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Effects of land use on greenhouse gas fluxes and soil properties of wetland catchments in the Prairie Pothole Region of North America

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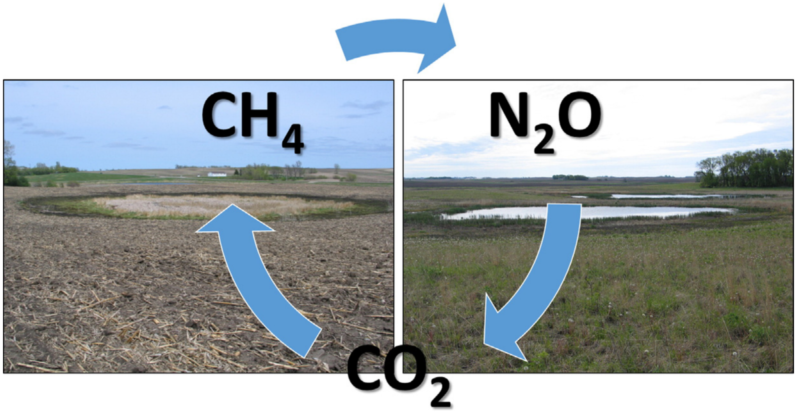
HIGHLIGHTS

- Soil carbon sequestration can be enhanced through wetland restoration.
- Methane emissions may offset wetland soil carbon sequestration.
- Greenhouse gas fluxes and soil properties were assessed from wetland catchments.
- All variables were affected by land use, but relations were variable.
- Restoration type must be considered when assessing wetland greenhouse gas fluxes.

GRAPHICAL ABSTRACT



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ABSTRACT

Wetland restoration has been suggested as policy goal with multiple environmental benefits including enhancement of atmospheric carbon sequestration. However, there are concerns that increased methane (CH_4) emissions associated with restoration may outweigh potential benefits. A comprehensive, 4-year study of 119 wetland catchments was conducted in the Prairie Pothole Region of the north-central U.S. to assess the effects of land use on greenhouse gas (GHG) fluxes and soil properties.

Results showed that the effects of land use on GHG fluxes and abiotic soil properties differed with respect to catchment zone (upland, wetland), wetland classification, geographic location, and year. Mean CH_4 fluxes from the uplands were predictably low (<0.02 g CH_4 m^{-2} day^{-1}), while wetland zone CH_4 fluxes were much greater (<0.001–3.9 g CH_4 m^{-2} day^{-1}). Mean cumulative seasonal CH_4 fluxes ranged from roughly 0–650 g CH_4 m^{-2}, with an overall mean of approximately 160 g CH_4 m^{-2}. These maximum cumulative CH_4 fluxes were nearly 3 times as high as previously reported in North America. The overall magnitude and variability of N_2O fluxes from this study (<0.0001–0.0023 g N_2O m^{-2} day^{-1}) were comparable to previously reported values.

Results suggest that soil organic carbon is lost when relatively undisturbed catchments are converted for agriculture, and that when non-drained cropland catchments are restored, CH_4 fluxes generally are not different than the pre-restoration baseline. Conversely, when drained cropland catchments are restored, CH_4 fluxes are noticeably higher. Consequently, it is important to consider the type of wetland restoration (drained, non-drained) when assessing restoration benefits. Results also suggest that elevated N_2O fluxes from cropland catchments

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likely would be reduced through restoration. The overall variability demonstrated by this study was consistent with findings of other wetland investigations and underscores the difficulty in quantifying the GHG balance of wetland systems.

1. Introduction

Investigations into global climate patterns and carbon cycles historically have recognized three overarching carbon pools consisting of marine and terrestrial environments, and the atmosphere (Tans et al., 1990; Sundquist, 1993; Canadell et al., 2007; Denman et al., 2007). Research associated with quantifying and modeling carbon pools (Tans et al., 1990; Fan et al., 1998; Pacala et al., 2001) has resulted in more refined efforts to segregate the terrestrial portion into major constituents such as soils, forests, agricultural lands, and inland aquatic ecosystems (Ciais et al., 1995; Houghton et al., 1999; Pacala et al., 2001; Bridgham et al., 2006, 2013; Euliss et al., 2006; CCSP, 2007; Sundquist et al., 2009; Zhu et al., 2010, 2011; Zhu and Reed, 2012; Byrd et al., 2013). As data have become available and coarse-scale models refined, a variety of studies have recognized the contribution of inland aquatic ecosystems (e.g., wetlands, peatlands, reservoirs) to the terrestrial carbon budget (Armentano and Menges, 1986; Gorham, 1991; Algesten et al., 2003; Bridgham et al., 2006, 2013; Cole et al., 2007; Downing et al., 2008; Battin et al., 2009). Despite this, soil organic carbon (OC) and greenhouse gas (GHG) flux data characterizing wetland ecosystems are relatively sparse, often region- or classification-specific, and associated with a high degree of uncertainty (Bridgham et al., 2006, 2013; Euliss et al., 2006; CCSP, 2007; Phillips and Beeri, 2008; Gleason et al., 2009; Badiou et al., 2011; Pennock et al., 2010; Finocchiaro et al., 2014).

