bases were in place at least two weeks before measurements started and remained in place throughout the summer and fall. During gas sampling, the chamber bases were fitted with a removable, opaque, nonreflective, flat PVC cover with a rubber septum port for sampling as well as a port fitted with 4 mm diameter tubing for pressure compensation, as described by *Livingston and Hutchinson* [1995]. The chambers were sealed with nonreactive vacuum grease (Dow Corning, Inc.), as described by *Nkongolo et al.* [2010]. This vacuum grease sealing method was lab tested, and was found to create an effective seal while having no effect on CH_4 flux rates, comparable with using water as a sealant (unpublished data). Water was determined unsuitable as a sealant in the field due to the risk of water spilling into the plot treatment area, thereby changing the soil moisture content during gas flux analysis, possibly impacting the CH_4 flux result.

[15] Gas was collected for analysis at three time points, in tedlar bags filled using a vac-u-tube (SKC Inc.) fitted with a needle, every 15 min for a total of 30 min. Tests showed that the concentration of CH_4 inside the tedlar bags remained unchanged for at least three weeks (data not shown). These bags were usually analyzed within one week of sampling, and the longest they were stored before analysis was two weeks. Tedlar bags were chosen for sampling rather than the more commonly used syringe to vial collection method, because both evacuated and noble gas-filled exetainers fitted with rubber septa were found to contribute CH_4 to the samples.

[16] Methane concentration was analyzed by gas chromatograph with attached flame ionization detector (GC-FID) (Trace GC, Thermo Instruments Inc.). The FID temperature was 190°C, and a Porapak Q column (Varian Inc.) of 25 m and 0.32 mm ID was used at 45°C. The carrier gas was He at a maximum of 10 ml min^{-1}. Since the changes in CH_4 concentrations were generally linear with time, the fluxes were calculated using linear regression and the ideal gas law [*Livingston and Hutchinson*, 1995]. Net CH_4 consumption by the soil was expressed using negative numbers, while positive numbers were used to express net release by the soil into the atmosphere.

2.4. Soil Analyses

[17] During gas collection, instantaneous moisture and temperature measurements were taken of the top 5 cm of the soil in each plot, just outside the chamber base, by a 5TE probe (Decagon Devices). Relative humidity, pressure and precipitation were measured hourly at a nearby Forest Service eddy covariance tower; more information is provided by *Clark et al.* [2010]. Soil water potentials were computed from pedotransfer functions using observed soil moisture measurements as described by *Vereecken et al.* [1989]. This equation, modified from its original version from *van Genuchten* [1980] was evaluated by *Cornelis et al.* [2001] to be the best fit pedotransfer function in the literature based on a large variety of soils. As the Pinelands soils are composed of sand and organic matter (see site description), the percentage of sand for the pedo-transfer function was assumed to be the remainder when the % C and N were subtracted.

[18] Soil cores (5 cm ID and 30.5 cm long) and adjacent soil from the top 5 cm were collected on gas-sampling dates.

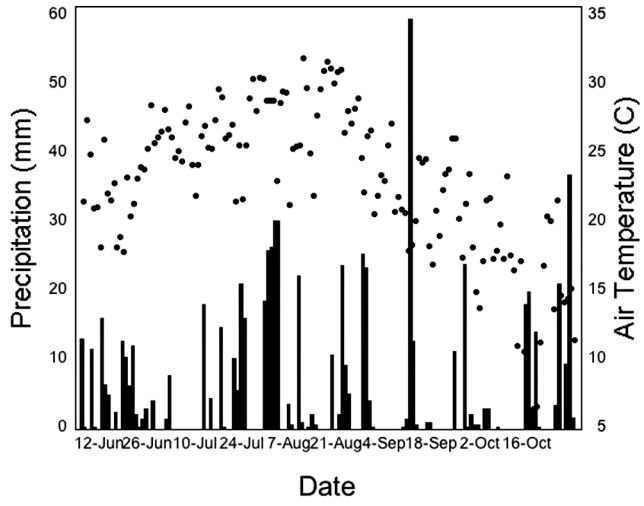

Figure 1. Average daily 24 h temperature (dots, scale on right) and total daily precipitation during the 2009 study period (bars, scale on left).

Topsoil was extracted within a few hours with KCl for NH_4^+ and NO_2^-+NO_3^-. Adjacent soil was weighed before and after oven drying to produce gravimetric water content for the analysis of NH_4^+ and NO_2^-+NO_3^- data. Extracts were analyzed colorimetrically with an Astoria-Pacific AutoAnalyzer 3 (Clackamus, Oreg.). The indophenol method was used to analyze NH_4^+ [*Standard Methods Committee*, 1976] and NO_2^-+NO_3^- was analyzed according to the N-1-naphthylenediamine dihydrochloride (NED) method following hydrazine reduction [*Environmental Monitoring and Support Laboratory*, 1983].

