



Historical soil drainage mediates the response of soil greenhouse gas emissions to intense precipitation events

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Abstract Precipitation events are increasing in intensity in the Midwestern US due to climate change. This is resulting in flooding of poorly-drained upland soils, which can feed back on climate change by altering greenhouse gas (GHG) emissions, including nitrous oxide (N₂O) and carbon dioxide (CO₂). The objective of this study was to determine if soil drainage history affects the response of soil GHG emissions to rain events. To do this, we measured N₂O and CO₂ fluxes from poorly-drained (PD) and well-drained (WD) soils in an agricultural field in Urbana, Illinois

before and after large rain events. We also performed a lab experiment to separate effects of soil drainage history from contemporary effects of ponding. Finally, we utilized stable isotope techniques to measure gross N₂O dynamics and to determine the contributions of nitrifiers and denitrifiers to net N₂O fluxes. We found that ponding of WD soils led to pulses of net N₂O efflux caused by stimulation of gross N₂O production by denitrifiers. In contrast, PD soils had high net N₂O effluxes only between large rain events, and gross N₂O production was inhibited following ponding. Soil CO₂ efflux was greater from PD soils under lab conditions, but autotrophic respiration obscured this trend in the field. Soil GHG emissions were a result of different contemporary ponding status as well as historical soil drainage, suggesting that historical soil redox regimes regulate soil GHG dynamics in response to precipitation. These soil drainage legacy effects are likely important in predicting soil GHG feedback effects on climate change.

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Introduction

The frequency and magnitude of intense precipitation events is increasing globally (USGCRP 2009; Min et al. 2011). In the Midwestern US, heavy rainfall has

led to higher frequency, duration, and spatial extent of ponding of upland mesic soils (Gleason 2008; Villarini et al. 2013). Changes in soil redox conditions associated with contemporary ponding can alter rates of biogeochemical processes that contribute to soil–atmosphere fluxes of greenhouse gases (GHGs), such as nitrous oxide (N_2O) and carbon dioxide (CO_2) which feedback on climate change. Depressions in the landscape that are more prone to ponding contribute disproportionately to ecosystem level GHG fluxes (Ambus and Christensen 1994; Ball et al. 1997; Li et al. 2018; Turner et al. 2016). However, as the spatial extent of ponding increases in the future, soil GHG dynamics in these newly ponded areas may not be similar to those in historically ponded areas. This can result from differences in soil chemistry, structure, microbial community composition, and other factors developed from long-term differences in soil moisture or drainage patterns (Averill et al. 2016; DeAngelis et al. 2010; Groffman and Tiedje 1991; Hawkes et al. 2017; Hawkes and Keitt 2015; Zeglin et al. 2013). Here, we differentiate soils based on soil drainage classification determined by the presence of ponding after large rain events. We define soil drainage legacy as differences in soil biotic and abiotic properties as a result of differences in historical soil drainage. The role of soil drainage legacy on the response of soil GHG dynamics to intense precipitation events has not been previously explored, yet it may be important in accurately predicting soil GHG feedback effects on climate change.

Water inundation effects on soil GHG dynamics in upland ecosystems that experience episodic ponding differ from those in perennially flooded ecosystems, such as wetlands and peatlands. In flooded ecosystems, soil–atmosphere GHG fluxes are dominated by methane (CH_4) due to the depletion of terminal electron acceptors (TEAs) higher on the redox ladder, such as oxygen (O_2) and nitrate (NO_3^-), which are needed for CO_2 and N_2O production (Estop-Aragonés et al. 2013; Knowles 1982). In soils that experience fluctuating redox conditions, these TEAs are replenished during periods when soils are unsaturated and oxic. When the soils inundate, the reduction of these replenished TEAs can then be coupled with organic C oxidation to anaerobically produce CO_2 . This phenomenon can be important at the ecosystem level, with the reduction of iron (Fe) accounting for up to 40% of

CO_2 emissions in upland soils that experience fluctuating redox conditions (Dubinsky et al. 2010). Soil NO_3^- pools are replenished by nitrification during oxic periods, and can drive N_2O production from denitrification, a multi-step anaerobic process which reduces NO_3^- to N_2O and then reduces N_2O to dinitrogen (N_2) when NO_3^- is limiting relative to electron donors such as C (Firestone et al. 1980). After rain events, topographic depressions can act as transient hot spots of soil N_2O emissions due to increased soil moisture (Turner et al. 2008, 2016; Yanai et al. 1965). Furthermore, NO_3^- and dissolved organic matter can accumulate in topographically depressed areas, possibly as a result of lateral movement of water, further fueling these hotspots of denitrification (Turner et al. 2008, 2016; Yanai et al. 1965). Although depressions may not perpetually act as N_2O hot spots, short-lived high N_2O emissions can act as hot moments that have been shown to account for up to 51% of cumulative annual N_2O emissions (Kroon et al. 2007; Molodovskaya et al. 2012; Parkin and Kaspar 2006; Saha et al. 2017). Understanding the controls over GHG emissions from different soil drainage classes that become transient hot spots under different conditions could, therefore, be important to accurately predict how soil GHG fluxes will respond to rainfall intensification associated with climate change.

Changes in soil chemistry, physical structure, and microbial community composition caused by historical soil drainage may control the response of biogeochemical processes to contemporary environmental conditions, such as ponding. Short-term legacy effects resulting from different precipitation and moisture regimes on the scale of days to months have been shown to affect soil CO_2 emissions (Groffman and Tiedje 1988; Evans and Wallenstein 2012; Averill et al. 2016). Soil moisture hysteresis can also affect soil N_2O fluxes (Groffman and Tiedje 1988; Banerjee et al. 2016). Over the long term, repeated ponding and soil redox fluctuations can affect organic C availability for heterotrophic microbial activity by slowing plant growth (Grable and Siemer 1968; Kanwar et al. 1988), facilitating the release of labile C from organo-mineral complexes (De-Campos et al. 2012; Huang and Hall 2017; Thompson et al. 2011), and breaking down soil aggregates (Adu and Oades 1978; De-Campos et al. 2009). The breakdown of soil aggregates by ponding can also alter the distribution of O_2 in soil and destroy

hypoxic microsites that act as hotspots of N_2O production via denitrification after soil drainage (Algayer et al. 2014; Sey et al. 2008). Fluctuating soil redox in depressions in surface soils can increase the bioavailability of Fe oxides over time by changing their mineralogy towards increasingly poorly crystalline forms that are more reactive than crystalline minerals (Ginn et al. 2017; Thompson et al. 2011). Additionally, soil microbial communities can adapt to dynamic redox regimes (Banerjee et al. 2016; DeAngelis et al. 2010; Evans and Wallenstein 2012, 2014; Palta et al. 2016; Peralta et al. 2013; Pett-Ridge et al. 2006; Zeglin et al. 2013). Any of these factors or combination of these factors may control soil GHG emissions depending on historical soil drainage. Lasting changes to soil biotic and abiotic properties can occur over the course of a single growing season (Pett-Ridge et al. 2006; De-Campos et al. 2009, 2012; Banerjee et al. 2016; Ginn et al. 2017) but can also take many years to develop (Thompson et al. 2011; Evans and Wallenstein 2012, 2014; Zeglin et al. 2013; Averill et al. 2016).

The goal of this study was to determine if historical soil drainage affects the response of CO_2 and N_2O emissions from upland soils to intense precipitation events. To test our hypothesis that CO_2 and N_2O dynamics would differ between soils with different historical drainage patterns, we measured in situ CO_2 and N_2O fluxes from poorly-drained and well-drained areas in an active agricultural field prior to and following large rain events. Soil drainage classifications were determined based on visual observations of ponding only in areas classified as poorly-drained in the days following large rain events (> 30 mm over 24 h). To separate the effects of contemporary conditions from soil drainage legacy effects, we performed a laboratory experiment in which soils from both drainage classes were subjected to the same flooding and drainage treatments. We also used stable isotope pool dilution techniques to measure gross N_2O production and consumption in the field, and stable isotope tracers to determine the dominant process responsible for N_2O production in the lab.

