Net soil–atmosphere fluxes mask patterns in gross production and consumption of nitrous oxide and methane in a managed ecosystem

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Abstract. Nitrous oxide (N\textsubscript{2}O) and methane (CH\textsubscript{4}) are potent greenhouse gases that are both produced and consumed in soil. Production and consumption of these gases are driven by different processes, making it difficult to infer their controls when measuring only net fluxes. We used the trace gas pool dilution technique to simultaneously measure gross fluxes of N\textsubscript{2}O and CH\textsubscript{4} throughout the growing season in a cornfield in northern California, USA. Net N\textsubscript{2}O fluxes ranged 0–4.5 mg N m\textsuperscript{-2} d\textsuperscript{-1} with the N\textsubscript{2}O yield averaging 0.68±0.02. Gross N\textsubscript{2}O production was best predicted by net nitrogen (N) mineralization, soil moisture, and soil temperature (\(R^2=0.60\), \(n=39\), \(p<0.001\)). Gross N\textsubscript{2}O reduction was correlated with the combination of gross N\textsubscript{2}O production rates, net N mineralization rates, and CO\textsubscript{2} emissions (\(R^2=0.74\), \(n=39\), \(p<0.001\)). Overall, net CH\textsubscript{4} fluxes averaged −0.03±0.02 mg C m\textsuperscript{-2} d\textsuperscript{-1}. The methanogenic fraction of carbon mineralization ranged from 0 to 0.27 % and explained 40 % of the variability in gross CH\textsubscript{4} production rates (\(n=37\), \(p<0.001\)). Gross CH\textsubscript{4} oxidation exhibited a strong positive relationship with gross CH\textsubscript{4} production rates (\(R^2=0.67\), \(n=37\), \(p<0.001\)), which reached as high as 5.4 mg C m\textsuperscript{-2} d\textsuperscript{-1}. Our study is the first to demonstrate the simultaneous in situ measurement of gross N\textsubscript{2}O and CH\textsubscript{4} fluxes, and results highlight that net soil–atmosphere fluxes can mask significant gross production and consumption of these trace gases.

1 Introduction

Greenhouse gas emissions from soils are major contributors to climate change (Ciais et al., 2013). While carbon dioxide (CO\textsubscript{2}) is the most abundant greenhouse gas in the atmosphere, both nitrous oxide (N\textsubscript{2}O) and methane (CH\textsubscript{4}) are more potent with 298 and 34 times the global warming potential of CO\textsubscript{2} on a 100-year timescale, respectively (Myhre et al., 2013). Both N\textsubscript{2}O and CH\textsubscript{4} are produced and consumed in soils by microbially mediated redox-sensitive processes. However, most studies only measure net soil–atmosphere exchange of N\textsubscript{2}O and CH\textsubscript{4}. This approach cannot differentiate between production and consumption of these trace gases and thus limits our ability to infer controls on these processes and to diagnose model inaccuracies in predicting net N\textsubscript{2}O and CH\textsubscript{4} fluxes. This hinders predictions of how soil–atmosphere N\textsubscript{2}O and CH\textsubscript{4} fluxes will respond to future changes in land use practices or climate change.

Agricultural soils account for nearly two-thirds of global soil emissions of N\textsubscript{2}O, which is produced from nitrification and denitrification of fertilizer nitrogen (N) that supports agroecosystem productivity (Ciais et al., 2013). Managing soil N\textsubscript{2}O emissions from agroecosystems can go beyond direct reductions in N\textsubscript{2}O production from decreased fertilizer inputs because denitrifying bacteria can consume N\textsubscript{2}O to dinitrogen gas (N\textsubscript{2}), completing the N cycling. Nitrous oxide consumption is not generally considered to be an important process in upland soils because it is an anaerobic process. Rates of N\textsubscript{2}O reduction to N\textsubscript{2} decrease as O\textsubscript{2} and NO\textsubscript{3} availability increases (Weier et al., 1993; Firestone et
Theoretically, this results in a high N2O yield (\(N_2O / (N_2O + N_2)\)) in unsaturated soil where diffusive re-supply of \(O_2\) and the production of \(NO_3^-\) from nitrification would inhibit \(N_2O\) reduction. Thermodynamics also predict that high soil \(NO_3^-\) from fertilizer N inputs in agricultural soils would lead to high \(N_2O\) yields. However, \(N_2O\) yields average 0.375 ± 0.035 in agricultural soil and span the entire range from 0 to 1 in oxic, upland soils (Schlesinger, 2009; Stevens and Laughlin, 1998). This high variability, in part, reflects the difficulty in measuring rates of \(N_2O\) reduction to \(N_2\), particularly under field conditions (Groppman et al., 2006). It also reflects other important factors that influence the \(N_2O\) yield, such as soil type (Woli et al., 2010), labile C (Weier et al., 1993), and pH (Stevens et al., 1998). The lower-than-expected average \(N_2O\) yield in agricultural soils and large range in \(N_2O\) yields in upland soil in general also suggests that \(N_2O\) reduction to \(N_2\) could play an important role in mitigating soil \(N_2O\) emissions to the atmosphere in agroecosystems.

Upland soils globally consume atmospheric \(CH_4\) at a rate similar to the accumulation of \(CH_4\) in the atmosphere (Ciais et al., 2013), and thus changes in the \(CH_4\) sink strength of soils could influence atmospheric \(CH_4\) concentrations. The inhibition of \(CH_4\) oxidation associated with fertilizer application of \(NO_3^-\) (Aronson and Helliker, 2010), urea (Mosier et al., 1991), and \(NH_4^+\) (Bedard and Knowles, 1989) is thought to cause lower net rates of \(CH_4\) uptake in agricultural systems compared to natural ecosystems (Nesbit and Breitenbeck, 1992; Bender and Conrad, 1994; Koschorreck and Conrad, 1993; Dutaur and Verchot, 2007; Mosier et al., 1991). Inhibition by \(NH_4^+\) has been attributed to enzymatic substrate competition due to the similarities between the \(CH_4\) monooxygenase and \(NH_4^+\) monooxygenase enzymes (Gulledge and Schimel, 1998) as well as toxicity effects from nitrite produced during \(NH_4^+\) oxidation (King and Schnell, 1994). However, the effect of N on \(CH_4\) oxidation varies by soil (Gulledge et al., 1997), and at least some of this effect is due to inhibition by salts included in the fertilizer applications (Adamsen and King, 1993; Dunfield et al., 1993; Gulledge and Schimel, 1998; Nesbit and Breitenbeck, 1992). In addition, the response of \(CH_4\) oxidation to \(NH_4^+\) and \(NO_3^-\) may depend on the methanotrophic community; for example the high affinity type II methane-oxidizing bacteria that dominate under low (<1000 ppm) \(CH_4\) conditions (Bender and Conrad, 1992) may be less sensitive to mineral N availability (Jung et al., 2011; Reay and Nedwell, 2004; Wang and Ineson, 2003). Thus, there remains uncertainty surrounding N inhibition of \(CH_4\) oxidation as the mechanism leading to low net rates of \(CH_4\) uptake in agricultural soils.