[19] The soil % content of N and C were analyzed at the start and the end of the growing season by elemental analyzer (Carlo Erba Instrumentazione, SA, Milan, Italy, model NA1500). Soil N and C analysis was performed on dried soils, used for gravimetric water content measurement, from the first date of collection ("pre-fertilization") and the last "fertilization day" of the field season in 2009.

[20] In July 2010, additional soil was collected from each plot for bulk density measurements. Bulk density was determined by removing and combining 3 identical cores with a corer of internal diameter 2.54 cm and length 15.24 cm. These were then dried in a drying oven at 110°C for 48 h and the dry weight determined. The bulk density was determined by dividing the dry weight by the volume of soil collected, which was 308.73 cc for each plot.

[21] Also in July 2010, a supplemental investigation was conducted of the treatment impacts on soil O_2 in the field site and in a growth chamber with soil removed from the field site. In the field, one O_2 sensor each was implanted at 5 cm depth into two lower site, high N plots. One plot was treated with high N while the other was watered. This effect was also measured in a climate-controlled growth chamber (Conviron, Inc.) simulating summer field conditions with soil collected from a water-saturated location 5 m from the lower site. Six pots were created out of opaque PVC pipe 25 cm ID and 60 cm long, with flat pieces of PVC cemented on one end. Pots were filled in the field with intact pillars of soil 30 cm deep, and transported back to the growth chamber without disturbance. Two pots were not amended, another two were watered to saturation, while a final two were watered to saturation with high N amendment. Each pot had an O_2 sensor implanted 5 cm into the soil continuously collecting O_2 data for 7 days, starting 3 h prior to amendment. A 5TE sensor was used to collect periodic temperature and moisture measurements throughout.

2.5. Statistics

[22] All statistical analysis was performed using JMP 8 (SAS, Inc.) and graphs were made with KaleidaGraph (Synergy Software, Inc.). The statistical tests performed included principal components analysis (PCA), analysis of covariance (ANCOVA), repeated–measures and single analyses of variance (ANOVA), t-test comparisons, Tukey's Honestly Significant Difference post-hoc tests and individual linear regressions. The probabilistic significance cut-off was $p < 0.05$. One outlier CH_4 release event, on 26 October 2009 in a high N plot, was 10 fold higher than any other CH_4 flux event and was therefore removed from all analyses. Since O_2 sensors were implanted in the field site after midway through the field season, the O_2 data collected during the field investigation in 2009 were not included in multivariate statistics.

Table 2. Soil Properties by Site Across All Treatments[a]

Environmental Variable	Sample Size (U, L)	Upper Site	Lower Site	*p*-values
Bulk Density (gcc^{-1})	18, 18	1.37 ± 0.13	0.22 ± 0.24	<0.0001*
% C content June	18, 18	23.77 ± 11.69	45.91 ± 1.94	<0.0001*
% C content October	18, 18	9.36 ± 8.99	38.84 ± 9.2	<0.0001*
% N content June	18, 18	0.86 ± 0.42	1.36 ± 0.2	<0.0001*
% N content October	18, 18	0.29 ± 0.31	1.12 ± 0.41	<0.0001*
Soil Moisture (ml H_2O ml^{-1} soil)	240, 240	0.13 ± 0.04	0.40 ± 0.15	<0.0001*
Soil water potential (MPa)	240, 240	−0.022 ± 0.017	−0.0055 ± 0.0034	<0.0001*
Soil temperature (°C)	240, 240	25.61 ± 7.44	20.92 ± 4.57	<0.0001*
Soil NH_4 content (mg N g^{-1} dry soil)	214, 216	21.21 ± 26	29.95 ± 41.38	<0.0092*
Soil NO_2+NO_3 content (mg N g^{-1} dry soil)	214, 216	4.67 ± 12.5	12.79 ± 30.02	<0.0003*

[a]Means ± standard deviation are given along with significance levels of t-test comparisons. Soil temperature, moisture and NH_4 and NO_2+NO_3 content averages are from all dates/times of CH_4 flux measurements. Bulk density is given for the top 15 cm of soil, while all other measurements are for the top 10 cm of soil. The % N and C content are given for the very first pre-fertilization date of all plots (June) and for the last fertilization date of all plots (October). Asterisks next to *p*-values indicate significance at $p < 0.05$, and *p*-values given are for one-way t-test differences between the two sites. U, L = Upper Site, Lower Site.