Methods

Study site

The study was conducted in an agricultural field located at the University of Illinois Crop Sciences Research and Education Center in Urbana, Illinois ($40^\circ 4' 26.42''\text{N}$, $88^\circ 14' 19.63''\text{W}$). For over the past 50 years, the field has been primarily rain-fed and is annually planted in maize in odd years and soybeans in even years, including in 2014 and 2015. Mean annual temperature in Urbana is 10.9°C , and mean annual precipitation is 1045 mm (Illinois Climate Network 2017). Precipitation data for the time period of this study were measured 0.5 km away from the study site (Illinois Climate Network 2017). During the period of 1989–2012, the daily average air temperature for the growing season (June–September) ranged between 22 and 24°C ; the monthly average rainfall ranged between 70 and 110 mm for this period (Illinois Climate Network 2017).

The study field extends approximately 80 m from north to south along a drainage gradient that causes varying frequency and duration of ponding in response to rain. This ponding occurs despite underlying tile drainage typical of the Midwest, US. Soils in the northern end of the field are classified as somewhat poorly-drained silt loams from the Flanagan soil series, while soils in the southern end are classified as poorly-drained silty clay loams from the Drummer soil series. These geographically associated soil series occur along a slope profile forming a drainage sequence with the Drummer soil in depressed areas; in other words, the characteristics that distinguish the two soil series are caused by the differing historical drainage patterns along the slope profile. We established two circular sampling areas (10 m diameter) separated by 60 m along this soil drainage gradient and for simplicity in terminology hereafter refer to the drainage class on the north end as well-drained (WD) and on the south end as poorly-drained (PD). The PD soils exhibit ponding when over 30 mm of precipitation fall over 24 h whereas the WD soils never experience ponding. Both the PD and WD soils are under the same management practices.

Quasi-continuous in situ measurements

To characterize how soil redox in the two drainage classes responded to precipitation, we measured quasi-

continuous in situ bulk soil O₂ concentrations and volumetric water content as proxies for soil redox. Soil O₂ data were collected from 10, 20, and 30 cm depth at one location in each drainage class beginning 10 May 2015 using Apogee SO-110 oxygen sensors fitted with AO-001 diffusion heads (Apogee Instruments, Logan, UT). Sensor voltage was measured every minute, and 30-min averages were recorded on a CR-100 datalogger (Campbell Scientific, Logan, UT). We converted voltage measurements to relative percent O₂ using a unique calibration factor for each probe determined prior to field deployment. The probes were calibrated based on mV measurements at 0% O₂ (dinitrogen gas) and 20.95% O₂ (ambient air) in sealed jars containing water to create a humid environment that mimicked mesic soil conditions. We used an empirical function provided in the Apogee SO-110 owner's manual to correct soil O₂ concentrations for temperature in the diffusion head as measured by the SO-110 sensor and atmospheric pressure measured at a nearby weather station (Illinois Climate Network 2017). Soil moisture was measured quasi-continuously using Decagon 5TM probes with EM50 data loggers at 10 cm and 30 cm depth from the PD class from April 2015 through September 2015 (Decagon, Pullman, WA); data are absent from the WD drainage class due to a non-operational datalogger.

Field measurements of net GHG fluxes

We measured in situ net GHG fluxes in the WD and PD classes on 11 dates during June–July 2014, a period when we expected large rain events to occur. We aimed to quantify fluxes before and after large rain events (> 30 mm) that could cause ponding and were successful in doing so for one event in late June. On each sampling date, we randomly placed six 26 cm diameter, 10 cm tall polyvinylchloride collars in each drainage class, inserting each collar approximately 3 cm into the soil surface. After a 30 min equilibration period, a vented acrylonitrile–butadiene–styrene plastic chamber top with a rubber septum port was placed on each collar (Matson et al. 1990). Gas samples were collected at 0, 5, 15, 30, and 45 min after the chambers were sealed; they were stored in 10 mL pre-evacuated glass vials sealed with thick rubber septa (Geo-Microbial Technologies, Inc., Ochelata, OK) and aluminum crimps (Wheaton Industries, Inc., Millville, NJ). All gas samples were analyzed on a Shimadzu GC

2014 gas chromatograph (GC) equipped with an electron capture detector (ECD), flame ionization detector, and thermal conductivity detector to measure concentrations of N₂O, CH₄, and CO₂, respectively. We determined net trace gas fluxes from the change in gas 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 there was no significant relationship between gas concentration and time ($p > 0.05$). There were no significant net CH₄ fluxes measured in this study.

Soil physical and chemical properties were also measured from each gas sampling location to provide insight into possible mechanisms driving observed patterns in soil GHG fluxes. After the last gas sample was collected from a chamber, we measured the chamber temperature and the soil temperature at 10 cm depth in the chamber footprint using an Acorn Temp 5 meter (Oakton Instruments, Vernon Hills, IL). A 0–10 cm depth soil sample was collected from each chamber footprint and transported at ambient temperature to the laboratory for same day processing. A subsample of each homogenized soil sample was shaken in 2 M KCl for 1 h, and another was shaken in 0.5 N HCl for 24 h to extract inorganic N and acid-extractable Fe, respectively. KCl extracts were analyzed colorimetrically for NH₄⁺ and NO₃⁻ on a Lachat Quick Chem flow injection analyzer (Lachat Instruments, Milwaukee, WI, USA). HCl extracts were analyzed for total Fe and Fe(II) concentrations using a modified ferrozine method (Liptzin and Silver 2009) on a Genesys 5 spectrophotometer (Thermo Scientific Spectronic, Waltham, MA). We measured gravimetric soil moisture by oven-drying a soil sample at 105 °C for at least 48 h. As part of a separate study, we collected three 0–10 cm cores from each drainage class with a 5 cm diameter core (AMS, Inc., American Falls, ID) to measure soil pH and bulk density (Suriyavirun et al. 2019).

Field measurements of gross N₂O fluxes

To determine how gross N₂O production and consumption may have contributed to the patterns in in situ net N₂O fluxes we observed in 2014, we performed field measurements of gross N₂O fluxes following two large rain events from June to July 2015. We employed the ¹⁵N₂O pool dilution technique

(Yang et al. 2011) with the same two-piece static flux chambers used for the net trace gas flux measurements. We volumetrically mixed 99% SF₆ (Matheson Tri Gas, Inc., Waverly, TN), 99% N₂O at 98 atom% ¹⁵N enrichment (Isotech, Richmond, CA, USA), and ultra-high purity helium (Airgas, Radnor, PA) in gas sample bags (Restek Corporation, Bellefonte, PA) to create a spiking gas consisting of 7.7 ppm SF₆ and 13.1 ppm N₂O at 98% atom ¹⁵N enrichment. We added 10 mL spiking gas to the chamber headspace immediately after the chamber top was placed on the collar, with the goal of increasing chamber headspace gas concentrations by 25 ppb N₂O and 10 ppb SF₆, achieving 5 atom% ¹⁵N enrichment of the chamber headspace N₂O pool. Gas samples (90 mL) were collected 0, 5, 15, 30, and 45 min after spiking gas injection and were stored in pre-evacuated 60 mL glass vials sealed with Teflon-coated rubber septa (Macherey-Negal, Inc., Bethlehem, PA) and aluminum crimps (Wheaton Industries, Inc., Millville, NJ).

All gas samples were analyzed for trace gas concentrations and ¹⁵N isotopic composition of N₂O in order to calculate gross rates of N₂O production and consumption. A 5 mL aliquot was removed from each gas sample vial for determination of N₂O, SF₆, CH₄, and CO₂ concentrations on the GC. For this experiment, the GC was equipped with a 4 m × 1 mm Hayesep Q column to allow adequate separation between N₂O and SF₆ on the ECD. The remaining gas in each sample vial was analyzed for ¹⁵N isotopic composition of N₂O using an IsoPrime 100 isotope ratio mass spectrometer (IRMS) interfaced to a trace gas preconcentration unit (Isoprime Ltd., Cheadle Hulme, UK) and a GX-271 autosampler (Gilson, Inc., Middleton, WI). To calculate rates of gross N₂O production and consumption we used the pool dilution model described by Yang et al. (2011) and von Fischer and Hedin (2007). The iterative model solves for N₂O production based on the dilution of the isotopically enriched chamber headspace pool of N₂O by natural abundance N₂O. Gross consumption rates were estimated using the empirical loss of ¹⁵N–N₂O, using SF₆ as a tracer to account for physical loss. 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 (Yang et al. 2011). N₂O yield was calculated as the difference between gross N₂O production and consumption divided by gross N₂O production.

