



RESEARCH LETTER

10.1002/2013GL058691

Key Points:

- Summer precipitation may moderate a methane source-sink transition at this site
- CH₄ fluxes are small at this high water-table boreal-temperate forest site
- Multiyear datasets are needed to build predictive understanding

Supporting Information:

- Readme
- Supplementary Figures S1–S7 and Table S1

Correspondence to:

J. K. Shoemaker,
jshoemak@fas.harvard.edu

Citation:

Shoemaker, J. K., T. F. Keenan, D. Y. Hollinger, and A. D. Richardson (2014), Forest ecosystem changes from annual methane source to sink depending on late summer water balance, *Geophys. Res. Lett.*, 41, 673–679, doi:10.1002/2013GL058691.

Received 14 NOV 2013

Accepted 1 JAN 2014

Accepted article online 6 JAN 2014

Published online 24 JAN 2014

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

Julie K. Shoemaker¹, Trevor F. Keenan², David Y. Hollinger³, and Andrew D. Richardson¹
¹Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, Massachusetts, USA, ²Department of Biological Sciences, Macquarie University, North Ryde, Sydney, Australia, ³USDA Forest Service-Northern Research Station, Durham, New Hampshire, USA

Abstract Forests dominate the global carbon cycle, but their role in methane (CH₄) biogeochemistry remains uncertain. We analyzed whole-ecosystem CH₄ fluxes from 2 years, obtained over a lowland evergreen forest in Maine, USA. Gross primary productivity provided the strongest correlation with the CH₄ 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 CH₄ in 2011 and a small net sink in 2012. Interannual variability in the summer hydrologic cycle apparently shifts the ecosystem from being a net source to a sink for CH₄. The small magnitude of the CH₄ fluxes and observed control of CH₄ fluxes by forest productivity and summer precipitation provide novel insight into the CH₄ cycle in this globally important forest ecosystem.

1. Introduction

Global forests remove CO₂ from the atmosphere at a rate of ~2.4 Pg C per year [Pan *et al.*, 2011]. The role of forests in methane (CH₄) cycling, however, has not been well constrained, in part because of difficulties in assessing CH₄ fluxes at the landscape scale. Most of what is known about forest CH₄ fluxes is derived from chamber measurements at the level of the soil surface, which show that many forest soils are net consumers of atmospheric CH₄ [Meronigal and Guenther, 2008]. Globally, CH₄-consuming bacteria in terrestrial soils are believed to account for approximately 5% of total CH₄ oxidation, the second largest sink of atmospheric CH₄, while anaerobic (saturated) soils are strong sources of CH₄ [Denman *et al.*, 2007]. The division between what constitutes a CH₄ producing versus consuming soil is murky with upland soils demonstrated to emit CH₄ under certain circumstances [Savage *et al.*, 1997; Whalen *et al.*, 1991; Yavitt *et al.*, 1990, 1995], 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 has 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, 2013; Smeets *et al.*, 2009; Wang *et al.*, 2013]. Here we present and analyze the first multiyear 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 gross primary productivity (GPP) during both years, with soil moisture accounting for significant variance during dry periods. Our results suggest that multiyear studies will be critical to developing model structures capable of reproducing net fluxes and predicting changes in future CH₄ fluxes from forested ecosystems.

2. Methods

2.1. Site Description

Research was conducted at the Howland Forest AmeriFlux site located about 56 km north of Bangor, Maine, USA (45°15'N, 68°44'W, 60 m above sea level) 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.

2.2. 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 (Figure 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 supporting information.

2.3. 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.

2.4. 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 supporting information.

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 4-day mean aggregated eddy covariance CH₄ fluxes independently. See supporting information for description of our three-stage training process.