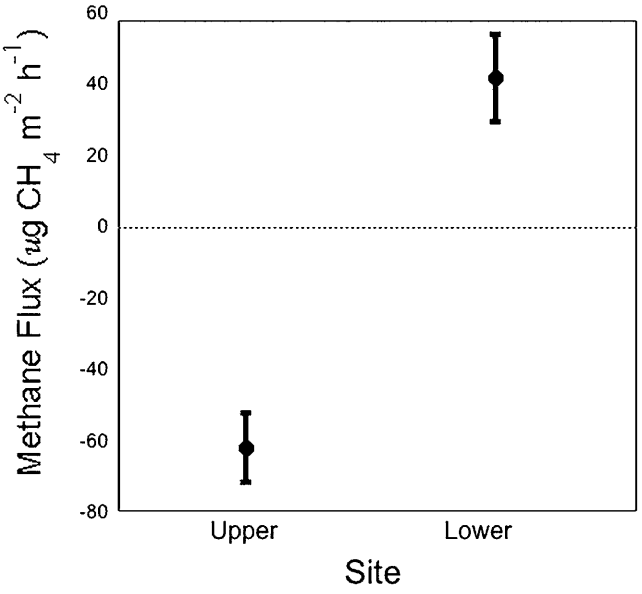

Figure 2. Averages by site bounded by the standard error of the mean of CH_4 flux across all plots, including treatments and controls, for the duration of the growing season. The values were significantly different at $p < 0.0001$. Sample size (n) for each site is 240 measurements.

[23] In order to establish the rate of flux across time, all CH_4 flux measurements were evaluated by linear regression. In order to weight the measurements of CH_4 flux by the accuracy of the multiple measurements for each time point, a weight statistic W was used in a subset of the statistical analyses. W was calculated as the inverse of the standard error of the slope of the line of best fit of the linear regression for CH_4 flux for each ring.

3. Results

3.1. Environment and Soil Properties

[24] The average ± standard deviation of daily air temperature was 22.7 ± 5.5°C and total rainfall was 533 mm during the 144 day study period (see Figure 1 for variation in these parameters across time). Soil properties found to be significantly different between sites are described in Table 2 for all treatments. Significantly different soil properties include bulk density, soil moisture, water potential, temperature, NH_4 and NO_2+NO_3. The mean ± standard error of the soil moisture across the growing season of the upper site was 0.13 ± 0.04 ml H_2O ml^{-1} soil, while the lower site had a moisture of 0.40 ± 0.15 ml H_2O ml^{-1} soil.

[25] Overall, there was a decrease in both N and C between June and October (i.e., across time, $p < 0.0001$ in both cases), but this difference was more pronounced in the upper site, and the site term was also significant ($p < 0.0001$) for both % N and % C (see Table S1 in the auxiliary materials).[1] Across the field season, N decreased 66.27% in the upper site and 17.65% in the lower site, and C decreased 60.62% in the upper site and 15.40% for the lower site.

3.2. CH_4 Flux Effects

[26] Across all plots for the duration of the field season, the average CH_4 flux was an unweighted −9.58 μg CH_4 m^{-2} h^{-1}, weighted −10.66 μg CH_4 m^{-2} h^{-1}. The average for all control plots across sites was −18.21 μg CH_4 m^{-2}

[1] Auxiliary materials are available in the HTML. doi:10.1029/2012JG001962.