N₂O source lab experiment

In September 2015, we collected 24 intact soil cores (0–10 cm depth) from each of the WD and PD classes for a laboratory ¹⁵N tracer experiment to estimate the relative importance of nitrifiers and denitrifiers in producing N₂O. We collected the cores from relatively dry soils to reduce the potential for soil compaction. We used a 2.5 cm diameter corer (AMS, Inc., American Falls, ID) fitted with removable plastic sleeves to collect the intact cores. We discarded cores that were clearly compacted during collection; the bulk density of the cores used in the experiment were comparable to that of cores collected using a 5 cm diameter corer (1.03 ± 0.10 and 1.09 ± 0.10 g dry soil cm⁻³ using the 2.5 cm corer in PD and WD soils, respectively compared to 1.05 ± 0.06 and 0.97 ± 0.02 g dry soil cm⁻³ using the 5 cm corer for PD and WD soils, respectively). We removed sleeved soil cores from the corer and capped them at both ends prior to transport to the laboratory at ambient temperature. Soil cores were incubated upright, with the upper cap removed, in a dark growth chamber (model PGR15, Conviron, Winnipeg, Canada) set to mimic mean typical summertime diurnal temperature fluctuations (12 h at 20 °C and 12 h at 30 °C) determined from quasi-continuous in situ surface soil (5 cm depth) temperature measurements at the site in 2011–2013 (Sanford unpublished data). Soil evaporation during the 2-day pre-incubation was minimized by placing a tub of water in the growth chamber to increase humidity and by loosely covering the cores with aluminum foil.

We imposed a flooding treatment and a drainage treatment to determine if N₂O production pathways differed between PD and WD soils under different moisture conditions. After 2 days of the preincubation described above, we flooded all 24 of the cores from each drainage class with rainwater. Half of the cores (n = 12 for each drainage class) were drained after 2 days (referred to as the Drained treatment), and half of the cores remained flooded for the full 5-day incubation period (referred to as the Flooded treatment). Net fluxes of N₂O, CO₂, and CH₄ were measured prior to flooding the cores (day 1) and on days 2 through 4 of the treatment incubations. Each day the same two intact soil cores from a given treatment were placed together in a sealed jar for net trace gas flux measurements to yield six replicate

measurements per treatment. Real-time trace gas concentrations in the jar headspace were measured over 8 min using a cavity ring down spectrometer (CRDS; Model G2508, Picarro, Santa Clara, CA); trace gas fluxes were estimated from the linear change in concentrations, excluding the first minute of data when the gases were mixing between the jar, CRDS internal headspace, and the tubing connecting the jar to the Picarro (with a total of 174 mL volume sample loop). Fluxes were considered significant if the change in gas concentration exceeded three times the reported 5-min detection limit (0.015 ppm for N₂O and 0.6 ppm for CO₂, Model G2508, Picarro, Santa Clara, CA).

To estimate N₂O production from nitrifiers and denitrifiers, we used short-term laboratory incubations with either ¹⁵N-labeled NH₄⁺ or ¹⁵N-labeled NO₃⁻ (n = 6 for each treatment). The production of ¹⁵N₂O from soils receiving ¹⁵NH₄⁺ represents nitrifier nitrification and nitrifier denitrification as N₂O source processes (van Groenigen et al. 2015) and from soils receiving ¹⁵NO₃⁻ represents heterotrophic denitrification. We did not account for abiotic processes, which can be important sources of N₂O in arid and semi-arid systems (Wang et al. 2017) but are likely less important in our mesic study site. On the final day of the treatment incubation (day 5), the soil samples were extruded from their cores and composited in Ziploc bags in the pairs that had been used for the CRDS trace gas flux measurements. We did this to ensure homogenous ¹⁵N enrichment in the soil. The homogenized soil samples were subsampled to measure gravimetric moisture and for 2 M KCl extraction to determine initial background NH₄⁺ and NO₃⁻ concentrations. We split the remaining soil into two subsamples for ¹⁵N label addition: 1 mL of 99 atom% ¹⁵N enrichment NH₄Cl (Cambridge Isotope Laboratories, Inc., Andover, MA) at a solution concentration of 6.38 µg N mL⁻¹ was added to one subsample, and 1 mL of 99 atom% ¹⁵N enrichment KNO₃ (Cambridge Isotope Laboratories, Inc., Andover, MA) at a solution concentration of 5.83 µg N mL⁻¹ was added to the other. The initial ¹⁵N enrichment of the NH₄⁺ pool averaged 15.2 atom% and ranged 3.6–33.2 atom%. The initial ¹⁵N enrichment for the NO₃⁻ pool averaged 17.8 atom% and ranged 4.1–36.9 atom%. After 15 min, 25 g of each soil sample was extracted in 100 mL of 2 M KCl. The remaining

soil was sealed in a 250 mL canning jar with a lid fitted with a rubber septum. After 4 h, a 90 mL gas sample was collected from the jar, and then the soil in the jar was extracted for NH₄⁺ and NO₃⁻ in 2 M KCl. Soil NH₄⁺ and NO₃⁻ in the KCl extracts were prepared for ¹⁵N isotope analysis by acid-trap diffusion (Herman et al. 1995) and analyzed for ¹⁵N isotopic composition on an IsoPrime 100 IRMS interfaced to a Vario Micro Cube elemental analyzer (Isoprime Ltd., Cheadle Hulme, UK; Elementar, Hanau, Germany). The gas samples were analyzed for trace gas concentrations on a GC and for ¹⁵N–N₂O on an IRMS as described above. Net CO₂ and N₂O emissions were calculated by the change in concentration over the course of the incubation. We calculated a minimal detectible flux based on the standard deviation of three standard gas samples (1001 ppm CO₂ and 1.08 ppm N₂O) run on the GC. The calculated detection limit for N₂O was 0.007 ppm h⁻¹ for CO₂ was 5.6 ppm h⁻¹. We estimated fluxes below this detection limit as zero. We estimated nitrifier-derived net N₂O fluxes based on ¹⁵N₂O produced from soils amended with ¹⁵NH₄⁺ scaled by the mean ¹⁵N enrichment of the NH₄⁺ pool measured at the 15 min and final time points. Denitrifier-derived net N₂O fluxes were similarly estimated using the samples amended with ¹⁵NO₃⁻. The sum of the nitrifier- and denitrifier-derived N₂O fluxes estimated in this way exceeded the net N₂O flux determined simply from the change in N₂O concentration (i.e., the net flux of ¹⁴N₂O + ¹⁵N₂O) due to N₂O reduction to N₂ via denitrification during the soil incubations. This does not affect our aim to determine the relative contribution of nitrifiers and denitrifiers to N₂O. Therefore, we calculated the proportional contribution of each process to the sum of nitrifiers- and denitrifiers-derived N₂O fluxes and then proportionally adjusted the N₂O flux estimates for each process so that their sum equaled the net N₂O flux.