A major confounding factor in studies assessing controls on \(CH_4\) oxidation is the simultaneous occurrence of methanogenesis and \(CH_4\) oxidation. Net changes in \(CH_4\) concentrations under oxic soil conditions are assumed to reflect only \(CH_4\) oxidation (e.g., Nesbit and Breitenbeck, 1992) because methanogenesis occurs only under highly reducing conditions (Conrad, 1996). However, von Fischer and Hedin (2002) demonstrated that \(CH_4\) production occurred in a wide range of dry, oxic soils with water-filled pore space as low as 20%. Similarly, Teh et al. (2005) documented the occurrence of methanogenesis under well-aerated conditions in an upland tropical forest soil. Macroaggregates can support net \(CH_4\) efflux in unsaturated soil (Jackel et al., 2001; Sey et al., 2008), likely because \(O_2\) consumption in the centers of the aggregates exceeds diffusive re-supply of \(O_2\) to create reducing conditions (Seixton et al., 1985). Microsites of methanogenesis could also occur in the rhizosphere where high rates of \(O_2\) consumption from rhizosphere priming could create reducing conditions (Cheng et al., 2003). Because the controls on methanogenesis and \(CH_4\) oxidation are likely very different, the co-occurrence of these processes means that we must measure gross rates of both processes simultaneously to elucidate the mechanisms driving patterns in net soil–atmosphere \(CH_4\) fluxes.

We used the stable isotope trace gas pool dilution technique to measure gross \(N_2O\) and \(CH_4\) fluxes in cornfield soils throughout the growing season in order to improve our understanding of trace gas dynamics in upland soils of agroecosystems. Fertilized agroecosystems are typically large net \(N_2O\) sources and small net \(CH_4\) sinks (Haile-Maraiam et al., 2008; Kessavalou et al., 1998; Gelfand et al., 2013; Nangia et al., 2013; Robertson et al., 2000). However, little is known about the rates of gross production and consumption of these gases in upland soils, or their controlling factors. Different controls on production and consumption processes may result in complex responses of net soil–atmosphere gas fluxes to climate or land management. Thus, the objectives of this study were to quantify field rates of gross \(N_2O\) and \(CH_4\) production and consumption, and explore environmental and plant-mediated controls on these rates.

## 2 Materials and methods

### 2.1 Study site

The study site was a cornfield planted on a drained peatland located on Twitchell Island (38.11°N, 121.65°W) in the Sacramento–San Joaquin River delta region of northern California. The region is very productive agriculturally, producing USD 500 million in crops in 1993 (Ingebretsen and Ikehara, 1999). The climate is Mediterranean with a winter wet season and summer dry season. The mean annual temperature is 15.1 °C, and mean annual precipitation is 335 mm (Hatala et al., 2012). The soils consist of mucky clay over buried peat and are classified as fine, mixed, superactive, thermic Cumulic Endoaquolls (Drexler et al., 2009). The field was fertilized once, at seeding, at a rate of 118 kg N ha\(^{-1}\) with UAN 32, which consists of 45 % ammonium nitrate, 35 % urea, and 20 % water. The water table was
maintained around 50 cm soil depth throughout the growing season via subsurface irrigation.

2.2 Study design

We measured gross and net fluxes of CO₂, CH₄, and N₂O at five time points during the growing season from May to November 2012 on the following days after seeding (DAS): 11 (germination stage), 24 (seedling stage), 59 (peak growth stage), 94 (flowering stage), and 171 (senesced stage). The corn began senescing around DAS 104 and was harvested on DAS 178. We performed measurements in row and inter-row locations with the assumption that plant effects, if any, would be greater in the rows where the corn was growing (Cai et al., 2012; Haile-Mariam et al., 2008; Kessavalou et al., 1998). We established three parallel transects spaced 50 m apart. We measured gross production and consumption of CH₄ and N₂O as well as net fluxes of CO₂, CH₄, and N₂O along the northernmost transect and measured only net fluxes in the other two transects. In each transect, we used paired measurements in the bed (in between corn rows) and furrow (in row) with replicate pairs spaced 10 m apart (n = 4 pairs per transect). After each gas flux measurement was completed, we measured air, chamber headspace, and soil temperature at the surface flux chamber location. We also used an auger to sample the soil from the chamber footprint in 10 cm increments to 50 cm depth for the gross flux transect and only 0–10 cm depth in the net flux transects. The soils were processed the next day for determination of gravimetric soil moisture and net rates of nitrogen (N) mineralization and nitrification as described below.

2.3 Laboratory assays

We determined net rates of N mineralization and nitrification from 6-day laboratory incubations. We mixed each soil core by hand and subsampled 15 g for extraction in 75 mL of 2 M KCl, 10 g for determination of gravimetric soil moisture, and 50 g for incubation in Mason jars kept in the dark at ambient temperature. The jars were covered in perforated plastic wrap to minimize evaporation during the incubation. After 6 days, the soils in the jars were mixed and 15 g of soil was sampled the next day for determination of gravimetric soil moisture, and only 0–10 cm depth in the net flux transects. The soils were processed the next day for determination of gravimetric soil moisture and net rates of nitrogen (N) mineralization and nitrification as described below.

