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Forest ecosystem changes from annual methane source to sink depending on late summer water balance

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Key Points

Summer precipitation may moderate a methane source-sink transition at this site

Ecosystem-scale photosynthesis correlates with methane fluxes over short and long timescales

Multiyear flux datasets are needed to build predictive understanding
Abstract

Forests dominate the global carbon cycle, but their role in methane (CH$_4$) biogeochemistry remains uncertain. We analyzed whole-ecosystem CH$_4$ fluxes from two years, obtained over a lowland evergreen forest in Maine, USA. Gross primary productivity (GPP) provided the strongest correlation with the CH$_4$ flux in both years, with an additional significant effect of soil moisture in the second, drier, year. This forest was a neutral to net source of CH$_4$ in 2011 and a small net sink in 2012. Inter-annual variability in the summer hydrologic cycle apparently shifts the ecosystem from being a net source to a sink for CH$_4$. The small magnitude of the CH$_4$ fluxes and observed control or CH$_4$ fluxes by forest productivity and summer precipitation provide novel insight into the CH$_4$ cycle in this globally important forest ecosystem.

Introduction

Global forests remove CO$_2$ from the atmosphere at a rate of ~2.4 Pg C per year [Pan et al., 2011]. The role of forests in methane (CH$_4$) cycling, however, has not been well constrained, in part because of difficulties in assessing CH$_4$ fluxes at the landscape scale. Most of what is known about forest CH$_4$ fluxes is derived from chamber measurements at the level of the soil surface, which show that many forest soils are net consumers of atmospheric CH$_4$ [Megonigal and Guenther, 2008]. Globally, CH$_4$-consuming bacteria in terrestrial soils are believed to account for approximately 5% of total CH$_4$ oxidation, the second largest sink of atmospheric CH$_4$ while anaerobic (saturated) soils are strong sources of CH$_4$ [Forster et al., 2007]. The division between what constitutes a CH$_4$ producing vs consuming soil is murky with upland soils demonstrated to emit CH$_4$ under
certain circumstances [Savage et al., 1997; Whalen et al., 1991; Yavitt et al., 1995; Yavitt et al., 1990] and localized (often discrete) soil flux measurements are difficult to scale up due to their high spatial and temporal variability.

Forests with high water tables and organic-rich soils, such as many boreal forests, provide an especially complex picture with dry and wet soil conditions intermixed due to small-scale topographic variability. Such forests have the most potential to produce and emit significant quantities of CH₄. In addition, direct interaction of trees with forest CH₄ emissions have also been posited, either aerobically [Keppler et al., 2006], through internal anaerobic rot [Covey et al., 2012], or with the trees acting as conduits for soil-produced CH₄ dissolved in the transpiration stream [Nisbet et al., 2009; Pangala et al., 2013]. Determining what controls the magnitude and seasonality of forest CH₄ fluxes above the canopy will define the roles of forest soils and trees in the global CH₄ cycle.

Recent improvements in fast-response CH₄ analyzers have made it possible to measure ecosystem-scale CH₄ fluxes by eddy covariance [Peltola, 2011; Smeets et al., 2009; Wang et al., 2013]. Here we present and analyze the first multi-year eddy covariance time series of CH₄ fluxes from a forested ecosystem. The results show that the site was a neutral to small net source of CH₄ during 2011 but a net sink during 2012. Importantly, no strong CH₄ sources, either from the soils or trees, are indicated by this study. The strongest correlate for the 4-day averaged CH₄ flux dynamics was GPP during both years, with soil moisture accounting for significant variance during dry periods. Our results suggest that multi-year studies will be critical to developing model structures capable of reproducing net fluxes and predicting changes in future CH₄ fluxes from forested ecosystems.
Methods

Site Description

Research was conducted at the Howland Forest AmeriFlux site located about 35 miles north of Bangor, Maine, USA (45°15’ N, 68°44’ W, 60 m asl) on forestland owned by the Northeast Wilderness Trust. Howland Forest is a boreal-temperate transition forest, with stands dominated by red spruce (*Picea rubens* Sarg.) and eastern hemlock (*Tsuga canadensis* (L.) Carr.) with lesser quantities of other conifers and hardwoods. The soils have never been cultivated and the upland soils are classified as Skerry fine sandy loam, Aquic Haplorthods. Peats have formed in the poorly drained positions dominated by sphagnum. Fernandez et al. [1993], and Hollinger et al. [1999; 2004] have previously described the climate, soils, and vegetation at the site.