Statistical analysis

We used R version 3.5.1 (R Core Team 2014) to perform statistical analyses and Microsoft Excel version 14.7.7 (Microsoft Corporation, Redmond, WA, USA) to run the iterative pool dilution model. Differences in soil physical and chemical variables measured in the field from WD and PD soils were assessed using two-tailed Student's *t* test. Statistical

significance was determined at $p < 0.05$. We used two-way analysis of variance (ANOVA) with drainage class and date as factors to compare field fluxes and soil properties before and after one large rain event spanning June 23rd and 24th 2014. This was done using the `anova` function in the `car` package in R (Fox and Weisberg 2011). Type III sums of squares were used to test for the presence of an interaction. If no interaction was detected, then type II sums of squares were used. When needed, data were either square root transformed or log-transformed to meet the assumptions of normality. A small constant of one was added prior to transformation when values below one were present. We used linear mixed effects models with drainage class and day of experiment as the two fixed factors, and soil core ID as the random factor to assess differences in net CO_2 and N_2O emissions from flooded cores during days 2 through 4 of the N_2O source lab experiment. This was done using the `lme` function from the `nlme` package (Pinheiro et al. 2017). We tested the significance of the fixed factors in this model using a likelihood ratio test performed using the `anova` function in `car` (Fox and Weisberg 2011). We used two-way ANOVA with treatment and drainage class as the factors to compare nitrification and denitrification derived N_2O fluxes from the N_2O source lab experiment. We conducted multiple pairwise comparisons corrected using Tukey's HSD to compare means across all factors for both the field and lab measurements. This was done using the `lsmeans` package (Lenth 2016).

Results

Soil properties

Soil O_2 dynamics differed between the PD and WD classes from May 2015 through August 2015 (Fig. 1). During this time, the PD soils consistently had lower soil O_2 concentrations at 10 cm depth compared to the WD soils. After large rain events (i.e., over 30 mm in 24 h), 10 cm depth soil O_2 concentration in the PD class fell to as low as 0% and took up to a week to rebound to pre-rain levels (Fig. 1a, b). In contrast, soil O_2 in the WD class never dropped below 10% at 10 cm depth. Soil O_2 decreased with depth in both classes but was generally lower in the PD class across both depths (Fig. 1b, c). Volumetric soil moisture at

10 cm depth in the PD drainage class was close to 20% under dry conditions, and increased to around 35% in response to rain events (Fig. 1a, d). In general, 10 cm depth O_2 concentrations from PD soils began to decrease when soil moisture increased above approximately 30%.

Despite their proximity and similar management, soils from the two drainage classes had different chemical properties (Table 1). Soil from the PD class had higher concentrations of total organic C (TOC, $p < 0.01$) and total N ($p = 0.05$) compared to soils from the WD class. Soils from the PD class also had higher pH compared to soils from the WD class, averaging 5.85 ± 0.06 compared to 5.35 ± 0.07 , respectively ($p < 0.01$). Soil bulk density was not significantly different between the two drainage classes, averaging 1.01 ± 0.05 g dry soil cm^{-3} .

Biogeochemical responses to rain events

Large rain events had strong and opposing effects on net N_2O fluxes between the two drainage classes (Fig. 2a, b), suppressing emissions in the PD class and stimulating them in the WD class ($F_{1,20} = 20.1$, $p < 0.001$). In response to a 64 mm rain event spanning June 23 and 24, 2014, N_2O emissions from the WD class increased from 3.0 ± 0.12 to 26 ± 12 ng N $\text{cm}^{-2} \text{h}^{-1}$ ($p < 0.05$), whereas N_2O emissions from the PD class decreased from 15 ± 3.3 to 4.6 ± 2.0 ng N $\text{cm}^{-2} \text{h}^{-1}$ ($p < 0.05$). This same pattern occurred in response to other rain events for which over 30 mm of precipitation fell within 24 h during June–July 2014 (Fig. 2a, b). There was no significant effect of sampling day on soil NH_4^+ concentrations ($F_{1,20} = 0.22$, $p = 0.6$), but there was a significant effect of drainage class ($F_{1,20} = 4.4$, $p < 0.05$), with PD soils having higher NH_4^+ concentrations (Fig. 2d). Soil NO_3^- concentrations decreased in response to the rain event ($F_{1,20} = 7.4$, $p = 0.01$), but this response did not differ between the two drainage classes ($F_{1,20} = 2.8$, $p = 0.1$) (Fig. 2e). HCl-extractable Fe(II) concentrations, used here as a biogeochemically relevant indicator of soil redox, were consistently higher for PD than WD soils ($F_{1,20} = 9.4$, $p < 0.01$) and did not change in response to the rain event ($F_{1,20} = 0.49$, $p = 0.49$) (Fig. 2f).

Field measurements of gross N_2O production and consumption rates during June–July 2015 elucidated

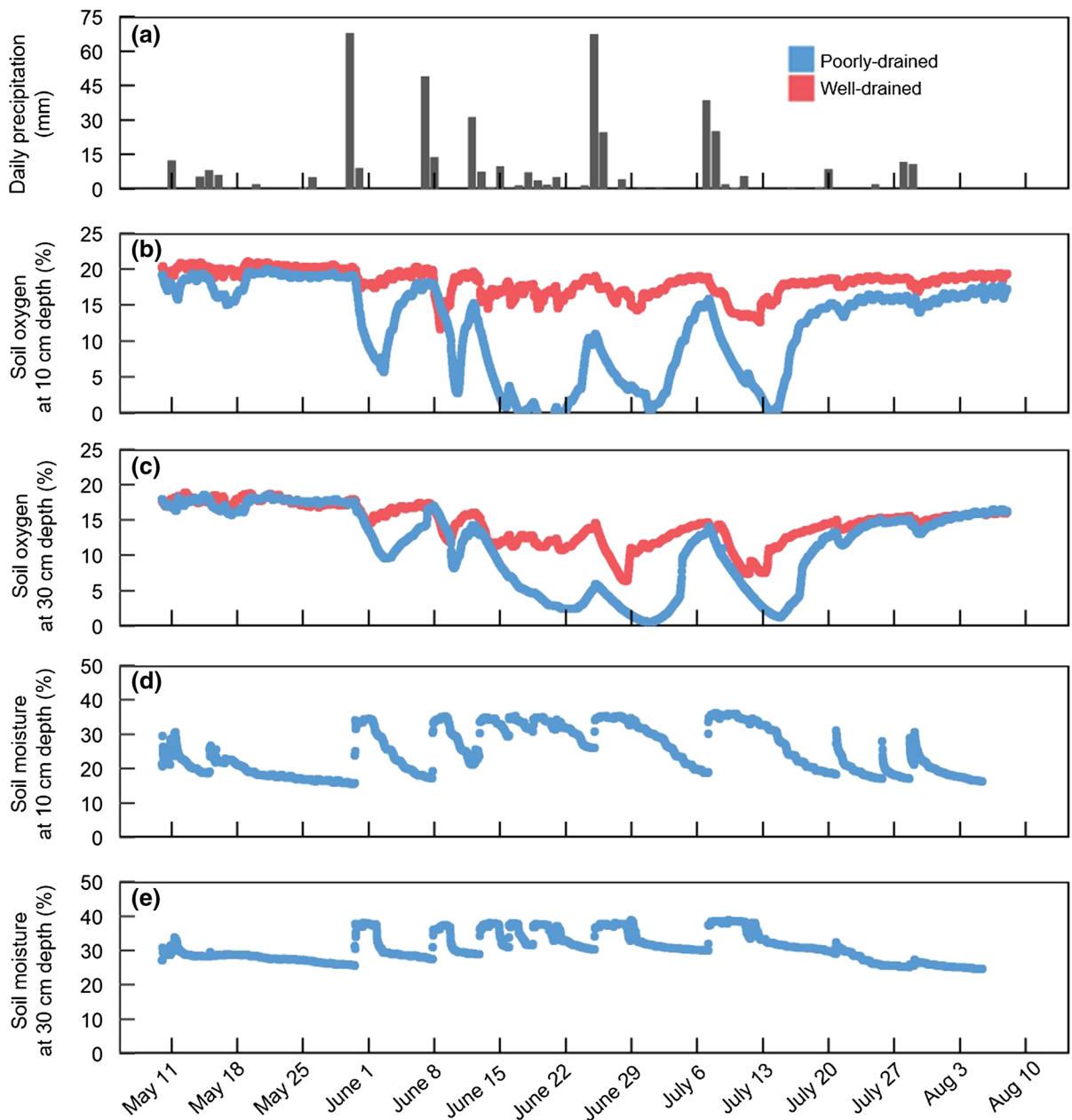


Fig. 1 Daily precipitation (a), bulk soil O₂ concentration at 10 cm depth (b) and 30 cm depth (c), volumetric soil moisture at 10 cm depth (d) and 30 cm depth (e) by drainage class. Data

were collected from May through August 2015. Missing soil moisture data for the well-drained class was due to datalogger failure

the contribution of these two processes to net N₂O fluxes (Fig. 3). There was a significant drainage class by day interaction effect on N₂O yield ($F_{3,39} = 3.0$, $p < 0.05$), defined as net N₂O production divided by gross N₂O production (Table 2). The N₂O yield remained consistent in the WD class over the four sampling days in 2015, averaging 0.48 ± 0.08 . In the