3. Results

Many variables including GPP, air temperature, PPFD, CO₂ flux, and soil moisture and soil temperature at 10 and 20 cm were significantly correlated (Kendall rank correlation, $p < 0.01$) with the CH₄ flux signal in both years, but any combination of these variables explains only a small fraction of the variation in the CH₄ fluxes (multiple $r^2 < 0.05$) at the 30 min 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 (Figure S3) using a combination of environmental drivers (GPP, air temperature, wind direction, wind speed, relative humidity, soil moisture, soil temperature, and water table

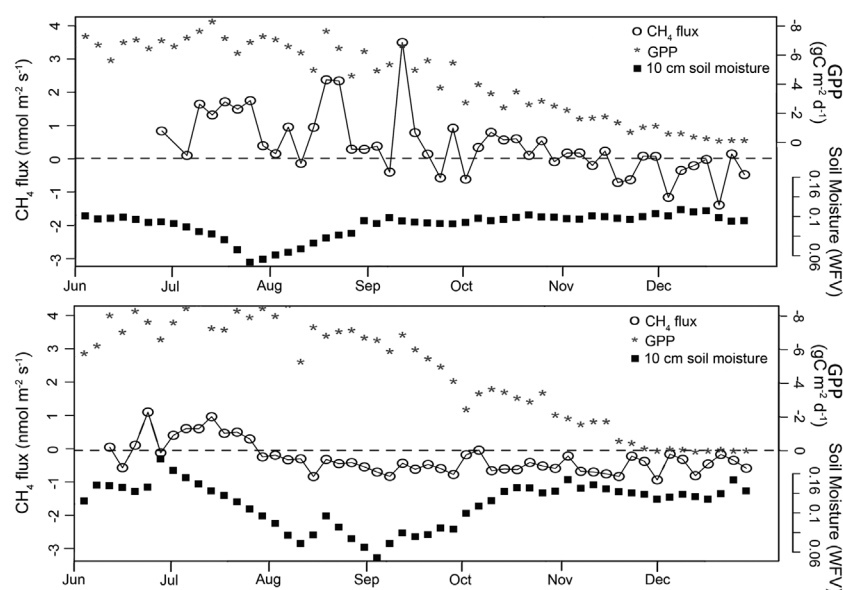


Figure 1. The 4 day mean CH_4 fluxes (open circles) with 4 day mean GPP (grey stars) and volumetric soil moisture at 10 cm (black squares). (top) Data from 2011. (bottom) Data from 2012. The dotted black line highlights the line of 0 flux, above which the forest is a net source of CH_4 to the atmosphere and below which the forest is a net sink for CH_4 .

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 the time of the 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 (Figure 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 h 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 (Figure 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 versus 76 mm). This precipitation change led to a large difference in summer/fall soil moisture between the years (Figure 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 give a mean (± 1 sd) precipitation of 200 ± 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 year 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 (Figures 2 and S5). GPP was chosen because it