2.4 Gas flux measurements

We used the stable isotope trace gas pool dilution technique to measure field rates of gross N₂O and CH₄ production and consumption (von Fischer and Hedin, 2002; Yang et al., 2011). We injected 10 mL of isotopically enriched spiking gas into the headspace of a 2.8 L surface flux chamber inserted 6 cm into the soil surface. The spiking gas consisted of 70 ppm N₂O at 98 atom % ¹⁵N enrichment, 280 ppm CH₄ at 99 atom % ¹³C enrichment, and 28 ppm SF₆ to achieve a ¹⁵N-N₂O enrichment of 5.42 atom % and ¹³C-CH₄ enrichment of 5.61 atom %. This spiking gas injection increased the chamber headspace gas composition by 25 N₂O, 100 CH₄, and 10 ppb SF₆. We sampled the chamber headspace at 5, 15, 30, 45, and 60 min after spiking gas injection. We analyzed samples on a Shimadzu GC-14A gas chromatograph (Columbia, MD, USA) equipped with a thermal conductivity detector, flame ionization detector, and electron capture detector for determination of CO₂, CH₄, N₂O, and SF₆ concentrations. We analyzed separate samples for ¹⁵N-N₂O and ¹³C-CH₄ on an IsoPrime 100 continuous flow isotope ratio mass spectrometer interfaced with a trace gas preconcentration unit (Isoprime Ltd, Cheadle Hulme, UK) and Gilson GX271 autosampler (Middleton, WI). The trace gas analyzer was equipped with a combustion furnace using palladium to catalyze the conversion of CH₄ to CO₂ for isotopic analysis after CO and CO₂ were scrubbed from the sample (Fisher et al., 2006). One out of the 40 gross N₂O flux measurements and three out of the 40 gross CH₄ flux measurements were lost due to autosampler needle clogs that occurred during isotopic analysis.

Gross N₂O and CH₄ production and consumption rates were estimated using the pool dilution model as described by Yang et al. (2011) and von Fischer and Hedin (2002). The iterative model solves for gross production rates based on the isotopic dilution of the isotopically enriched chamber headspace pool of N₂O or CH₄ by natural abundance N₂O or CH₄ emitted by the soil. Gross consumption rates were estimated from the empirical loss of the ¹⁵N-N₂O or ¹³C-CH₄ tracer, using the loss of the SF₆ tracer to account for physical losses such as diffusion. We note that gross N₂O consumption rates are not equivalent to N₂ production via denitrification because heterogeneous ¹⁵N₂O distribution in the soil and complete denitrification intracellularly could lead to underestimates of N₂ production (Well and Butterbach-Bahl, 2013; Yang et al., 2013). We assumed that the isotopic composition of produced N₂O was 0.3431 atom % ¹⁵N and the fractionation factor associated with N₂O reduction to N₂ was 0.9924. The justification for these assumptions is discussed by Yang et al. (2011). We assumed that the isotopic composition of produced CH₄ was 1.0473 atom %, based on measurements of the ¹³C isotopic composition of soil CH₄ in a nearby study site (Y. Teh, personal communication, 2011). We assumed that the fractionation factor associated with CH₄ oxidation was 0.98 as justified by von Fischer and Hedin (2002). Sen-
sitivity analyses performed by both Yang et al. (2011) and von Fischer and Hedin (2002) showed that the pool dilution model output is not sensitive to these assumed values at the high isotopic enrichments used. Net fluxes of CO$_2$, N$_2$O, and CH$_4$ were determined from the change in concentration over time using an iterative model that fits an exponential curve to the data (Matthias et al., 1978). Fluxes were considered to be zero when the relationship between trace gas concentration and time was not significant at $p = 0.05$. The methanogenic fraction of C mineralization was calculated as the gross CH$_4$ production rate divided by the sum of the gross CH$_4$ production rate and CO$_2$ production rates.

2.5 Statistical analyses

We used SYSTAT version 13 (SPSS Inc., Evanston, IL, USA) to perform statistical analyses and Microsoft Excel 2007 (Microsoft Corporation, Redmond, WA, USA) to run the iterative pool dilution model. We log transformed the data to meet the normality assumptions of ANOVAs; soil moisture, soil temperature, soil C and N concentrations, and soil C : N ratios did not require transformation. We analyzed net and gross fluxes of CO$_2$, N$_2$O, and CH$_4$ using sampling date as the within-subjects factor and location (i.e., bed versus furrow) as the between-subject factor in repeated measures ANOVAs. We also analyzed net N mineralization and nitrification rates using sampling date as the within-subjects factor, and soil depth and location as the between-subjects factors in repeated measures ANOVAs. We explored relationships between trace gas fluxes and potential drivers (soil moisture, air and soil temperatures, soil NH$_4^+$ and NO$_3^-$ concentrations, net N mineralization and nitrification rates, soil C and N concentrations, etc.) using linear regressions. We determined the model that best fit observed trace gas flux data using backwards stepwise multiple linear regressions starting with all potential explanatory variables; the best model fit was determined by minimizing the Akaike information criterion. Statistical significance was determined at $p$ values $< 0.05$.

3 Results

3.1 Soil characteristics and N cycling

Air and soil temperature differed significantly among sampling dates ($p < 0.05$, Table 1). Mean air temperature spanned a small range from a low of 24.5 ± 0.7°C on DAS 171 to a high of 28.2 ± 0.7°C on DAS 94. Soil temperature was more variable, with the lowest mean soil temperature on DAS 171 at 14.8 ± 0.1°C and the highest mean soil temperature on DAS 59 at 24.2 ± 0.3°C.

In surface soils (0–10 cm depth), gravimetric soil moisture ranged from 0.24 ± 0.01 g H$_2$O g$^{-1}$ soil on DAS 94 to 0.38 ± 0.02 g H$_2$O g$^{-1}$ soil on DAS 11 (Table 1). Soil moisture decreased as the growing season progressed until DAS 171, when soil moisture increased to a value intermediate of that on DAS 59 and 94 (Table 1). Soil moisture was significantly higher in the row than in the inter-row on DAS 11 and 24 only (Table 3). Mean soil moisture increased significantly with depth (Table 2), although differences were not statistically significant for all dates (Table 3).