PD class, the N₂O yield was lower on 27 June and 9 July compared to 11 July and 15 July (Table 2). Large rain events occurred within 48 h before sampling on 27 June and 9 July (Fig. 3a). This increase in N₂O yield was a result of a greater increase in gross N₂O production relative to gross N₂O consumption as soils dried on 11 July and 15 July, leading to a higher

Table 1 Soil chemical and physical properties by drainage class (mean \pm standard error)

	n	t	p	Poorly-drained	Well-drained
Total organic C (%)	12	3.7	< 0.01	2.37 \pm 0.05	2.16 \pm 0.02
Total N (%)	12	2.1	0.05	0.182 \pm 0.003	0.176 \pm 0.001
pH	3	5.4	< 0.01	5.85 \pm 0.06	5.35 \pm 0.07
Bulk density (g cm ⁻³)	3	1.4	0.30	1.05 \pm 0.06	0.97 \pm 0.02

A Student's t-test was performed to compare each soil chemical and physical property between the two drainage classes. Sample size (n), t-value (t), and p-value (p) from the Student's t-test are reported

proportion of produced N₂O being released to the atmosphere. Overall, net N₂O fluxes were inhibited in PD soils and were stimulated in WD soils following large rain events (Fig. 3b). This is the same pattern observed in 2014 (Fig. 2b) and appeared to be driven by suppressed gross N₂O production in PD soils following large rain events (Fig. 3c). Soil NO₃⁻ concentrations were greater in the WD class on 27 June, and were similar on all other sampling dates (Fig. 3e). Soil NH₄⁺ concentrations were greater in the PD class compared to the WD class on 27 June, 9 July, and 11 July, and did not differ between drainage classes on 15 July (Fig. 3f).

Large rain events also differentially affected CO₂ fluxes in the two drainage classes ($F_{1,20} = 23.8$, $p < 0.001$) (Fig. 2c). On 23 June 2014, before the rain event, CO₂ fluxes averaged $25.9 \pm 3.13 \mu\text{g C cm}^{-2} \text{ h}^{-1}$ from PD soils compared to $16.2 \pm 0.88 \mu\text{g C cm}^{-2} \text{ h}^{-1}$ in WD soils. Afterwards, CO₂ fluxes decreased in the ponded PD soils ($p < 0.01$) whereas they did not change significantly in the WD soils, which did not have standing water. After this rain event, CO₂ fluxes were lower in the PD class ($2.33 \pm 0.56 \mu\text{g C cm}^{-2} \text{ h}^{-1}$) compared to the WD class ($20.7 \pm 4.70 \mu\text{g C cm}^{-2} \text{ h}^{-1}$; $p < 0.01$). Large rain events also inhibited CO₂ efflux from PD soils after large rain events on 30 June 2014 (Fig. 2c), as well 26 June and 7 July 2015 (Fig. 3g).

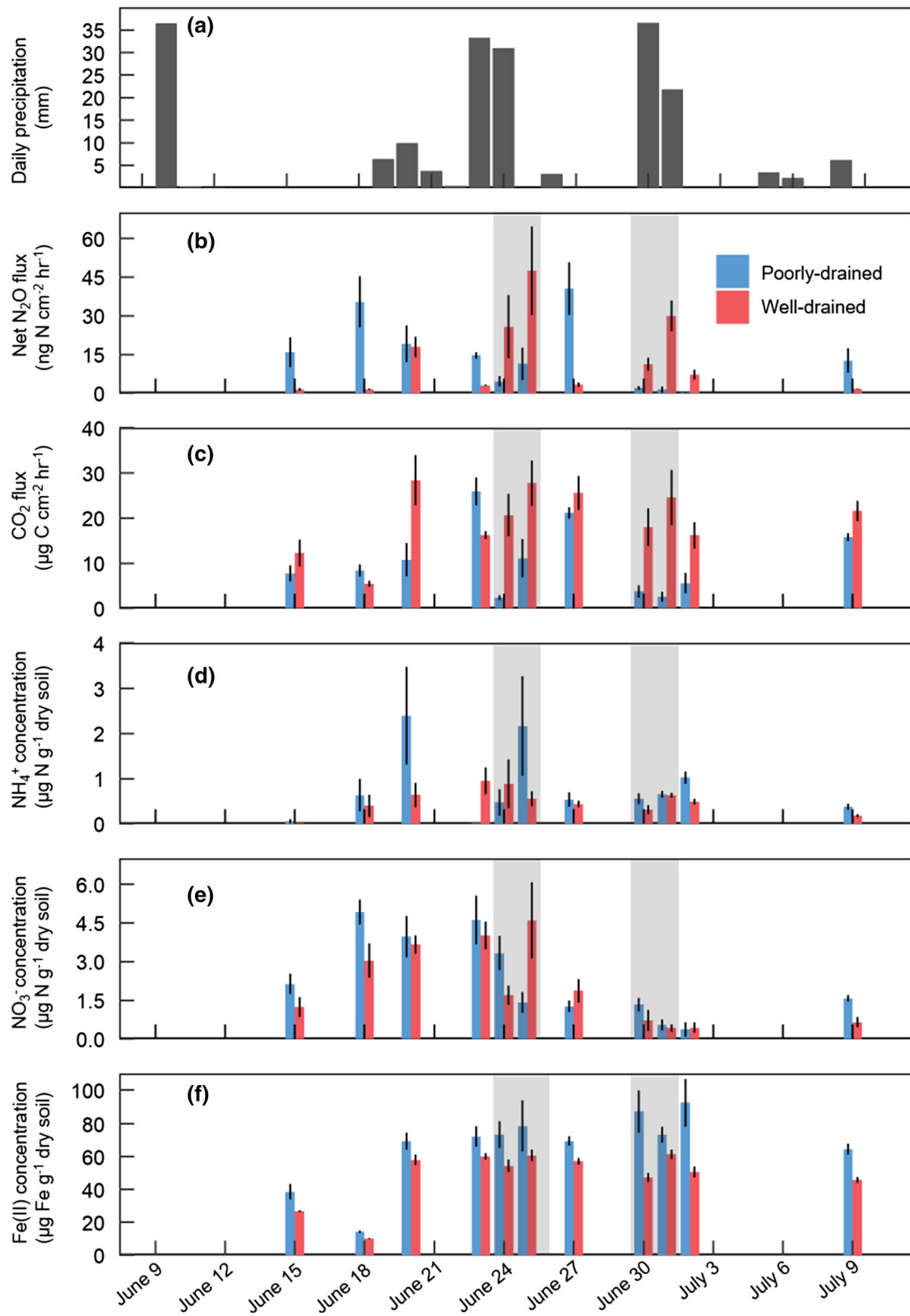
N₂O source laboratory experiment

One day of flooding stimulated net N₂O fluxes from both PD and WD classes (Fig. 4a). Fluxes were not detectable before the cores were flooded (day 1) and returned to non-detectable levels in the PD soil cores on day 3, after 2 days of flooding. During days 2 through 4, net N₂O fluxes were higher in the flooded

WD soils compared to the flooded PD soils [$X^2(1) = 26.0$, $p < 0.001$, Fig. 4a]. There was also a significant day effect that was driven by lower N₂O efflux from the WD soils on day 4 [$X^2(2) = 8.7$, $p = 0.01$]. There was a marginally significant interaction effect of drainage class and day on net N₂O efflux ($F_{2,30} = 5.5$, $p = 0.06$).