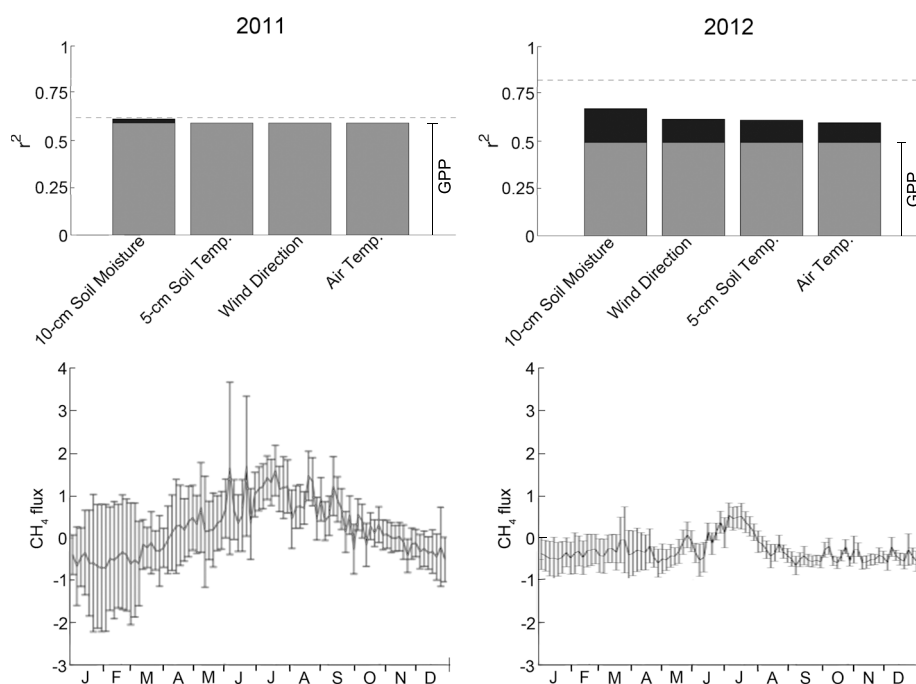


Figure 2. Results from the ANN for (left) 2011 and (right) 2012. Figure 2 (top) indicates the importance of various environmental drivers contributing to the model. Each environmental driver is shown separately with the black portion of the column indicating the additional predictive power this driver 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. Figure 2 (bottom) shows the ANN modeled fluxes for the entire year (black lines) ± 1 sd (vertical bars).

was the individual variable with the highest explanatory power in both years. The importance of each driver using this reduced approach is shown in Figure 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 (in addition to GPP) 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 day 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 (Figure 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 (Figure S7) we estimate net efflux (mean ± 1 sd) of $7 \pm 4.6 \text{ mmol m}^{-2} \text{ yr}^{-1}$ for 2011 and consumption $-18 \pm 2.7 \text{ mmol m}^{-2} \text{ yr}^{-1}$ for 2012. Using the ANN, annual fluxes were $6 \pm 11 \text{ mmol m}^{-2} \text{ yr}^{-1}$ for 2011 and $-9 \pm 3.7 \text{ mmol m}^{-2} \text{ yr}^{-1}$ for 2012 (Figure 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.

4. 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 (Figure 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 day mean CH₄ emissions for 2011 and 2012 individually (Figure 2), while the 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 CH₄ 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 CH₄ 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 CH₄ emissions only indirectly through cross correlations. The a priori assumption would be that CH₄ fluxes are controlled by soil moisture [Adamsen and King, 1993; Castro *et al.*, 1994, 1995] due to the dependence of both CH₄ oxidation and CH₄ production on soil diffusivity (through O₂ 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 CH₄ 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 CH₄ emissions. First, CH₄ production rates have been linked to photosynthesis through root exudation in some wetlands [King and Reeburgh, 2002]. Carbon isotope studies have shown that most CH₄ 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 CH₄ emissions to be driven by GPP [Hatala *et al.*, 2012].

However, trees may also be influencing the seasonal and diurnal cycles if dissolved CH₄ 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 CH₄ 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 CH₄ 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 CH₄ oxidation linked to increased soil respiration activity. We interpret these results as indicating a significant role for GPP in influencing CH₄ 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 CH₄ flux may involve a threshold: once volumetric soil moisture exceeds some level (here ~0.1 volumetric water fraction), there are sufficient anoxic pore spaces to support CH₄ production near the surface and correlations become weak, while below this threshold, soil moisture is an important factor in controlling the balance between CH₄ production and CH₄ 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 that 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 (Figure S6). Similar challenges have been observed with modeling CH₄ fluxes [Mastepanov *et al.*, 2012; Moore *et al.*, 2011; Treat *et al.*, 2007], as well as CO₂ fluxes [Richardson *et al.*, 2007] from a variety of environments. Net CH₄ emission is the result of two processes acting in opposition, CH₄ production and CH₄ oxidation, and it appears that a correlative model based on emissions may lack the appropriate structure needed to extrapolate fluxes over longer time scales, despite success over shorter time scales. Achieving an appropriate model structure and complexity are necessary for improving the CH₄ components of larger Earth system models and predicting natural CH₄ 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 CH₄ 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 CH₄ flux.

In the context of the overall climate impact of greenhouse gas fluxes at this site, the CH₄ fluxes are small contributors (see supporting information) relative to the total CO₂ uptake. This contrasts with other

ecosystems, such as boreal wetlands where the climate impact of CH₄ fluxes can be larger than the climate benefit of their CO₂ uptake [Whiting and Chanton, 2001].