Flux measurements

Fluxes were measured at a height of 29 m with systems consisting of a model SAT-211/3K 3-axis sonic anemometer (Applied Technologies Inc., Longmont, CO, USA) and a fast-response CH₄/CO₂/H₂O cavity ring down spectrometer (model G1301-f in 2011 and G2311-f in 2012; Picarro Inc., Santa Clara, CA) with data recorded at 5 Hz. The CO₂ flux measurements were also independently quantified with a co-deployed fast response CO₂/H₂O infrared gas analyzer (model Li-7200, Li-Cor Inc., Lincoln, NE, USA). In 2011, H₂O concentrations measured with the Li-7200 were used for density correction of CO₂ and CH₄ fluxes measured with the G1301-f because that instrument could not output all three concentrations simultaneously. Fluxes were calculated and filtered according to Hollinger et al. [1999; 2004]. In 2012, fluxes were calculated via the same equations and assumptions (600 s time constant running mean filter, double rotation, etc.) using
commercially available software (EddyPro version 4, Li-Cor Inc., Lincoln, NE, USA). In both years, the CO₂ fluxes were nearly identical between the Picarro and Licor analyzers (Fig S1). The sign convention used is that flux to the ecosystem is defined as negative. Further details on the filtering of the flux data are available in the SI.

Environmental Data

Profiles of soil temperature and soil moisture were measured hourly at 5, 10, 20, 50, and 100 cm using Hydra probes (Stevens Water Monitoring Systems Inc., Beaverton, OR, USA) 20 near the base of the tower. Water table depth was measured using a barometrically compensated pressure transducer (model WL400, Global Water, Gold River, CA, USA) in a shallow well. Solar radiation (photosynthetic photon flux density, PPFD), air temperature, and precipitation were measured from the top of the flux tower as described previously [Hollinger et al., 2004]. We note that the measurement scale for the soil data differs from that of the flux data.

Statistical Analyses

The half-hourly CH₄ flux data were low-pass filtered to give a set of mean fluxes, each representing a 4-day window. This was combined with Monte-Carlo resampling in order to obtain an estimate of the uncertainty on these mean fluxes. Details are available in the SI.

We used an Artificial Neural Network (ANN) to characterize the climatic sensitivity of ecosystem-atmosphere CH₄ exchange and to estimate annual CH₄ budgets. This methodology choice is supported by a recent study showing the effectiveness of ANNs for gap-filling CH₄ fluxes [Dengel et al., 2013]. An ANN is an inductive approach based
on statistical multivariate modeling [Bishop, 1995; Rojas, 1996] by which one can map
drivers directly onto observations [Moffat et al., 2010]. We used a feed-forward ANN
with a sigmoid activation function trained with a back propagation algorithm. An
ensemble of 100 ANNs was trained both on the hourly and running mean aggregated
eddy-covariance CH$_4$ fluxes independently. See SI for description of our 3-stage training
process.

**Results**

Many variables including GPP, air temperature, PPFD, CO$_2$ flux, and soil moisture and
soil temperature at 10 and 20 cm were significantly correlated (Kendall rank correlation,
p<<0.01) with the CH$_4$ flux signal in both years, but any combination of these variables
explains only a small fraction of the variation in the CH$_4$ fluxes (multiple r$^2$$<0.05$) at the
30 minute time step. The neural network approach was able to explain a maximum of 8-
10% of the total variability in the data for each year (Fig S3) using a combination of
environmental drivers (GPP, air temperature, wind direction, wind speed, relative
humidity, soil moisture, soil temperature, and water table depth). The individual driver
with the highest explanatory power in the ANN was air temperature in 2011 and GPP in
2012. These low correlations emerge because of the large random errors (noise) in the
measurement, which argues for the use of statistical approaches for time averaging of the
data to reduce uncertainties and permit elucidation of the trends.