Soil NH$_4^+$ concentrations differed significantly among sampling dates and were lowest at the beginning (DAS 11) and end (DAS 171) of the study (Table 3). The inclusion of an outlier plot on DAS 94 increased the mean NH$_4^+$ concentration to 62.5 ± 46.4 µg N g$^{-1}$. Soil NH$_4^+$ concentrations decreased significantly from 0–10 to 20–30 cm depth (Tables 2–3) and were higher in rows than inter-rows (Table 3). Across all sampling dates, concentrations at 0–10 cm depth averaged 34.8 ± 20.1 % in rows and 12.9 ± 2.0 µg N g$^{-1}$ in inter-rows. Soil NO$_3^-$ concentrations were lower on DAS 11 than all other sampling dates (Table 3), averaging 53.5 ± 7.2 % on DAS 11 and 215 ± 33 µg N g$^{-1}$ across all other sampling dates at 0–10 cm depth. Soil NO$_3^-$ concentrations decreased with depth (Tables 2–3). On DAS 59 and 94 only, soil NO$_3^-$ concentrations were higher in rows (387 ± 117 µg N g$^{-1}$) than in inter-rows (156 ± 23 µg N g$^{-1}$) (Table 3).

Across the entire data set ($n = 216$), net N mineralization rates averaged 3.3 ± 0.5 % and net nitrification rates averaged 2.7 ± 0.6 µg N g$^{-1}$ d$^{-1}$. Net N mineralization and nitrification rates did not differ significantly among soil depths, sampling locations, or sampling dates (Table 3), although rates trended higher at 0–10 cm depth across all sampling dates and locations (Table 2). Across all sampling dates and soil depths, 96 % of the variability in net nitrification rates was explained by net N mineralization rates ($p < 0.001$, $n = 215$, Table 4).

Total C and N concentrations for soils sampled on DAS 11 differed between row and inter-row sampling locations (soil C, $F_{1,30} = 5.295$, $p = 0.03$; soil N, $F_{1,30} = 4.546$, $p = 0.04$) but not among soil depths (Table 2). Both soil C and N concentrations were higher in rows than in inter-rows, averaging 16.1 ± 0.8 % C and 0.99 ± 0.03 % N in rows and 13.7 ± 0.5 % C and 0.89 ± 0.02 % N in inter-rows. Soil C : N ratios averaged 15.8 ± 0.2 overall ($n = 40$), and did not differ significantly between sampling locations or among soil depths.

3.2 Gross and net N$_2$O fluxes

Across the entire data set, net N$_2$O fluxes ranged 0–4.5 and averaged 1.6 ± 0.2 mg N m$^{-2}$ d$^{-1}$ ($n = 112$). Net N$_2$O fluxes differed significantly among sampling dates ($F_{4,56} = 3.0$, $p = 0.03$) but not between sampling locations (Fig. 1a). Net N$_2$O fluxes were best predicted by net N mineralization, soil moisture, and soil CO$_2$ emissions together ($R^2 = 0.49$, Table 4).

Gross N$_2$O production ranged 0.09–6.6 mg N m$^{-2}$ d$^{-1}$ and gross N$_2$O reduction rates ranged 0.00–0.95 mg N m$^{-2}$ d$^{-1}$. The N$_2$O yield averaged 0.68 ± 0.02 ($n = 40$). Both gross N$_2$O production and consumption rates differed sig-
Table 1. Environmental and soil (0–10 cm depth) variables by sampling date (mean ± SE).

<table>
<thead>
<tr>
<th>Variable</th>
<th>F statistic</th>
<th>Sampling date</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>DAS 11 (n = 8)</td>
</tr>
<tr>
<td>Air temperature (°C)</td>
<td></td>
<td>24.5 ± 0.2 a, a</td>
</tr>
<tr>
<td>Soil temperature (°C)</td>
<td></td>
<td>24.5 ± 0.2 a, a</td>
</tr>
<tr>
<td>Soil moisture (g H$_2$O g$^{-1}$)</td>
<td>4.54, 4.44, 4.34</td>
<td>24.5 ± 0.2 a, a</td>
</tr>
</tbody>
</table>

Degrees of freedom are shown in subscripts, and statistically significant F statistics at P < 0.05 are indicated by bold text. Letters indicate statistically significant differences among sampling dates. * One transect was excluded from the repeated measures ANOVA because data are missing for one sampling date.

Table 2. Soil characteristics and N cycling rates across all sampling dates by soil depth in the gross flux transect (mean ± SE).

<table>
<thead>
<tr>
<th>Variable</th>
<th>N</th>
<th>P value</th>
<th>0–10 cm</th>
<th>10–20 cm</th>
<th>20–30 cm</th>
<th>30–40 cm</th>
<th>40–50 cm</th>
</tr>
</thead>
<tbody>
<tr>
<td>Soil moisture (g H$_2$O g$^{-1}$)</td>
<td>40</td>
<td>&lt;0.001</td>
<td>0.34 ± 0.01 a</td>
<td>0.35 ± 0.01 a</td>
<td>0.37 ± 0.01 ab</td>
<td>0.40 ± 0.01 b</td>
<td>0.46 ± 0.02 c</td>
</tr>
<tr>
<td>NH$_4^+$ concentration (µg N g$^{-1}$)</td>
<td>40</td>
<td>&lt;0.001</td>
<td>23.3 ± 9.6 a</td>
<td>15.2 ± 6.3 b</td>
<td>7.0 ± 1.8 b</td>
<td>5.0 ± 0.7 b</td>
<td>5.7 ± 0.8 b</td>
</tr>
<tr>
<td>NO$_3^-$ concentration (µg N g$^{-1}$)</td>
<td>40</td>
<td>&lt;0.001</td>
<td>183 ± 28 a</td>
<td>110 ± 22 b</td>
<td>58 ± 8.4 c</td>
<td>41.9 ± 6.1 c</td>
<td>29.5 ± 3.2 c</td>
</tr>
<tr>
<td>Net mineralization (µg N g$^{-1}$ d$^{-1}$)</td>
<td>40</td>
<td></td>
<td>5.9 ± 2.6</td>
<td>1.0 ± 0.9</td>
<td>1.5 ± 0.5</td>
<td>1.8 ± 0.7</td>
<td>3.3 ± 0.5</td>
</tr>
<tr>
<td>Net nitrification (µg N g$^{-1}$ d$^{-1}$)</td>
<td>40</td>
<td></td>
<td>6.7 ± 2.4</td>
<td>1.7 ± 0.8</td>
<td>2.1 ± 0.5</td>
<td>2.3 ± 0.7</td>
<td>3.8 ± 0.5</td>
</tr>
<tr>
<td>Soil C concentration (%)</td>
<td>8</td>
<td>*</td>
<td>14.1 ± 0.5</td>
<td>15.4 ± 1.6</td>
<td>14.8 ± 0.9</td>
<td>15.2 ± 1.6</td>
<td>15.0 ± 0.9</td>
</tr>
<tr>
<td>Soil N concentration (%)</td>
<td>8</td>
<td>*</td>
<td>9.3 ± 0.2</td>
<td>0.96 ± 0.07</td>
<td>0.98 ± 0.05</td>
<td>0.91 ± 0.06</td>
<td>0.93 ± 0.05</td>
</tr>
</tbody>
</table>