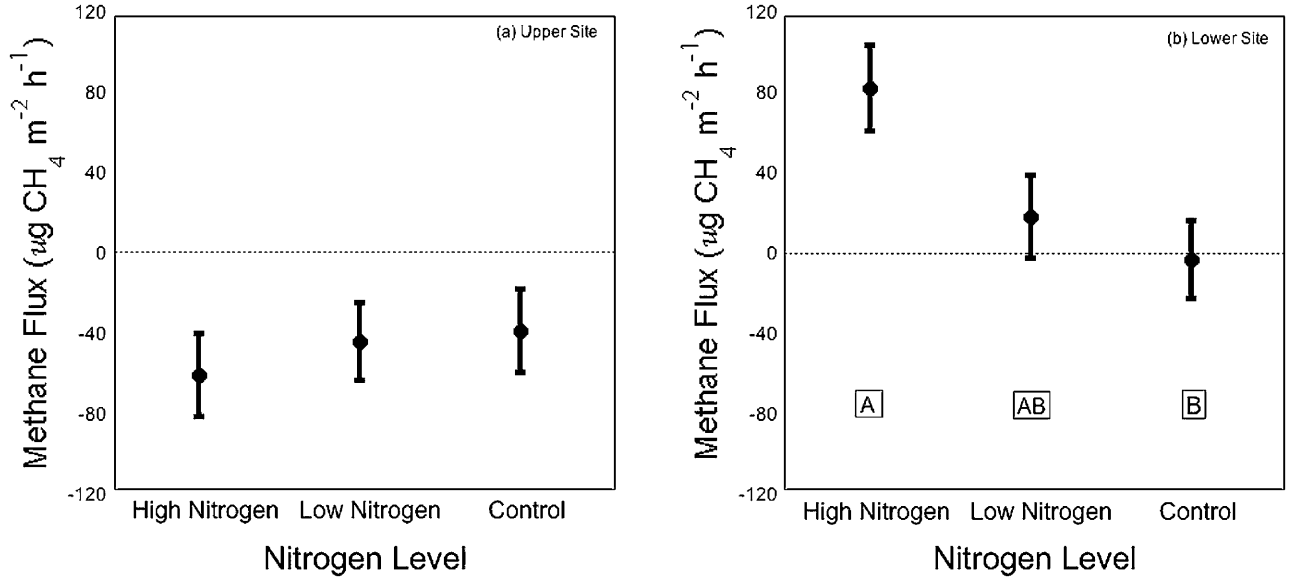

Figure 3. Averages bounded by the standard error of the mean of CH_4 flux across all plots for the duration of the growing season, by N treatment for (a) upper and (b) lower sites. Different letters indicate differences in average values of CH_4 flux between treatments within each site by Tukey's HSD. Each sample size (n) is 80 measurements.

Table 3. Single Variable Linear Regression Intercepts and Coefficients of Variation (of the Form y = mx + b) for the Impact of Environmental Variables on CH_4 Flux (μg CH_4 m^{-2} h^{-1}) of All Observations[a]

Environmental Variable	Slope (m)	Intercept (b)	Sample Size (n)	R^2 Value	*p*-value
Bulk Density (g cc^{-1})	−94.2 ± 12.7	65.6 ± 12.8	36	0.103	<0.0001*
% C Content June	3.2 ± 0.6	−118.6 ± 21.6	36	0.062	<0.0001*
% C Content October	3.0 ± 0.5	−80.2 ± 13.6	36	0.084	<0.0001*
% N Content June	75.3 ± 19.9	−91.2 ± 23.5	36	0.030	<0.0002*
% N Content October	86.2 ± 14.3	−69.813.0	36	0.072	<0.0001*
Soil Moisture (ml H_2O ml^{-1} soil)	366.4 ± 44.0	−107.0 ± 14.0	480	0.127	<0.0001*
Soil Water Potential (MPa)	14963.8 ± 3468.9	124.5 ± 22.4	480	0.073	<0.0001*
Soil Temperature (°C)	−4.5 ± 1.2	96.0 ± 29.6	480	0.028	<0.0002*
Soil NH_4 Content (mg N g^{-1} dry soil)	0.6 ± 0.3	−25.5 ± 11.2	430	0.013	<0.0185*
Soil NO_2+NO_3 Content (mg N g^{-1} dry soil)	0.9 ± 0.4	−17.8 ± 9.6	430	0.013	<0.0196*

[a]The estimates are bounded by standard errors. Asterisks next to *p*-values indicate significance at $p < 0.05$.

h^{-1}, unweighted. Variation in CH_4 flux between sites, and between treatments by site, are shown in Figures 2 and 3, respectively. Table 3 gives the equations, degrees of freedom, significance probability (*p*) values and coefficients of variation (R^2) for significant linear regressions of single environmental variables on CH_4 fluxes. When all treatments are averaged across the measurement period, upper site plots consumed CH_4 at −61.44 μg CH_4 m^{-2} h^{-1}, unweighted, while the lower site released CH_4 at 42.49 μg CH_4 m^{-2} h^{-1}, unweighted. There was no significant difference between the watered and unwatered controls (data not shown).

[27] The CH_4 flux data were analyzed with all environmental variables by PCA, and the first 5 components accounted for a cumulative 83.82% of the variation observed. The environmental variables with the largest eigenvectors in the first component were bulk density, soil moisture, as well as %N and %C from both June and October. The dominant factors in the second component were air and soil temperature, NH_4 and NO_x concentrations and precipitation. The first five principal components were saved and included in a full factorial ANCOVA of all treatment, condition and location factors. The overall R^2 value of this ANCOVA was 0.84, indicating that 84% of the variation was explained in this test. Site, fertilization status, condition (whether the site was established in 2008 or 2009), fertilization status by condition, site by condition and principal components 1, 2, 4 and 5 were significant (Table S2).