Averaging the fluxes by time of day, we observed more CH$_4$ efflux during the daytime
and more CH$_4$ consumption at night. This pattern was only present during summer
months (Fig S4). We used a wavelet coherence analysis as an alternate approach for
examining the significance of this diurnal structure. Using this analysis we found
coherent periodic behavior in both the CH$_4$ and GPP signals at the 18-28 hour time scale over the summer and early fall seasons, although the time periods when this relationship was significant were intermittent. The coherence between the CH$_4$ flux and GPP signals was stronger than between CH$_4$ flux and air temperature. Due in part to the intermittent nature of the coherence, it was not possible to determine whether CH$_4$ flux lagged GPP, which could potentially indicate a causal relationship.

The use of 4-day mean fluxes elucidated the seasonal pattern in the CH$_4$ flux data. CH$_4$ fluxes were mostly positive during the summer months, trending negative in the late summer or fall, then remaining consistently negative through the winter months (Fig 1). By comparison, the CO$_2$ fluxes (here processed as GPP) showed the opposite pattern with the highest rates of CO$_2$ uptake during the midsummer, followed by decreasing uptake through the fall into the winter.

The spring and summer precipitation patterns differed between 2011 and 2012. While the total annual precipitation measured at the tower was lower in 2011 (870 mm) than in 2012 (940 mm), the precipitation during July and August was much greater during 2011 than 2012 (224 vs 76 mm). This precipitation change led to a large difference in summer/fall soil moisture between the years (Fig 1). Historical precipitation data (http://www.ncdc.noaa.gov/cdo-web/) from Millinocket station (located ~50 km north of Howland forest) for July and August for 1970-2010 gives a mean ($\pm$ 1sd) precipitation of 200 $\pm$ 73 mm for those months combined. In 2011 Millinocket recorded July-August precipitation of 282 mm during 2011, compared with 127 mm for 2012, indicating that 2011 was wetter than the 40-yr average whereas 2012 was drier than average.
Using a wide selection of variables (air temperature, soil temperature, soil moisture, wind direction, water table depth, relative humidity, and wind speed) the ANN produced a model explaining nearly 65% and 90% of the variability in the 4-day CH$_4$ fluxes during 2011 and 2012. However, to reduce the redundancy due to correlations between many of these drivers, we forced the ANN to use GPP and then tested for the additional explanatory power (if any) attained by each remaining driver (Fig 2, S5). GPP was chosen because it was the individual variable with the highest explanatory power in both years. The importance of each driver using this reduced approach is shown in Fig 2. We observe that, in 2011 and 2012 respectively, variation in GPP accounted for 60% and 50% of the variability in the 4-day CH$_4$ fluxes. Including soil moisture increases the explanatory power of the model by >10% during 2012 (the drier year) but has negligible influence in 2011 (the wetter year). Therefore, a model using only GPP and 10-cm soil moisture was able to explain ~ 60 and 70% of the variability in 4-d mean CH$_4$ fluxes for 2011 and 2012. All other drivers provide negligible improvement to the model fit. This order of importance of drivers was supported by separate linear regression analysis (Table S1).