5. Conclusions

We provide the first multiyear set of CH₄ fluxes measured by eddy covariance over a forested ecosystem. Multiyear data sets of CH₄ fluxes capturing a wide variety of environmental conditions are critical to developing model structures that are capable of adequately predicting future CH₄ fluxes. GPP provided the strongest correlation with the calculated 4 day mean CH₄ fluxes during each year. Including soil moisture as a driver for CH₄ production improved the fit of the model only during 2012, which had a drier than average summer. Despite the potential for CH₄ efflux from this temperate-boreal transition site, our observations suggest that neither the soils nor the trees are large sources of CH₄ from the forest to the atmosphere. This study finds evidence for a link between GPP and CH₄ flux, and a small sink/source transition controlled by summer hydrologic conditions.

Acknowledgments

This research was supported by the Office of Science (BER), U.S. Department of Energy. We also recognize contributions from Robert Evans, Holly Hughes, Kathleen Savage, John Lee and Eric Davidson. We thank Ankur Desai and an anonymous reviewer for their helpful comments.

The Editor thanks Ankur Desai and an anonymous reviewer for their assistance in evaluating this paper.

References

- Adamsen, A. P. S., and G. M. King (1993), Methane consumption in temperate and subarctic forest soils: Rates, vertical zonation, and responses to water and nitrogen, *Appl. Environ. Microbiol.*, 59(2), 485–490.
- Bishop, C. M. (1995), *Neural Networks for Pattern Recognition*, Oxford Univ. Press, Oxford, United Kingdom.
- Castro, M. S., J. M. Melillo, P. A. Steudler, and J. W. Chapman (1994), Soil moisture as a predictor of methane uptake by temperate forest soils, *Can. J. For. Res.*, 24(9), 1805–1810.
- Castro, M. S., P. A. Steudler, J. M. Melillo, J. D. Aber, and R. D. Bowden (1995), Factors controlling atmospheric methane consumption by temperate forest soils, *Global Biogeochem. Cycles*, 9(1), 1–10.
- Chanton, J. P., J. E. Bauer, P. A. Glaser, D. I. Siegel, C. A. Kelley, S. C. Tyler, E. H. Romanowicz, and A. Lazrus (1995), Radiocarbon evidence for the substrates supporting methane formation within northern Minnesota peatlands, *Geochim. Cosmochim. Acta*, 59(17), 3663–3668.
- Covey, K. R., S. A. Wood, R. J. Warren, X. Lee, and M. A. Bradford (2012), Elevated methane concentrations in trees of an upland forest, *Geophys. Res. Lett.*, 39, L15705, doi:10.1029/2012GL052361.
- Dengel, S., D. Zona, T. Sachs, M. Aurela, M. Jammot, F. J. W. Parmentier, W. Oechel, and T. Vesala (2013), Testing the applicability of neural networks as a gap-filling method using CH₄ flux data from high latitude wetlands, *Biogeosci. Discuss.*, 10(5), 7727–7759.
- Denman, K. L., et al. (2007), Couplings between changes in the climate system and biogeochemistry, in *Climate Change 2007: The Physical Science Basis, Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, edited by S. Solomon et al., pp. 539–544, Cambridge Univ. Press, Cambridge, U.K., and New York.
- Fernandez, I. J., Y. Son, C. R. Kraske, L. E. Rustad, and M. B. David (1993), Soil carbon dioxide characteristics under different forest types and after harvest, *Soil Sci. Soc. Am. J.*, 57(4), 1115–1121.
- Hatala, J. A., M. Detto, and D. D. Baldocchi (2012), Gross ecosystem photosynthesis causes a diurnal pattern in methane emission from rice, *Geophys. Res. Lett.*, 39, L06409, doi:10.1029/2012GL051303.
- Hollinger, D. Y., S. M. Goltz, E. A. Davidson, J. T. Lee, K. Tu, and H. T. Valentine (1999), Seasonal patterns and environmental control of carbon dioxide and water vapour exchange in an ecotonal boreal forest, *Global Change Biol.*, 5(8), 891–902.