Letters indicate statistically significant differences among soil depths. * Data from DAS 11 only.

Figure 1. Mean (a) net N$_2$O flux and (b) CO$_2$ efflux for all three transects (n = 24 per sampling date except n = 16 on DAS 94) in inter-rows (black bars) and rows (grey bars). Error bars represent standard errors, and different letters indicate statistically significant differences among sampling dates.

Gross N$_2$O reduction rates increased with gross N$_2$O production rates ($R^2 = 0.60$, n = 39, $p < 0.001$, Fig. 3a). Rates were also positively correlated with soil CO$_2$ emissions ($R^2 = 0.36$, n = 39, $p < 0.001$); this relationship was stronger when the corn was not actively growing (DAS 11, 24, and 171), with 80% of the variability in gross N$_2$O reduction rates explained by CO$_2$ emissions on these dates (n = 24, $p < 0.001$, Fig. 3b). Gross N$_2$O reduction was most strongly correlated with the combination of gross N$_2$O production rates, net N mineralization rates, and CO$_2$ emissions ($R^2 = 0.74$, n = 39, $p < 0.001$, Table 4).
Table 3. Results from repeated measures ANOVAs with sampling date, the interaction of sampling date and soil depth, and the interaction of sampling date and sampling location as the within-subjects, and soil depth and sampling location as the between-subjects factors.

<table>
<thead>
<tr>
<th></th>
<th>Sampling date</th>
<th>Soil depth</th>
<th>Sampling location</th>
<th>Sampling date*</th>
<th>Soil depth*</th>
<th>Sampling location*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Soil moisture (g H₂O g⁻¹⁻¹)</td>
<td>F₄,120 = 135</td>
<td>F₄,30 = 31</td>
<td>F₁,30 = 5.1</td>
<td>F₁₆,120 = 1.9</td>
<td>F₄,120 = 4.6</td>
<td></td>
</tr>
<tr>
<td>NH₄⁺ concentration (µg N g⁻¹ d⁻¹)</td>
<td>F₄,120 = 7.9</td>
<td>F₄,30 = 7.7</td>
<td>F₁,30 = 4.0</td>
<td>F₁₆,120 = 0.90</td>
<td>F₄,120 = 1.9</td>
<td></td>
</tr>
<tr>
<td>NO₃⁻ concentration (µg N g⁻¹ d⁻¹)</td>
<td>F₄,120 = 17</td>
<td>F₄,30 = 36</td>
<td>F₁,30 = 18</td>
<td>F₁₆,120 = 1.0</td>
<td>F₄,120 = 7.1</td>
<td></td>
</tr>
<tr>
<td>Net mineralization (µg N g⁻¹ d⁻¹)</td>
<td>F₄,120 = 1.5</td>
<td>F₄,30 = 1.5</td>
<td>F₁,30 = 1.5</td>
<td>F₁₆,120 = 1.1</td>
<td>F₄,120 = 1.7</td>
<td></td>
</tr>
<tr>
<td>Net nitrification (µg N g⁻¹ d⁻¹)</td>
<td>F₄,120 = 1.4</td>
<td>F₄,30 = 0.22</td>
<td>F₁,30 = 1.9</td>
<td>F₁₆,120 = 0.31</td>
<td>F₄,120 = 1.8</td>
<td></td>
</tr>
</tbody>
</table>

Degrees of freedom are shown in subscripts, and statistically significant F statistics at \( P < 0.05 \) are indicated by bold text.

Table 4. Coefficients for multiple linear regressions predicting trace gas fluxes using soil variables.