Despite the fact that the principal environmental drivers were the same in both years, models derived from the 2011 fluxes did a poor job predicting CH$_4$ fluxes in 2012, and vice versa (Fig. S6). We also trained the model on the 4-day means from both years together and while the ANN produced a model that explained 40% of the variability in all the data this represented a substantial decrease in goodness-of-fit compared to modeling each year individually.
We estimated the annual CH$_4$ budgets for 2011 and 2012 for Howland forest in two ways; using either the ANN or a linear model combined with Monte Carlo resampling. Using the linear modeling approach (Fig S7) we estimate net efflux (mean ± 1sd) of 7 ± 4.6 mmol m$^{-2}$ yr$^{-1}$ for 2011 and consumption -18 ± 2.7 mmol m$^{-2}$ yr$^{-1}$ for 2012. Using the ANN, annual fluxes were 6 ±11 mmol m$^{-2}$ yr$^{-1}$ for 2011, and -9 ± 3.7 mmol m$^{-2}$ yr$^{-1}$ for 2012 (Fig 2). Larger uncertainties were contributed by the first few months of the year due to the absence of measurements to constrain the model during these periods. This increase in variance was particularly large in the ANN because of its inherently nonlinear structure. Both approaches indicated that the annual CH$_4$ flux in 2011 was small but likely positive while the forest was a net consumer of CH$_4$ in 2012.

**Discussion**

The lowland evergreen forest studied was an intermittent source of CH$_4$ to the atmosphere, showing efflux from July through October during 2011, and from June through July 2012 while recording net uptake for the remainder of each year (Fig 1). Using an artificial neural network (ANN), we found that a combination of GPP and 10-cm soil moisture was able to explain 60 and 70% of the variability in 4-d mean CH$_4$ emissions for 2011 and 2012 individually (Fig 2), while use of all the drivers resulted in a model explaining nearly 90% of the variability during 2012 (the maximum explainable variance in 2011 is just above 60%). Additionally, a diurnal cycle was present in the CH$_4$ flux signal during the summer and fall that was consistent with that observed in GPP. The ANN, supported by linear modeling, consistently found GPP to be a stronger correlate of the 4-day mean CH$_4$ fluxes than air temperature.
Gross primary production is highly correlated with a wide variety of other environmental parameters, such as air temperature, PPFD, and soil temperature, and it could be argued that GPP is driving CH$_4$ emissions only indirectly through cross-correlations. The a priori assumption would be that CH$_4$ fluxes are controlled by soil moisture [Adamsen and King, 1993; Castro et al., 1994; Castro et al., 1995] due to the dependence of both CH$_4$ oxidation and CH$_4$ production on soil diffusivity (through O$_2$ availability) with temperature being a secondary controlling variable [Castro et al., 1995] due to the positive influence of temperatures on reaction rates (positive Q10 values). However, both the neural network and linear modeling approaches found GPP to be the stronger predictor of CH$_4$ emissions when treating each year individually, or together, with soil moisture only important during 2012.

There are several mechanistic reasons why changes in GPP may lead to changes in CH$_4$ emissions. First, CH$_4$ production rates have been linked to photosynthesis through root exudation in some wetlands [King and Reeburgh, 2002]. Carbon isotope studies have shown that most CH$_4$ released from wetlands is derived from “new carbon” rather than from dissolved soil organic matter [Chanton et al., 1995]. In a rice paddy, wavelet coherence analysis found the diurnal cycle in CH$_4$ emissions to be driven by GPP [Hatala et al., 2012]. However, trees may also be influencing the seasonal and diurnal cycle if dissolved CH$_4$ is emitted through transpired soil water [Nisbet et al., 2009], such that GPP could be more proxy than mechanism. It is more difficult to directly connect CH$_4$ oxidation and GPP, although microbial priming could link these processes. In this case, carbon leakage from the roots of trees and other plants increases total microbial activity; because many CH$_4$ oxidizing bacteria are capable of consuming a wide variety of
methylated substrates their population dynamics could respond to overall soil carbon degradation rates, leading to higher rates of CH$_4$ oxidation linked to increased soil respiration activity. We interpret these results as indicating a significant role for GPP in influencing CH$_4$ flux, both in its high frequency and low frequency variability although we acknowledge that the mechanism is not yet clear.