- Hollinger, D. Y., et al. (2004), Spatial and temporal variability in forest-atmosphere CO₂ exchange, *Global Change Biol.*, 10(10), 1689–1706.
- Keppler, F., J. T. G. Hamilton, M. Brab, and T. Rockman (2006), Methane emissions from terrestrial plants under aerobic conditions, *Nature*, 439(12), 187–191.
- King, J. Y., and W. S. Reeceburgh (2002), A pulse-labeling experiment to determine the contribution of recent plant photosynthates to net methane emission in arctic wet sedge tundra, *Soil Biol. Biochem.*, 34(2), 173–180.
- Mastepanov, M., C. Sigsgaard, T. Tagesson, L. Ström, M. P. Tamstorf, M. Lund, and T. R. Christensen (2012), Revisiting factors controlling methane emissions from high-arctic tundra, *Biogeosci. Discuss.*, 9(11), 15,853–15,900.
- Megonigal, J. P., and A. B. Guenther (2008), Methane emissions from upland forest soils and vegetation, *Tree Physiol.*, 28(4), 491–498.
- Moffat, A. M., C. Beckstein, G. Churkina, M. Mund, and M. Heimann (2010), Characterization of ecosystem responses to climatic controls using artificial neural networks, *Global Change Biol.*, 16(10), 2737–2749.
- Moore, T., A. Young, J. Bubier, E. Humphreys, P. Lafleur, and N. Roulet (2011), A multi-year record of methane flux at the Mer Bleue Bog, Southern Canada, *Ecosystems*, 14(4), 646–657.
- Nisbet, R. E. R., et al. (2009), Emission of methane from plants, *Proc. R. Soc. B*, 276(1660), 1347–1354.
- Pan, Y., et al. (2011), A large and persistent carbon sink in the world's forests, *Science*, 333(6045), 988–993.
- Pangala, S. R., S. Moore, E. R. C. Hornibrook, and V. Gauci (2013), Trees are major conduits for methane egress from tropical forested wetlands, *New Phytol.*, 197(2), 524–531.
- Peltola, O., I. Mammarella, S. Haapanala, G. Burba, and T. Vesala (2013), Field intercomparison of four methane gas analyzers suitable for eddy covariance flux measurements, *Biogeosciences*, 10(6), 3749–3765.
- Richardson, A. D., D. Y. Hollinger, J. D. Aber, S. V. Ollinger, and B. H. Braswell (2007), Environmental variation is directly responsible for short- but not long-term variation in forest-atmosphere carbon exchange, *Global Change Biol.*, 13(4), 788–803.
- Rojas, R. (1996), *Neural Networks: A Systematic Introduction*, Springer-Verlag, Berlin, Germany.
- Savage, K., T. R. Moore, and P. M. Crill (1997), Methane and carbon dioxide exchanges between the atmosphere and northern boreal forest soils, *J. Geophys. Res.*, 102(D24), 29,279–29,288.
- Smeets, C., R. Holzinger, I. Viganò, A. Goldstein, and T. Röckmann (2009), Eddy covariance methane measurements at a Ponderosa pine plantation in California, *Atmos. Chem. Phys.*, 9(21), 8365–8375.
- Treat, C. C., J. L. Bubier, R. K. Varner, and P. M. Crill (2007), Timescale dependence of environmental and plant-mediated controls on CH₄ flux in a temperate fen, *J. Geophys. Res.*, 112, G01014, doi:10.1029/2006JG000210.

- Wang, J. M., J. G. Murphy, J. A. Geddes, C. L. Winsborough, N. Basiliko, and S. C. Thomas (2013), Methane fluxes measured by eddy covariance and static chamber techniques at a temperate forest in central Ontario, Canada, *Biogeosciences*, 10(6), 4371–4382.
- Whalen, S. C., W. S. Reeburgh, and K. S. Kizer (1991), Methane consumption and emission by Taiga, *Global Biogeochem. Cycles*, 5(3), 261–273.
- Whiting, G. J., and J. P. Chanton (2001), Greenhouse carbon balance of wetlands: Methane emission versus carbon sequestration, *Tellus, Ser. B*, 53(5), 521–528.
- Yavitt, J. B., D. M. Downey, G. E. Lang, and A. J. Sexton (1990), Methane consumption in two temperate forest soils, *Biogeochemistry*, 9(1), 39–52.
- Yavitt, J. B., T. J. Fahey, and J. A. Simmons (1995), Methane and carbon dioxide dynamics in a northern hardwood ecosystem, *Soil Sci. Soc. Am. J.*, 59(3), 796–804.