<table>
<thead>
<tr>
<th>Dependent variable</th>
<th>N</th>
<th>( R^2 )</th>
<th>Effect</th>
<th>Coefficient</th>
<th>SE</th>
<th>( P ) value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Log(Nitrogen mineralization, µg N m⁻² d⁻¹)</td>
<td>215</td>
<td>0.96</td>
<td>Constant</td>
<td>0.162</td>
<td>0.020</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Log(Nitrogen mineralization, µg N m⁻² d⁻¹)</td>
<td>215</td>
<td>0.96</td>
<td>Log(Soil moisture, g H₂O g⁻¹)</td>
<td>0.906</td>
<td>0.012</td>
<td>&lt; 0.001</td>
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<tr>
<td>Log(CO₂ emissions, g C m⁻² d⁻¹)</td>
<td>96</td>
<td>0.15</td>
<td>Constant</td>
<td>0.466</td>
<td>0.195</td>
<td>0.02</td>
</tr>
<tr>
<td>Log(CO₂ emissions, g C m⁻² d⁻¹)</td>
<td>96</td>
<td>0.15</td>
<td>Soil moisture (g H₂O g⁻¹)</td>
<td>-1.019</td>
<td>0.416</td>
<td>0.02</td>
</tr>
<tr>
<td>Log(CO₂ emissions, g C m⁻² d⁻¹)</td>
<td>96</td>
<td>0.15</td>
<td>Soil temperature (°C)</td>
<td>0.022</td>
<td>0.007</td>
<td>0.002</td>
</tr>
<tr>
<td>Log(N₂O flux, mg N m⁻² d⁻¹)</td>
<td>56</td>
<td>0.49</td>
<td>Constant</td>
<td>-1.671</td>
<td>0.743</td>
<td>0.03</td>
</tr>
<tr>
<td>Log(N₂O flux, mg N m⁻² d⁻¹)</td>
<td>56</td>
<td>0.49</td>
<td>Log(Soil moisture)</td>
<td>1.342</td>
<td>0.274</td>
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<td>Log(N₂O flux, mg N m⁻² d⁻¹)</td>
<td>56</td>
<td>0.49</td>
<td>Log(Soil temperature)</td>
<td>4.356</td>
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<td>Log(N₂O flux, mg N m⁻² d⁻¹)</td>
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<td>0.49</td>
<td>Log(Soil temperature)</td>
<td>1.404</td>
<td>0.288</td>
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<tr>
<td>Log(N₂O production, mg N m⁻² d⁻¹)</td>
<td>39</td>
<td>0.60</td>
<td>Constant</td>
<td>1.743</td>
<td>0.453</td>
<td>0.001</td>
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<tr>
<td>Log(N₂O production, mg N m⁻² d⁻¹)</td>
<td>39</td>
<td>0.60</td>
<td>Log(Soil moisture)</td>
<td>0.516</td>
<td>0.139</td>
<td>0.001</td>
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<tr>
<td>Log(N₂O production, mg N m⁻² d⁻¹)</td>
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<td>0.60</td>
<td>Log(Soil temperature)</td>
<td>2.226</td>
<td>0.839</td>
<td>0.01</td>
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<tr>
<td>Log(N₂O production, mg N m⁻² d⁻¹)</td>
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<td>Log(Soil temperature)</td>
<td>-0.043</td>
<td>0.013</td>
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<tr>
<td>Log(N₂O production, mg N m⁻² d⁻¹)</td>
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<td>Constant</td>
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<td>Log(Soil moisture)</td>
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<td>0.258</td>
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<td>Log(N₂O reduction)</td>
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<td>0.74</td>
<td>Log(N₂O production)</td>
<td>0.983</td>
<td>0.226</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Log(N₂O reduction)</td>
<td>39</td>
<td>0.74</td>
<td>Log(SO₂ emissions)</td>
<td>1.199</td>
<td>0.292</td>
<td>&lt; 0.001</td>
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<td>Log(CH₄ production, mg C m⁻² d⁻¹)</td>
<td>37</td>
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<td>Constant</td>
<td>2.264</td>
<td>0.199</td>
<td>&lt; 0.001</td>
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<tr>
<td>Log(CH₄ production, mg C m⁻² d⁻¹)</td>
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<td>0.17</td>
<td>Log(CH₄ production)</td>
<td>0.921</td>
<td>0.348</td>
<td>0.01</td>
</tr>
<tr>
<td>Log(CH₄ oxidation)</td>
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<td>0.79</td>
<td>Constant</td>
<td>0.794</td>
<td>0.621</td>
<td>0.21</td>
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<td>Log(CH₄ oxidation)</td>
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<td>0.79</td>
<td>Log(CH₄ production)</td>
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<td>Log(Soil temperature)</td>
<td>-0.086</td>
<td>0.024</td>
<td>0.001</td>
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<tr>
<td>Log(CH₄ oxidation)</td>
<td>37</td>
<td>0.79</td>
<td>Log(SO₂ emissions)</td>
<td>1.096</td>
<td>0.335</td>
<td>&lt; 0.001</td>
</tr>
</tbody>
</table>

3.3 Gross and net CH₄ fluxes

Net CH₄ fluxes ranged from −1.3 to 0.44 mg C m⁻² d⁻¹ but net fluxes were not detectable for 94 out of 112 measurements. Overall net CH₄ fluxes averaged −0.03 ± 0.02 mg C m⁻² d⁻¹. Using the trace gas pool dilution technique, we detected gross CH₄ production in 36 out of 37 measurements. Gross CH₄ production reached as high as 5.4 mg C m⁻² d⁻¹ with rates trending higher throughout the growing season (Fig. 2b). However, rates were only significantly different between DAS 11 and 94 \( (F_{4,12} = 4.1, p = 0.03) \). Gross CH₄ production rates were marginally significantly higher in rows than in inter-rows \( (F_{1,3} = 5.8, p = 0.10) \). Overall, gross CH₄ production rates were weakly correlated to soil CO₂ emissions \( (R^2 = 0.17, \) Table 4) but exhibited a stronger positive correlation with the methanogenic fraction of C mineralization \( (R^2 = 0.40, n = 37, p < 0.001, \) Fig. 4a), which ranged from 0 to 0.27 % and averaged 0.06 ± 0.01 %. The strength of the relationship increased to \( R^2 = 0.60 (n = 23, p < 0.001) \) when considering only dates when the corn was not actively growing (Fig. 4a). When only peak growth sampling dates were con-
Figure 3. Gross N\textsubscript{2}O reduction rates versus (a) gross N\textsubscript{2}O production and (b) CO\textsubscript{2} efflux. Symbols represent sampling on different days after seeding (DAS): circles are DAS 11, triangles are DAS 24, pluses are DAS 59, crosses are DAS 94, and squares are DAS 171. (a) The line represents the regression line for all sampling dates together, \( \log_{10}(y) = [1.567 \times \log_{10}(x)] - 2.573 \) \( (R^2 = 0.60, n = 39, p < 0.001) \), and (b) the line represents the regression line for sampling dates when the corn was not at peak growth (DAS 11, 24, and 171), \( \log_{10}(y) = [3.663 \times \log_{10}(x)] + 0.822 \) \( (R^2 = 0.80, n = 24, p < 0.001) \).