There was a significant interaction effect on denitrifier-derived N₂O fluxes ($F_{1,16} = 5.9$, $p < 0.05$), with higher fluxes under the flooded treatment in the WD class compared to all other soils (Fig. 5a). Denitrifier-derived N₂O fluxes accounted for over 72% of the total net N₂O flux for all treatments across both drainage classes. The flooded treatment exhibited higher nitrifier-derived net N₂O fluxes than the drained treatment ($F_{1,18} = 9.8$, $p < 0.01$, Fig. 5b); there was no significant drainage class or interaction effect on these fluxes ($F_{1,18} = 0.85$, $p = 0.4$, $F_{1,18} = 0.84$, $p = 0.4$, respectively). There was a significant treatment effect on total net N₂O flux ($F_{1,43} = 12.27$, $p < 0.01$), and a marginally significant drainage class and interaction effects ($F_{1,43} = 3.8$, $p = 0.06$; $F_{1,43} = 3.8$, $p = 0.06$ respectively). Total net N₂O flux from the WD class under the flooded treatment was higher compared to all other drainage class and treatment combinations ($p < 0.05$).

Soil CO₂ fluxes were suppressed from all soils the day after flooding, but the fluxes rebounded during the experimental treatment incubation (Figs. 4b, 5d). During days 2 through 4 of the experiment, soil CO₂ fluxes in the flooded treatment were higher from the PD class compared to WD class [$X^2(1) = 11.0$, $p < 0.001$, Fig. 4b]. Additionally, CO₂ fluxes increased each day during this time [$X^2(2) = 10.9$, $p < 0.01$]. We also measured CO₂ efflux from soils during the N₂O source experiment (Fig. 5d). During this experiment, soil CO₂ fluxes were higher from the



◀ **Fig. 2** Daily precipitation (a), net N₂O flux (b), CO₂ flux (c), and soil concentrations of NH₄⁺ (d), NO₃⁻ (e) and Fe(II) (f) measured on 11 days during summer 2014. Error bars represent one standard error (n = 6). Shaded areas represent sampling days where over 30 mm of rain had fallen in the past 48 h

PD class compared to the WD class ($F_{1,44} = 11.6$, $p < 0.01$); overall, fluxes were higher in the flooded treatment compared to the drained treatment ($F_{1,44} = 17.2$, $p < 0.001$).

Soil NH₄⁺ concentrations were higher in the flooded treatment than the drained treatment ($F_{1,20} = 19.7$, $p < 0.001$) but did not differ significantly between the two drainage classes ($F_{1,20} = 1.2$, $p = 0.3$, Fig. S1a). Nitrate concentrations immediately before the ¹⁵N tracer addition were higher in the drained treatment than the flooded treatment ($F_{1,20} = 17.3$, $p < 0.001$) and were marginally higher in the WD class than the PD class ($F_{1,20} = 3.3$, $p = 0.08$) (Fig. S1b). Soil moisture was higher in the flooded treatment compared to the drained treatment ($F_{1,20} = 4.8$, $p < 0.05$, Fig. S1c). Before the soil cores were flooded, soil moisture did not differ between the two drainage classes, averaging 0.21 ± 0.01 g H₂O g⁻¹ and 0.22 ± 0.01 g H₂O g⁻¹ in the PD and WD soils, respectively.

Discussion

Both contemporary conditions and historical soil drainage mediated N₂O and CO₂ emissions from mesic soils in an agricultural field. Large rain events stimulated net N₂O flux in WD soils and inhibited it in PD soils (Fig. 2a, b). Hotspots of N₂O efflux along topographic gradients have previously been attributed to the effect of contemporary soil moisture (Turner et al. 2016). Indeed, large rain events only caused ponding in the PD soils where surface soil O₂ concentrations fell near 0% (Fig. 1b). However, N₂O emissions were not just due to different contemporary ponding status, as ponding treatments in the laboratory experiment stimulated N₂O production via heterotrophic denitrification to a greater degree in WD compared to PD soils (Fig. 5a). Soil CO₂ efflux was also inhibited after large rain events (Fig. 2a, c), but autotrophic respiration may have obscured any

patterns between rain events in the field due to the contribution of root respiration to soil respiration during the growing season. Under lab conditions, soil CO₂ efflux was consistently greater from PD soils (Fig. 4b). Ponding initially inhibited CO₂ efflux from both drainage classes, but CO₂ emissions rose as ponding duration increased (Figs. 4b, 5d). These results suggest that soil drainage legacy effects are important regulators of soil GHG emissions. Here, we discuss potential mechanisms driving these effects, and what implications they have for understanding how soil GHG emissions will respond to amplification of the hydrological cycle.

The increased residence time of N₂O under low redox conditions in the PD soils suggests that increased complete denitrification to N₂ could be responsible for the inhibition of net N₂O fluxes in PD soils under ponded conditions (Chapuis-Lardy et al. 2007). However, measurements of gross N₂O production and consumption in the field demonstrated that net N₂O fluxes were due to changes to gross N₂O production rather than N₂O consumption (Fig. 3c, d). The suppression of N₂O production under flooded soil conditions could directly result from the inhibition of the aerobic processes of nitrifier nitrification or nitrifier denitrification which can release N₂O as a byproduct or intermediate product of nitrification, respectively (van Groenigen et al. 2015). Inhibition of nitrifiers under anaerobic conditions can also indirectly decrease net N₂O efflux by limiting the nitrification-derived NO₃⁻ supply for N₂O production via denitrification. The latter is likely a more important mechanism because a laboratory ¹⁵N tracer experiment showed that denitrifiers dominated over nitrifiers as the N₂O source in both soil drainage classes (Fig. 5a, b). The use of loose (albeit unsieved) soil for this experiment may have caused some soil aggregates to disperse, thus releasing labile soil C to fuel denitrification (Schimel et al. 1989), and the even distribution of soil organic matter by soil homogenization for the experiment may have inhibited nitrification by favoring heterotrophs that compete better for NH₄⁺ under C-rich conditions (Booth et al. 2006). However, artifacts of soil structure treatment on soil N cycling rates are not always detectable or consistent across studies (Yang et al. 2017). Early in the growing season when soil NO₃⁻ concentrations are still high from fertilizer application and low plant