[28] In order to better evaluate the effect of the N treatments, an ANOVA was run without the pre-fertilization days. This ANOVA had an R^2 value of 0.13; site and the cross of site by N treatment were significant (Table S3). A stepwise multiple regression was also run on all environmental variables, and soil moisture ($p < 0.0001$) was the first factor to step in, followed by the concentration of $NO_2 + NO_3$ ($p < 0.118$), and finally soil water potential ($p < 0.159$). In the subsequent model, only soil moisture was significant ($p < 0.0001$), with a total R^2 value of 0.14. The linear regression of soil moisture by methane flux can be found in Figure 4.

[29] Finally, in order to evaluate the impact of time or cumulative effects of N treatments, the methane flux data were run in a repeated measures framework using averaged time points (across blocks) at each of 15 analogous fertilization statuses (Figure 5). The model was simplified to preserve degrees of freedom. All between plots interactions were significant ($p < 0.0010$), as were site ($p < 0.000$), N treatment ($p < 0.0288$) and site by N treatment ($p < 0.0131$). Due to lost degrees of freedom, F tests were not possible for within plot interactions. Univariate unadjusted epsilon probability values were used instead, and all tests were significant, including all within interactions ($p < 0.0001$), time ($p < 0.0001$), time by site ($p < 0.0001$), time by N treatment ($p < 0.0010$) and time by site by N treatment ($p < 0.0485$).

3.3. Oxygen Analysis

[30] The addition of N correlated with lower soil O_2 concentrations in the field plots and growth chamber pots studied, as analyzed using matched pairs t-tests. In the field, the O_2 sensors at 5 cm depth in the unfertilized plot found an average of 21.11% of the volume of air, while those in the fertilized plot were lower, at 20.52% ($p < 0.0001$). In the laboratory growth chamber, the average soil O_2 concentration of the unamended (control) pots in the growth chamber was 21.76% of the volume of air, the average of the watered pots was 21.80%, and the average for the N-fertilized and watered pots was 21.71%. The fertilized pots had significantly lower O_2 concentrations than the unamended pots ($p < 0.029$),

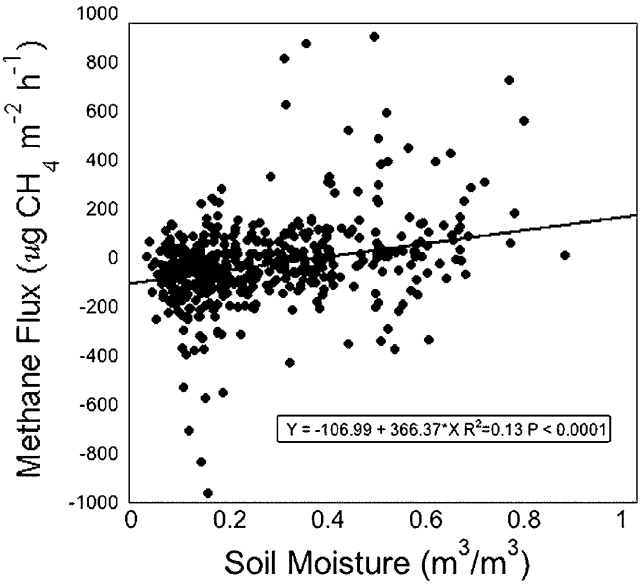

Figure 4. Linear regression of soil moisture by CH_4 flux across all plots and measurement dates in both sites. Soil moisture is given as the volume of water out of the total intact soil volume.