The role of soil moisture in forest CH$_4$ flux may involve a threshold: once volumetric soil moisture exceeds some level (here ~0.1WFV), there are sufficient anoxic pore spaces to support CH$_4$ production near the surface and correlations become weak, while below this threshold, soil moisture is an important factor controlling the balance between CH$_4$ production and CH$_4$ oxidation. It is also possible that the lower correlations are a result of spatial variability in soil moisture over the tower footprint related to the small-scale topography that was not captured by this study. However, the trends of drying and wetting, also observed in the precipitation data, would be expected to be felt to some degree throughout the landscape. Overall, we found soil moisture had a smaller overall influence than GPP but remains important under drier conditions.

Despite the high correlations of a model using GPP and soil moisture to the data in each year, the explanatory power of these models diminished almost to zero when applied to data on which the model was not trained (Fig S6). Similar challenges have been observed with modeling CH$_4$ fluxes [Mastepanov et al., 2012; Moore et al., 2011; Treat et al., 2007], as well as CO$_2$ fluxes [Richardson et al., 2007] from a variety of environments.

Net CH$_4$ emission is the result of two processes acting in opposition – CH$_4$ production and CH$_4$ oxidation, and it appears that a correlative model based on emissions may lack the appropriate structure needed to extrapolate fluxes over longer timescales, despite
success over shorter timescales. Achieving an appropriate model structure and
complexity is necessary for improving the CH$_4$ components of larger earth-system
models and predicting natural CH$_4$ emissions from forests under changing environmental
conditions. Multiple years of flux measurements under a range of conditions will be
needed to accurately characterize the climatic and physiological dependence of forest
CH$_4$ fluxes. Experimental methods combining ecosystem-scale flux measurements, soil
chamber flux measurements, and soil-gas profiles may also provide needed insight into
the mechanistic controls driving both the sign and magnitude of CH$_4$ flux.

In the context of the overall climate impact of greenhouse gas fluxes at this site, the CH$_4$
fluxes are small contributors (see SI) relative to the total CO$_2$ uptake. This contrasts with
other ecosystems, such as boreal wetlands where the climate impact of CH$_4$ fluxes can be
larger than the climate benefit of their CO$_2$ uptake [Whiting and Chanton, 2001].

Conclusions

We provide the first multi-year set of CH$_4$ fluxes measured by eddy-covariance over a
forested ecosystem. Multi-year data sets of CH$_4$ fluxes capturing a wide variety of
environmental conditions are critical to developing model structures that are capable of
adequately predicting future CH$_4$ fluxes. GPP provided the strongest correlation with the
calculated 4-day mean CH$_4$ fluxes during each year. Including soil moisture as a driver
for CH$_4$ production improved the fit of the model only during 2012, which had a drier
than average summer. Despite the potential for CH$_4$ efflux from this temperate-boreal
transition site, our observations suggest that neither the soils nor trees are large sources of
CH$_4$ from the forest to the atmosphere. This study finds evidence for a link between GPP
and CH$_4$ flux, and a small sink/source transition controlled by summer hydrologic conditions.

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References


**Figure Legends**

Figure 1: The 4-day running mean CH$_4$ fluxes (open circles) with 4-day mean GPP (grey stars) and volumetric soil moisture at 10 cm (black squares). Data from 2011 is shown in the top panel against data from 2012 in the lower panel. The dotted black line highlights the line of 0 flux, above which the forest is a net source of CH$_4$ to the atmosphere and below which the forest is a net sink for CH$_4$.

Figure 2: Results from the ANN for both years, with the top panels indicating the importance of various environmental drivers contributing to the model. Each environmental driver is shown separately with the black portion of the column indicating the additional predictive power this driver gives the model when combined with GPP (the grey portion of the column). The horizontal dotted lines indicate the maximum attainable predictive capacity if all drivers are used simultaneously. The bottom panels show the ANN modeled fluxes for the entire year (black lines) ± 1 sd (vertical bars).