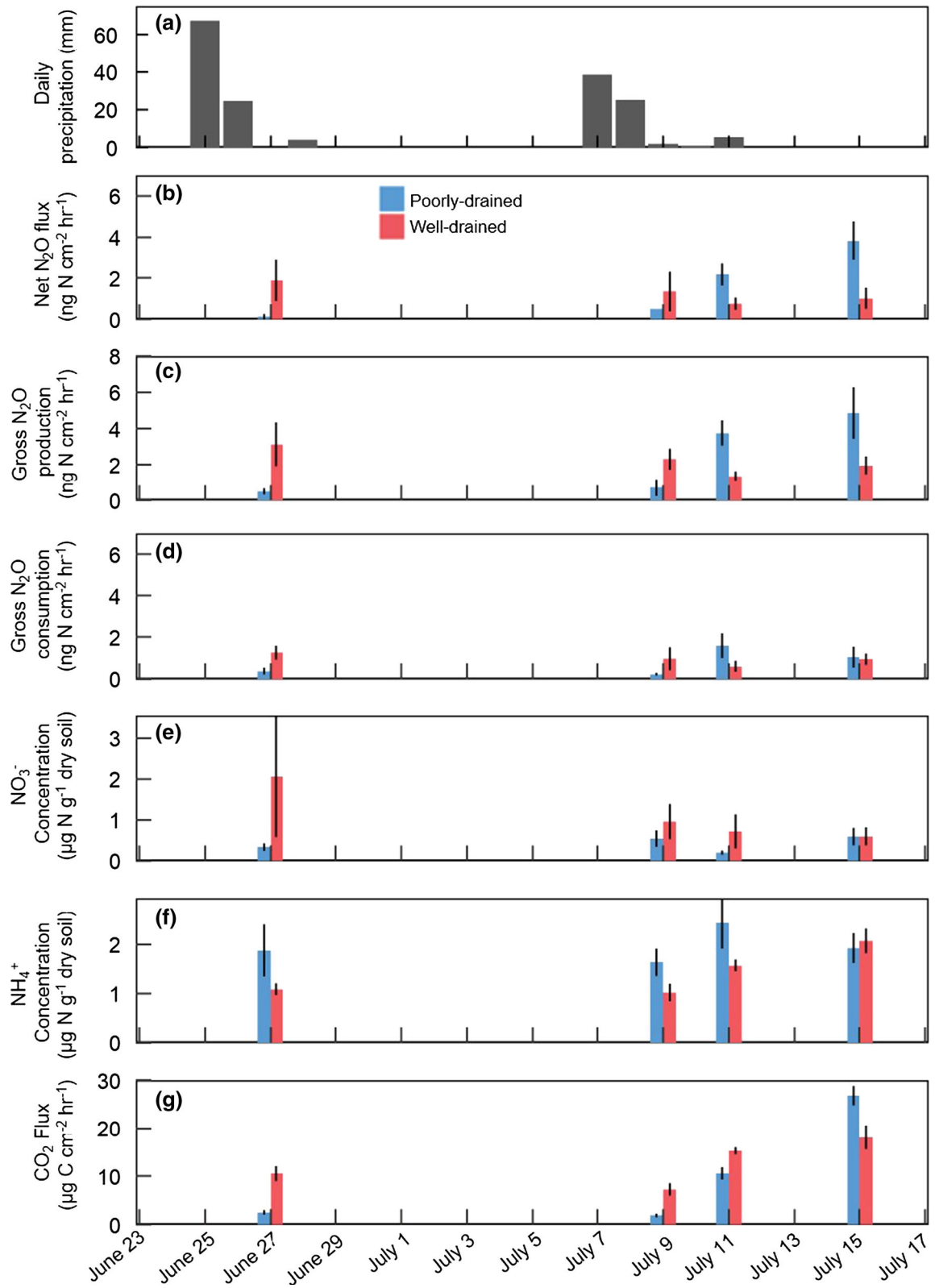


Fig. 3 Daily precipitation (a), net N₂O flux (b), gross N₂O production rate (c), gross N₂O consumption rate (d), NO₃⁻ concentration (e), NH₄⁺ concentration (f), and CO₂ flux (g) measured in the field on 4 days during summer 2015. Error bars represent one standard error (n = 6)

Table 2 N₂O yield from the 2015 field measurements (n = 6)

Date	N ₂ O yield (mean ± SE)	
	Poorly-drained	Well-drained
June 27*	0.15 ± 0.15 ^a	0.55 ± 0.08 ^{ab}
July 9*	0.16 ± 0.16 ^{ab}	0.44 ± 0.20 ^{ab}
July 11	0.60 ± 0.14 ^{ab}	0.47 ± 0.17 ^{ab}
July 15	0.83 ± 0.05 ^b	0.42 ± 0.16 ^{ab}

Letters indicate significant differences measured by Tukey corrected multiple comparisons ($p < 0.05$). Asterisks indicate dates within 48 h of rainfall

nitrogen demand, depressed areas can serve as N₂O hot spots when ponding creates conditions conducive for denitrification in the presence of ample NO₃⁻ supply (Molodovskaya et al. 2012; Saha et al. 2017). In contrast, our study took place later in the growing season when soil NO₃⁻ concentrations were low,

thereby limiting denitrification rates in ponded depressed areas to create N₂O cold spots (Turner et al. 2016).

The drainage class differences in in situ gross N₂O production rates following intense rain events cannot be explained solely by contemporary ponding status, as net N₂O efflux differed between soils from the two drainage classes when exposed to the same flooding treatments (Fig. 4a). Well-drained soils supported higher rates of denitrifier-derived N₂O production compared to PD soils under flooded conditions (Fig. 5a), possibly by retaining microsites of high O₂ concentrations within soil macroaggregates (Askaer et al. 2010) that could support coupled nitrification–denitrification under flooded conditions. Although minor soil compaction while collecting soil cores can alter soil pore structure, this pattern observed in the laboratory experiment is consistent with the patterns in N₂O dynamics that we observed in the field. Over time, soil drainage can alter the size class of soil aggregates, which affects the distribution of O₂ throughout the soil profile. Specifically, prolonged anaerobic conditions, as were observed in the PD class, can break down soil macroaggregates (De-Campos et al. 2009). Additionally, plants are more productive in WD compared to PD soils (Grable and Siemer 1968; Kanwar et al. 1988), and plant roots and

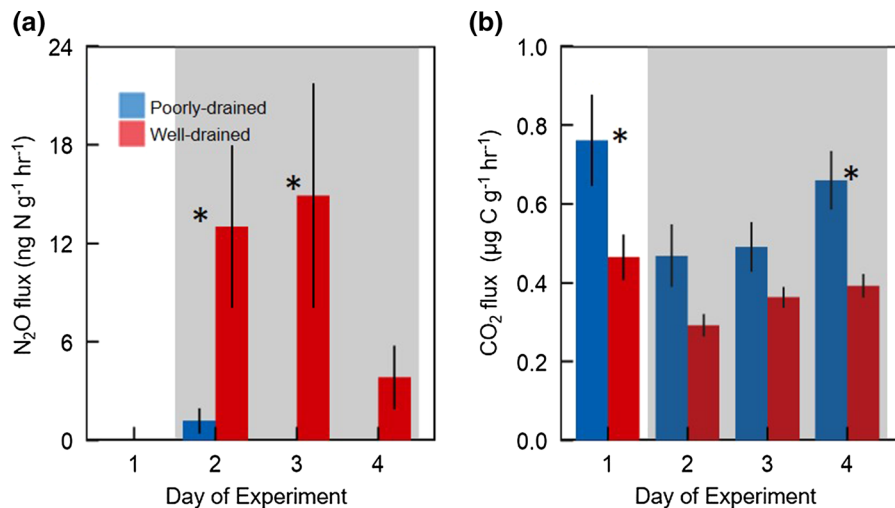
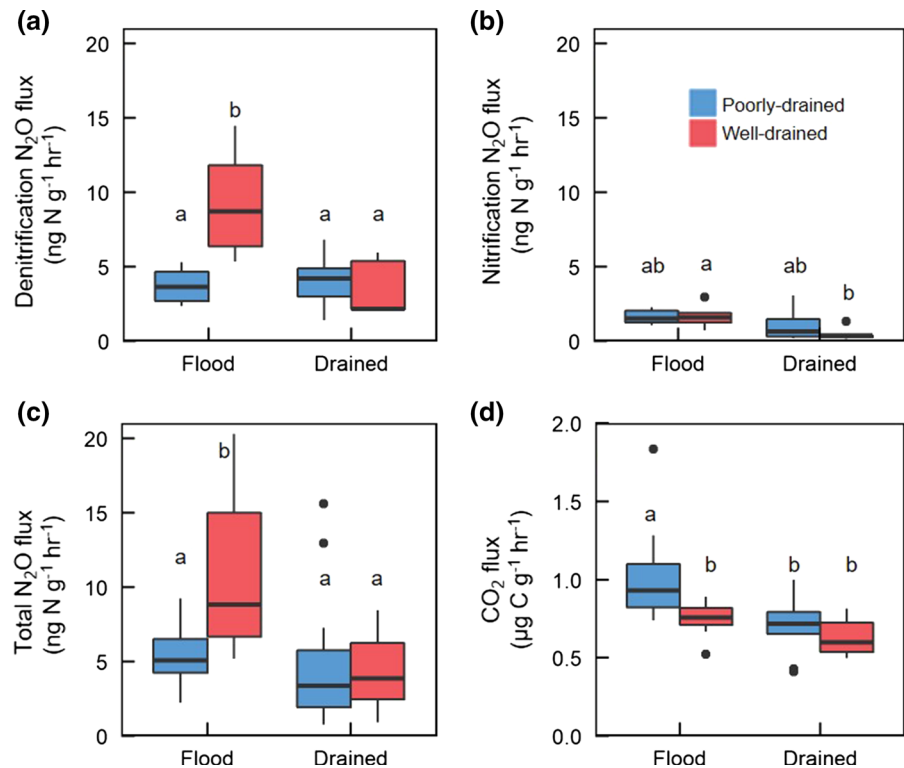