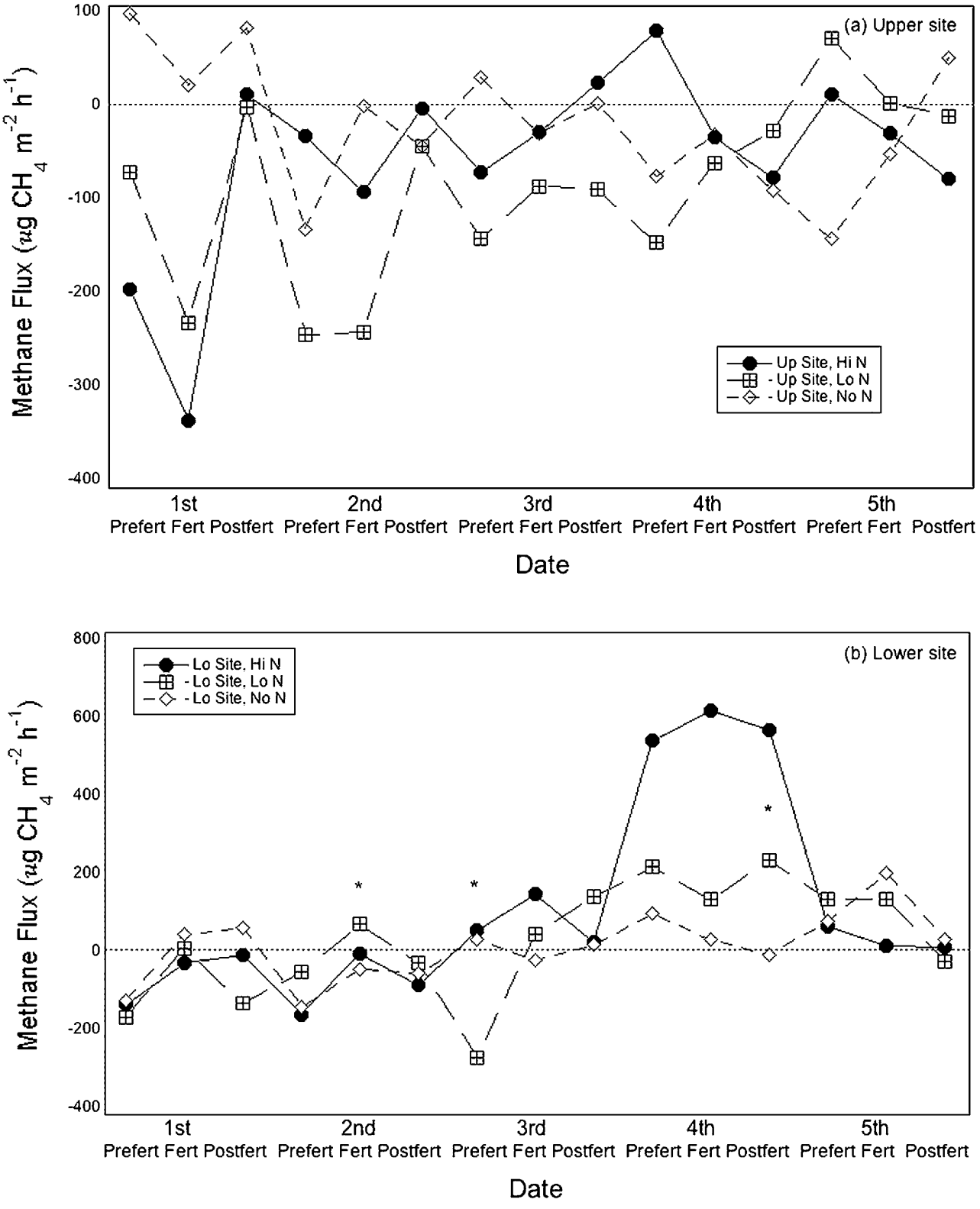

Figure 5. Average methane fluxes across time, pooled by fertilization stage for (a) upper and (b) lower sites. Dates of pre-fertilization are shown as "Prefert," fertilization dates are shown as "Fert," and post-fertilization dates are shown as "Postfert." Asterisks indicate dates where CH_4 fluxes were significantly different between treatments.

with no significant difference between the control and watered pots O_2 concentrations ($p < 0.732$) nor between the fertilized and watered pots ($p < 0.141$). There was no significant impact of treatment on CH_4 flux in the growth chamber ($p < 0.818$). The average CH_4 flux in growth chamber pots was -13.57 μg CH_4 m^{-2} h^{-1} for control, -6.26 μg CH_4 m^{-2} h^{-1} for watered pots, and -12.33 μg CH_4 m^{-2} h^{-1} for N-fertilized and watered pots.

4. Discussion

[31] Methane flux across the soil-air interface in this pine forest was the result of complex interactions between the soil microbial community and both environmental and climatic variation. Much of the observed variation in CH_4 flux was attributable to site location, soil moisture, and N treatment. However, a high level of replication in the experimental setup and a suite of environmental variables were needed to explain the full extent of variation in CH_4 flux. The effects of location, N treatment and their interaction were also found to differ across time, but this did not appear to be a seasonal trend. This may be due to differing thresholds for the microbial response to N amendment in the two sites.

[32] There were many differences in soil texture and composition between the two neighboring sites, which are likely due to long-term disparities in soil moisture from elevation-driven drainage dissimilarities. There were significant differences in soil conditions and nutrient status, including bulk density, % N and % C, as well as inorganic nitrogen content, throughout the season. All soil measures showed greater differences between well and poorly drained sites, rather than between plots within each site. Therefore, in a deviation from much of the published literature, the differences in soil moisture alone did not drive methane flux variation in this forest, but rather the complex effects of how those differences in water table affected the soil in the long term.