Figure 4. (a) Gross CH\textsubscript{4} production rates versus methanogenic fraction of C mineralization, and (b) gross CH\textsubscript{4} oxidation rates versus gross CH\textsubscript{4} production rates. Symbols represent sampling on different days after seeding (DAS): circles are DAS 11, triangles are DAS 24, pluses are DAS 59, crosses are DAS 94, and squares are DAS 171. The solid lines represent the regression line for all sampling dates together, (a) \( \log_{10}(y) = [18.953 \times \log_{10}(x)] + 2.245 \) \( (R^2 = 0.40, n = 37, p < 0.001) \) and (b) \( \log_{10}(y) = [1.308 \times \log_{10}(x)] - 1.028 \) \( (R^2 = 0.67, n = 37, p < 0.001) \). The dashed line represents the regression line for DAS 11, 24, and 171 only, \( \log_{10}(y) = [22.681 \times \log_{10}(x)] + 1.904 \) \( (R^2 = 0.60, n = 23, p < 0.001) \).

3.4 CO\textsubscript{2} emissions

Carbon dioxide emissions ranged 0.6–10.5 g C m\textsuperscript{−2} d\textsuperscript{−1} across the entire data set. Emissions trended higher in the rows than in the inter-rows after the corn germinated, but repeated measures ANOVA showed that CO\textsubscript{2} emissions differed significantly among sampling dates \( (F_{1,56} = 80.1, p < 0.001) \) but not between row and inter-row locations (Fig. 1b). The highest CO\textsubscript{2} emissions occurred on DAS 59 and 94, at the height of the growing season, averaging 6.7 ± 0.2 g C m\textsuperscript{−2} d\textsuperscript{−1}; the lowest emissions occurred on DAS 11 and 24 at the beginning of the growing season, averaging 2.6 ± 0.2 g C m\textsuperscript{−2} d\textsuperscript{−1}. The variability in CO\textsubscript{2} emissions was poorly explained by environmental and soil variables with soil moisture and soil temperature together as the best, yet weak, predictors \( (R^2 = 0.15, \text{Table } 4) \).

4 Discussion

4.1 N\textsubscript{2}O dynamics

Net N\textsubscript{2}O fluxes at our study site were comparable to those reported for other fertilized crop fields (Gelfand et al., 2013; Smith et al., 2011; Stevens and Laughlin, 1998; Nangia et al., 2013; Robertson et al., 2000), averaging 1.5 ± 0.2 mg N m\textsuperscript{−2} d\textsuperscript{−1} across the growing season. Prior field estimates of N\textsubscript{2}O yield using \(^{15}\)NH\textsubscript{4} or \(^{15}\)NO\textsubscript{3} addition at application rates of 200–300 kg N ha\textsuperscript{−1} span a wide range from 0.06 to 0.7 (Mosier et al., 1986; Rolston et al., 1976, 1978, 1982). In contrast, the N\textsubscript{2}O yield varied little throughout the growing season at our site, averaging 0.68 ± 0.02, despite significant differences in both net and gross N\textsubscript{2}O fluxes among sampling dates. This is similar to a field estimate of the N\textsubscript{2}O yield for a nearby pasture on the same soil type \( (0.70 ± 0.04; \text{Yang et al., 2011}) \). Soil NO\textsubscript{3}\textsuperscript{−1} concentrations in surface soils (0–10 cm depth) were 1–2 orders of magnitude greater in the cornfield than in the pasture, so it is surprising that the N\textsubscript{2}O yields were similar. Soil NO\textsubscript{3}\textsuperscript{−1} concentration was the strongest predictor of N\textsubscript{2}O yield in a US Midwest cornfield soil incubated in the laboratory (Woli et al., 2010).
Other factors such as soil pH, labile C availability, or soil aggregation may have played a more important role in controlling the N₂O yield in our cornfield (Sey et al., 2008).

The best predictors of gross N₂O production and consumption changed over the growing season, likely reflecting the influence of plant–microbial competition for N on N₂O dynamics. This is a novel finding because, to our knowledge, this is the first study that has made repeated measurements of gross N₂O dynamics over the growing season in the presence of active plant–microbial competition for N. When the corn was actively growing, 89% of the variability in gross N₂O production was explained by soil moisture, soil temperature, net N mineralization, and CO₂ emissions together. In contrast, when the corn was not actively growing, both gross N₂O production and reduction were best predicted by soil CO₂ emissions alone. This may reflect the role of CO₂ emissions as proxy for the availability of labile C as an electron donor for denitrification; during the growing season, the contribution of autotrophic respiration to soil CO₂ emissions obscured this role. Net N mineralization was an explanatory variable for gross N₂O production only during the growing season when plant uptake of N could have limited N₂O production.

Overall, gross N₂O reduction rates were strongly correlated to gross N₂O production rates. This relationship was also observed in a managed grassland with high soil mineral N concentrations and net soil N₂O emissions (Yang et al., 2011), but not in a salt marsh with low mineral N availability where net N₂O uptake by soil occurred (Yang and Silver, 2016). The strong relationship between N₂O production and reduction may have driven the well-constrained N₂O yields in both this study and the managed grassland study because N₂O reduction increased proportionally to N₂O production rates. Additional studies using the trace gas pool dilution technique in the field could elucidate whether or not this relationship holds only in soils with high mineral N concentrations to drive high rates of N₂O production.