Fig. 4 Net N₂O (a) and CO₂ (b) flux from the N₂O source experiment in 2015. Error bars represent one standard error (n = 6). The shaded area represents when all the cores were under flooded conditions. On day 1, soils were at field moisture. Asterisks indicate statistically significant differences between PD and WD soils on each day. For day 1, this was determined

using a paired t-test. For days 2–4, this was determined using Tukey HSD corrected multiple pairwise comparisons ($p \leq 0.05$). No significant net N₂O fluxes were detected on day 1 from either drainage class, and no significant net N₂O flux was detected from the PD soils on days 3 and 4

Fig. 5 Denitrification-derived net N_2O flux (a) nitrification-derived net N_2O flux (b), total net N_2O flux (c), and CO_2 flux (d) measured on day 5 of the 2015 N_2O source lab experiment. Letters represent significant differences between each mean determined using Tukey HSD corrected multiple pairwise comparisons ($p < 0.05$). The line in each box represents the mean ($n = 6$ for a–c, $n = 12$ for d), the upper and lower portions of each box correspond to the 25th and 75th percentiles, the whiskers extend to the upper and lower interquartile range, and dots represent outliers



fungal hyphae promote the formation of soil pores and aggregates (Horn and Smucker 2005; Six et al. 2004). Combined, these factors can create more macroaggregates within WD soils that can harbor aerobic microsites under flooded conditions (Gupta and Wang 2006; Askaer et al. 2010) that allow nitrification to occur (Banerjee et al. 2016), thus providing NO_3^- to fuel N_2O production via denitrification. As future increases in the magnitude and frequency of intense precipitation events extends ponding into currently WD soils, these newly ponded areas could, therefore, serve as N_2O hot spots throughout the growing season.

Poorly-drained soils maintained higher net N_2O fluxes than the WD soils during interludes between large rain events (Fig. 2a, b), causing a reversal in the locations of N_2O hot spots and cold spots observed during ponding events. As ponded soils drain, the release of stored N_2O can lead to pulses of N_2O emissions from soil that do not represent concurrent biological production of N_2O (Jarecke et al. 2016). However, the PD soils maintained higher net N_2O efflux even during relatively dry periods, such as 20 June 2014, when no rain had fallen in 10 days (Fig. 2a, b). This suggests that a biotic mechanism may explain

higher N_2O efflux during these periods. Soil O_2 concentrations at 10 cm depth experienced a higher magnitude decrease in PD soils compared to WD soils following large rain events, and remained lower compared to WD soils for approximately 1–2 weeks (Fig. 1a, b). For example, after the 90 mm rain event on 25–26 June 2015, 10 cm depth O_2 concentrations fell to 0.3% in the PD soils after 4 days, and didn't rise above 10% for another 3 days. Similar patterns were observed throughout the growing season. Thus, the PD soils potentially retained more anaerobic microsites conducive for denitrification that were intermixed with re-oxygenated pore spaces where nitrification could provide a NO_3^- supply. In contrast, the more porous WD soils were likely more quickly and uniformly oxygenated to limit N_2O production via denitrification. This reversal in N_2O hot spots and cold spots mediated by soil structure differences between drainage classes creates a mechanistic framework to predict when and where hot spots of soil N_2O emissions occur, allowing us to advance beyond the perspective of hot spots as occurring in fixed locations and hot moments as events that occur across the spatial domain (Bernhardt et al. 2017; McClain et al. 2003).

The contribution of autotrophic soil respiration to measured CO₂ fluxes likely obscured patterns in in situ heterotrophic soil respiration. Field sampling in this study occurred only during the peak growing season when roots were well-established. On most sampling dates, soil CO₂ fluxes were greater in the WD class than the PD class (Fig. 2c), but this likely reflected patterns in autotrophic soil respiration associated with higher plant productivity in the WD class (Grable and Siemer 1968; Kanwar et al. 1988). In the plant-free soil incubations in the laboratory, CO₂ fluxes were consistently higher in the PD soils than in the WD soils under these experimental treatments (Fig. 4b). Laboratory incubations are not representative of field conditions and reflect activity only in the soil depth increment sampled (i.e., 0–10 cm depth in this study) while not accounting for physical controls on soil–atmosphere gas fluxes. Nonetheless, this laboratory approach was necessary to disentangle the effects of contemporary ponding from that of historical drainage class in surface soils where C availability and, therefore, microbial activity contributing to GHG fluxes tends to be highest (e.g. Blume et al. 2002; Yang and Silver 2016). Our results suggest that historical soil drainage may affect the response of heterotrophic soil respiration to ponding in the field.

Heterotrophic respiration rates in both the PD and WD classes were inhibited initially by flooding but increased as flooding continued. This phenomenon was recently reported in association with Fe reduction releasing labile C from organo-mineral complexes in mineral soils collected from across a topographic gradient (Huang and Hall 2017). The recovery of heterotrophic respiration rates was more rapid in our study, with CO₂ emissions increasing within 4 days of flooding (Figs. 4b, 5d), compared to weeks in the other study. This suggests that flooding could stimulate heterotrophic respiration in Fe-rich mineral soils on time scales relevant to the short duration of ponding that occurs in the field. Furthermore, differences in potential Fe reduction rates between drainage classes may underlay the higher heterotrophic respiration rates observed in the PD class under both flooded and drained treatments. Redox fluctuations can decrease the crystallinity of Fe(III) oxides (Thompson et al. 2011) such that ponding and drainage cycles in depressions can form more reactive Fe(III) pools that can be more rapidly reduced by microbes. Faster redox fluctuations can also lead to the formation of larger

reactive Fe(III) pools that support higher Fe reduction rates (Ginn et al. 2017). While we did not measure rates of Fe reduction, the PD drainage class consistently had a larger pool of reduced Fe(II) compared to the WD class in the field (Fig. 2f). Higher heterotrophic respiration rates in the PD soils under flooding and subsequent drainage could, therefore, reflect the release of labile C from organo-mineral complexes caused directly by Fe reduction (Huang and Hall 2017; Pan et al. 2016) or indirectly by pH changes driven by Fe reduction (Grybos et al. 2009). Our findings contribute to growing evidence that the commonly accepted moisture-respiration relationship, which suggests that C mineralization is inhibited under anaerobic conditions (Linn and Doran 1984), does not hold in periodically flooded mineral soils.

Despite higher heterotrophic respiration rates in the PD class than the WD class, TOC was higher in the PD surface soils (Table 1). This would suggest that PD soils have higher organic C inputs compared to WD soils. However, lower crop productivity in the PD class compared to the WD class should lead to lower TOC inputs from root exudates or from crop residues (Grable and Siemer 1968; Kanwar et al. 1988). Therefore, transport of dissolved or particulate C into PD depressed areas, through hydrological flow or erosion (Nitzsche et al. 2017), must be an important source of TOC. Even if this redistribution of C from the WD class to the PD class contributed to the larger TOC pools in the PD class in comparison to the WD class, higher heterotrophic respiration rates in the PD class are unlikely to deplete the labile TOC pool over long time scales but rather these higher rates can be sustained by these C inputs.

Here, we documented how historical soil drainage mediates the response of GHG fluxes from mesic agricultural soils to contemporary conditions. Soils that have not historically ponded exhibited higher N₂O emissions and lower CO₂ emissions when inundated than soils with a long history of episodic ponding. This suggests that we cannot simply extrapolate our understanding of GHG dynamics in PD areas to areas that will experience increased ponding with climate change driven rainfall intensification. We proposed possible mechanisms related to drainage class differences in soil properties that could underlay this soil drainage legacy effect. Microbial community composition also differs by soil drainage history (Suriyavirun et al. 2019) but the functional importance of this

relative to the role of soil properties differences in driving the legacy effect on GHG fluxes is yet to be determined. Determining these mechanisms could not only elucidate the time scales over which this soil drainage legacy effect develops but would also aid in incorporating historical soil drainage into field and regional scale models to better predict how soil GHG emissions will respond to rainfall intensification and feedback on climate change.

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Compliance with ethical standards

Conflict of interest None.

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