[33] Soil moisture was the variable with the strongest correlation with CH_4 flux, with higher CH_4 release at greater soil moisture content. This is consistent with the published literature, since methanogens are known to be more active in anaerobic, poorly drained conditions, while methanotrophs need access to oxygen and CH_4 in order to be active [*Le Mer and Roger*, 2001]. The correlation between soil moisture and CH_4 consumption was significant, but low relative to those reported in the literature [*Groffman and Pouyat*, 2009; *Adamsen and King*, 1993]. A review of the literature found that at least 20 field CH_4 flux studies showed some measure of soil moisture (gravimetric, by volume or by water filled pore space) to be the most important factor in determining CH_4 flux (E. L. Aronson and B. R. Helliker, Review of non-wetland soil methane flux: Impacts of environment, climate change and methodology, submitted to *Geoderma*, 2011). Of those, 17 found increased moisture correlated with decreased CH_4 consumption (or increased release). Another three studies found the opposite response. A study performed in desert soils [*Angel and Conrad*, 2009] and one in boreal forest [*Ambus and Christensen*, 1995] found that both CH_4 release and consumption increased with dryer soils. The third study found both positive and negative relationships between water table height and CH_4 release in boreal forest [*van Huissteden et al.*, 2008]. Other studies found that soil moisture was relatively similar across sites and did not correlate with CH_4 flux as well as it did with vegetation or other factors [i.e., *Reay et al.*, 2005].

[34] The total magnitude of CH_4 flux in the well-drained upper site was -5.38 kg CH_4 ha^{-1} yr^{-1}, if extrapolated across the year. This number is similar in magnitude to the global average for forest CH_4 consumption reported by *Dutaur and Verchot* [2007] as -5.70 kg CH_4 ha^{-1} yr^{-1}, based on 92 temperate forest sites. The associated variance was 31.5 kg CH_4 ha^{-1} yr^{-1}, an order of magnitude larger than all other ecosystems they included in their analysis. Within temperate forests, *Dutaur and Verchot* [2007] showed coarse (sandy) soil CH_4 flux to be -7.5, and organic soils -4.6, kg CH_4 ha^{-1} yr^{-1}, a range that brackets the flux in the upland site. *Smith et al.* [2000] found sites across Europe to range in average CH_4 consumption rate from 0.1 to 9.1 kg CH_4 ha^{-1} yr^{-1}. That study found that the main determinant of whether soil was a net sink or source was the position of the surface relative to the water table, and that most soils were sinks [*Smith et al.*, 2000]. In the Pinelands, the poorly drained site represents a minority of the soil types and drainage regimes, so that the best estimate for overall flux comes from the well-drained site. If both the well- and poorly drained sites were weighted evenly, we would have found an average flux in the Pinelands of -0.84 kg CH_4 ha^{-1} yr^{-1}, which grossly underestimates the contribution of this site to the global CH_4 sink. Many of the papers included in the review by *Dutaur and Verchot* [2007] and a meta-analysis [*Aronson and Helliker*, 2010] took snapshots of the ecosystems they studied in both space and time, not accounting for key environmental variation within these sites. Low levels of replication within some previously published studies of CH_4 flux may be the reason their results are highly variable. When many of these results are taken together, the average flux across forests has a similar magnitude and level of variation to what we have found in the upland Pinelands forest in New Jersey.

[35] The control plots in the poorly drained, lower site did not release CH_4 overall, and without N amendment the lower site had a net flux near zero. This is in contrast with most water-saturated soils, which are known to emit CH_4 regularly. This finding hints that the patchiness of forests with respect to hydrology, when coupled with high N deposition, should result in drastic variation in CH_4 dynamics within the system. On average, under low N deposition, different locations within the forest may vary in magnitude of CH_4 consumed, but not in the direction of flux. The implication is that long-term or large-scale models and predictions based on limited observed flux may be more plausible than earlier observations suggested. However, observations in forests with high N deposition may not have the same predictive capacity because the cumulative effects of N deposition may be hard to quantify. For example, the poorly drained site borders on a seasonal stream about a hundred meters away, which may receive inorganic N from agricultural run-off upstream. These results indicate that such influxes may cause CH_4 release from soil that is otherwise not a net source or sink.