4.2 CH₄ dynamics

The small and zero net CH₄ fluxes we observed, which are typical of cornfields (Mosier et al., 2006), masked gross CH₄ fluxes which were 2 orders of magnitude greater. Net CH₄ fluxes were generally undetectable because CH₄ oxidation was tightly coupled to methanogenesis, especially at high gross CH₄ production rates. The ability of methanotrophs to adjust activity to match, but not exceed, rates of methanogenesis could reflect oxidation of soil-derived CH₄ at high concentrations near methanogenic microsites but not atmospheric CH₄ at low concentrations in the bulk soil. There are a few mechanisms that could drive a stimulatory effect of high CH₄ concentrations on CH₄ oxidation without increasing oxidation rates at atmospheric concentrations (Benstead and King, 1997). First, high microsite CH₄ concentrations can increase the number of methanotrophs as well as shift the methanotrophic community composition from high affinity type II methanotrophs, who consume CH₄ at low concentrations, to low affinity type I methanotrophs, who consume CH₄ only at high concentrations, in or near the methanogenic microsites (Bender and Conrad, 1992, 1995). Second, the enzyme affinity of type II methanotrophs can change from high affinity in the presence of atmospheric CH₄ concentrations to low affinity at high CH₄ concentrations, thereby reducing their capability to oxidize CH₄ at low concentrations (Dunfield et al., 1999). Third, high CH₄ availability may be needed to stimulate enzyme synthesis (Bender and Conrad, 1992, 1995; Nesbit and Breitenbeck), and thus methanotrophic activity may be induced only near methanogenic microsites and not in the bulk soil. Additional studies investigating gross CH₄ dynamics in soil aggregates or through the soil profile could provide insight into the mechanisms coupling CH₄ production and consumption. Regardless of the mechanisms, our observations suggest that using in situ methods that preserve spatial variability in soil CH₄ concentrations and allow for the occurrence of both CH₄ production and oxidation, such as the trace gas pool dilution technique, is important for accurately characterizing CH₄ dynamics in soil.

Gross CH₄ production rates were strongly positively correlated with the methanogenic fraction of C mineralization, an index of anaerobic soil microsites where electron acceptors are depleted relative to C supply (von Fischer and Hedin, 2007). Von Fischer et al. (2007) found that the methanogenic fraction was constrained below 0.04% and gross CH₄ production rates below 1 mg C m⁻² d⁻¹ in tropical and temperate forest soils with less than 60% water-filled pore space. Though the slope of the relationship between gross CH₄ production rates and the methanogenic fraction observed here was similar to that reported by von Fischer et al. (2007), the maximum methanogenic fraction observed here was nearly 7 times greater. The maximum gross CH₄ production rate was also an order of magnitude greater than the maximum rate of 0.5 mg C m⁻² d⁻¹ reported by von Fischer and Hedin (2002) for a range of unsaturated upland soils in which net CH₄ fluxes were near zero (−0.2 to 0.2 mg C m⁻² d⁻¹). This suggests a higher potential for the development of methanogenic microsites in these drained peatland soils, which are rich in C.

The near-zero net CH₄ fluxes measured in our cornfield are consistent with other studies in agricultural systems, but the relatively high gross CH₄ oxidation rates we documented challenge the paradigm that agricultural soils have low potential for CH₄ oxidation compared to unsaturated soils in natural ecosystems (Bender and Conrad, 1994; Koschorreck and Conrad, 1993; Mosier et al., 1991; Nesbit and Breitenbeck, 1992; Zhuang et al., 2013). Our soils had high NH₄⁺ and NO₃⁻ concentrations, which did not limit the ability of methanotrophs to completely consume soil-derived CH₄. Undisturbed soils in which CH₄ production and consumption occur simultaneously could behave differently than manipu-
lated soils incubated in the laboratory under conditions to isolate CH\(_4\) oxidation from CH\(_4\) production, and vice versa. Application of the trace gas pool dilution technique to other agricultural fields could reveal whether or not the tight coupling of CH\(_4\) production and consumption rather than low rates of CH\(_4\) production and oxidation could be responsible for the general observation of small and near-zero net CH\(_4\) fluxes in agricultural ecosystems. A greater understanding of limitations on gross CH\(_4\) oxidation under field conditions is needed to accurately predict how land use change will alter soil–atmosphere CH\(_4\) exchange and to better manage agricultural soils to be atmospheric CH\(_4\) sinks.

Our data provide circumstantial evidence that plants could mediate gross CH\(_4\) dynamics in upland soil both directly and indirectly. An increase in plant C inputs to the soil over the growing season may have directly driven a steady, though not statistically significant, increase in rates of methanogenesis by providing more C substrate to support methanogenesis. Both gross CH\(_4\) production and oxidation rates were approximately 2.5 times greater at DAS 171 compared to DAS 11. This trend in gross CH\(_4\) fluxes cannot be explained by changes in environmental variables such as soil temperature, which peaked in the middle of the growing season, and soil moisture, which decreased over the growing season. However, von Fischer and Hedin (2007) showed that methanogenesis was not limited by C supply in a wide range of upland soils, but rather, it was limited by the number of anaerobic microsites that could support methanogenesis in the soils. Our data also support the latter mechanism controlling methanogenesis: we observed a strong relationship between gross CH\(_4\) production and the methanogenic fraction of C mineralization (an index of the abundance of anaerobic soil microsites) on DAS 11, 24, and 171, when root respiration likely did not contribute significantly to CO\(_2\) effluxes. We also observed higher gross CH\(_4\) production and oxidation rates in rows than in inter-rows, suggesting that plants could indirectly control methanogenesis through rhizosphere priming, fueling biological O\(_2\) demand for C mineralization (Zhu et al., 2014) that creates a greater number of anaerobic soil microsites supporting methanogenesis.

5 Conclusions

Our study demonstrates that the anaerobic processes of N\(_2\)O reduction to N\(_2\) and methanogenesis can play important roles in mediating soil–atmosphere greenhouse gas fluxes in upland crop field soils where these processes have previously been discounted. Moreover, despite high soil NO\(_3^-\) and NH\(_4^+\) concentrations that theoretically inhibit N\(_2\)O reduction to N\(_2\) as well as CH\(_4\) oxidation, gross N\(_2\)O reduction rates were approximately one-third of gross N\(_2\)O production rates and CH\(_4\) oxidation kept pace with methanogenesis that reached relatively high rates for unsaturated soil. Our field measurements of gross N\(_2\)O and CH\(_4\) fluxes thus challenge our current understanding of the controls on the production and consumption of N\(_2\)O and CH\(_4\) in upland soils. The strong correlations that gross N\(_2\)O and CH\(_4\) fluxes exhibited with soil characteristics and soil N cycling process rates can help guide controlled studies to investigate the controls on the processes that lead to the production and consumption of N\(_2\)O and CH\(_4\). A better understanding of the controls on these processes can help refine modeling efforts to characterize the effects of anoxic microsites in unsaturated soil on greenhouse gas emissions (Riley et al., 2011) and also inform land management decisions to mitigate soil greenhouse gas emissions from crop fields.

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References