[36] The lower site had greater spatial and temporal variance in CH_4 flux. The well-drained site showed relatively little variation and did not respond as strongly to the treatments and environmental variations as the poorly drained site. Rather, the upper site consumed CH_4 at a relatively

steady rate throughout the experimental timeframe. The CH_4 flux measurements in the lower site, however, were highly variable. This highlights the importance of soil moisture in determining CH_4 flux in both sites, rather than intermittent precipitation events, which did not correlate with changes in CH_4 flux. The well-drained site, likely due to its low water holding capacity and relatively low water table, may have shown resilience to perturbations of inorganic nitrogen content, precipitation, and temperature. Resilience to N disturbance was seen in the microbial community in a nearby, similar site by *Krumins et al.* [2009].

[37] The interactive effects of site and N addition suggest that soil drainage conditions are important in predicting CH_4 responses to N levels. Upon first N application in the well-drained site, there was a nonsignificant effect of greater consumption with greater N addition that disappeared throughout the rest of the growing season. This may indicate that the microbial community in the well-drained soil is sensitive to N amendment, but undergoes rapid succession to a different, resistant community. Alternatively, the extant microbial community may have quickly adapted to the higher N condition. The first N applications did not impact CH_4 flux in the poorly drained site, but the high N treatment emitted more CH_4 after several applications. In the poorly drained site, therefore, the microbial community showed resistance to the perturbation of N amendment until a certain threshold is reached. At that point, either a well-adapted group of methanogens took over in the high N plots, or the N limitation of the existing methanogens was relieved; both explanations would result in the observed short burst of CH_4 release. The period of release may have ended because the methanotroph population grew in response and consumed the extra CH_4. There are multiple potential explanations for these observations, and in depth study of the microbial community may present findings that clarify which explanation is correct.

[38] The rate of CH_4 release in the poorly drained site increased with high N addition, when averaged across the growing season. This result is consistent with the conclusions drawn in a meta-analysis on the same topic [*Aronson and Helliker*, 2010]. However, this trend was not seen in the well-drained site, probably due to the excessive drainage provided by the sandy texture of the upper site soil. There is an overlying organic layer of variable depth which may hold onto water and soluble compounds; the sand below, however, is known to drain excessively [*Krumins et al.*, 2009], allowing rapid leaching. Soil texture is known to regulate CH_4 flux to a certain extent [*Dutaur and Verchot*, 2007], but there is little published information about the interactive effects of soil texture and moisture on CH_4 flux.

[39] The data here presented are limited to net flux of CH_4 across the soil surface, and therefore trends cannot be attributed to variation in the community or actions of methanogens or methanotrophs specifically. As methanotrophs are thought to be more responsive to nitrogen variation than methanogens [*Hanson and Hanson*, 1996], it is possible that the increase in CH_4 release in poorly drained high N plots, was due to suppression of methanotrophy. However, it has been shown that under low N conditions, the addition of N fertilizer can stimulate methane consumption [*Bodelier and Laanbroek*, 2004], but also methanogenesis [*Liu et al.*, 2011] so the origin of the observed responses is not clear. This is an active area of research and further study is necessary to identify clear causal relationships in CH_4 cycle responses to N addition [*Bodelier*, 2011].

[40] Indirect effects may play a large role in the control of CH_4 flux across and between the two sites. N addition may have stimulated oxygen-consuming microbial activities in the poorly drained soil other than CH_4 oxidation. The resultant decrease in redox potential of the soil may have stimulated methanogenesis, driving the patterns seen in response to N addition in the lower site. Unfortunately, the oxygen sensors were not placed inside of treatment areas, and were only in place for half of the field season, so this effect was not tested directly. When we returned to the field site the following summer we did see a decrease in soil O_2 concentration in response to N addition, both in the lab and in the field. However, there was no significant associated change in CH_4 flux when studied in the growth chamber. Analysis of the microbial community itself is needed to approach these questions.

5. Conclusions

[41] Although soil moisture was the greatest predictor of CH_4 flux across well- and poorly drained soils in this pine forest, it was necessary to create a complex statistical model using many environmental variables to capture the full variation in methane flux. The forest was a net sink for atmospheric CH_4 at rates that are similar to other forests across the globe. Drainage of the soil determined the response to environmental variation and treatments. The CH_4 flux rate in the well-drained soil showed either fast adaptation or resilience to perturbation, specifically N addition and natural variation in temperature and moisture. The poorly drained soil showed high variance that was driven by soil moisture and nitrogen addition, with a large release of CH_4 after a threshold of N addition was reached. These results are consistent with previous data on the inhibition of net CH_4 consumption by nitrogen addition. Further study of the microbial community should be performed to confirm the underlying cause of these trends in net CH_4 flux. The complex observed relationships between environmental variables and CH_4 flux indicate intricate relationships between environmental changes and microbial communities that deserve further study.

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