The Prairie Pothole Region (PPR) of North America (Fig. 1) covers approximately 821,859 km^2 and includes portions of five U.S. states and three Canadian provinces (Gleason et al., 2008). The PPR is characterized by relatively small (often <5 ha), highly productive, mineral-soil wetlands dispersed throughout an agriculture-dominated landscape, and prairie pothole wetlands have potential to be important ecosystems in terms of the North American carbon balance (Bridgham et al., 2006; Euliss et al., 2006; Badiou et al., 2011). Studies from North America, including the PPR, have shown that minimally disturbed wetland catchments in native grasslands have relatively high soil OC levels, and soils of wetland catchments in an agricultural setting are capable of sequestering OC when restored to a similar natural state (Follett et al., 2001; Desjardins et al., 2005; Euliss et al., 2006; Gleason et al., 2008, 2011; Badiou et al., 2011). Consequently, natural resource organizations have promoted the benefits of conservation and restoration programs for moderating atmospheric GHG levels, as well as for providing numerous other ecosystem services (Gebhart et al., 1994; Litynski et al., 2006; Gleason et al., 2008; PCOR, 2008; Hansen, 2009; Brinson and Eckles, 2011; Gleason et al., 2011). However, abiotic conditions that promote OC sequestration in soils also can be conducive for the production of methane (CH_4), a potent GHG that may offset the benefits of increased

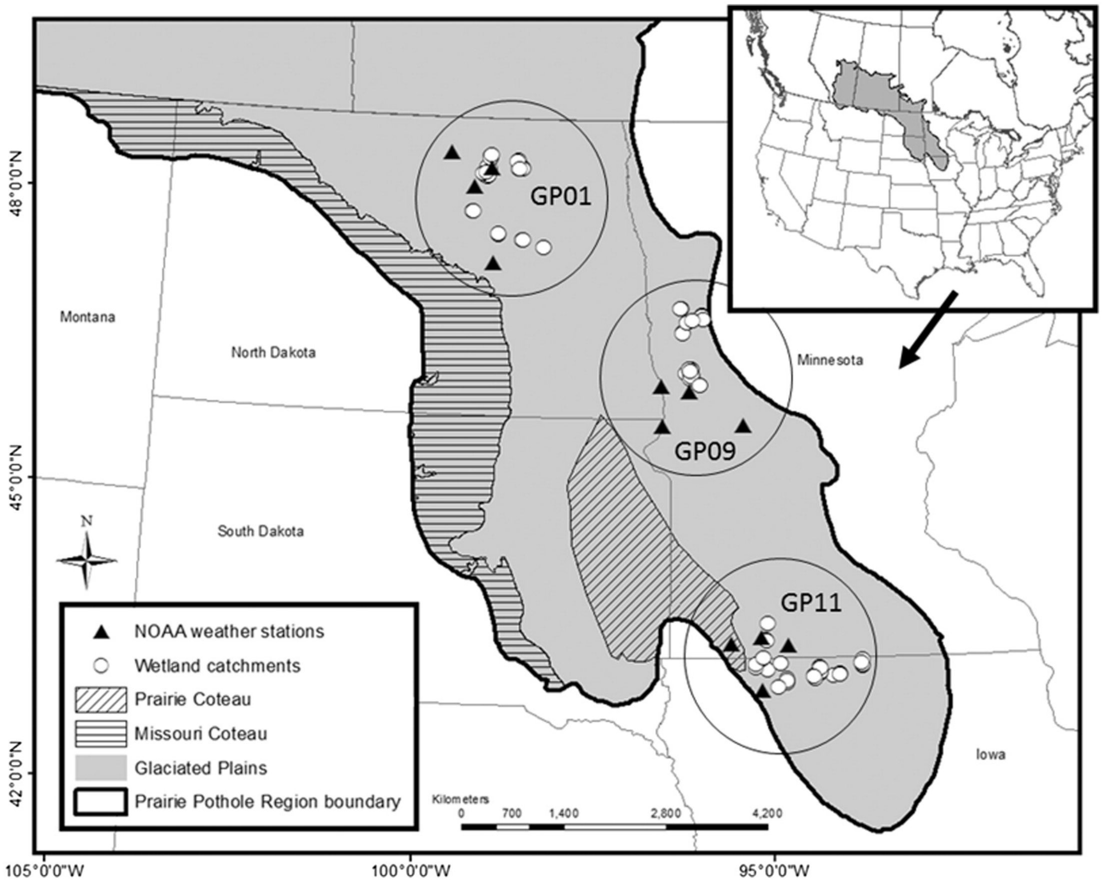

Fig. 1. Location of wetland catchments and National Oceanic and Atmospheric Administration (NOAA) weather stations within the three study points (GP01, GP09, GP11) in the glaciated plains area of the Prairie Pothole Region.

OC sequestration (Whiting and Chanton, 2001; van den Bos, 2003; Bridgham et al., 2006; Mitsch et al., 2013). Similarly, wetland catchments, especially those in croplands, have the potential to emit nitrous oxide (N_2O), a powerful GHG which can be produced at high levels following application of nitrogen-based fertilizers (Bremner and Blackmer, 1978; Eichner, 1990; Merbach et al., 2002; Venterea et al., 2005; Liu and Greaver, 2009).

Production and flux of GHGs in wetland catchments, as well as OC sequestration in soils, generally are controlled by highly variable abiotic factors such as soil moisture and temperature, water depth, hydroperiod (period of inundation), water chemistry, and redox conditions (Priemé, 1994; Segers, 1998; Le Mer and Roger, 2001; Smith et al., 2003; Whalen, 2005; Bedard-Haughn et al., 2006; Kayranli et al., 2010; Pennock et al., 2010). The makeup of soil microbial and vegetation communities, as well as availability of organic substrates, also can be important factors (Priemé, 1994; Le Mer and Roger, 2001; Smith et al., 2003; Whalen, 2005; Bedard-Haughn et al., 2006; Hernandez and Mitsch, 2006; Laanbroek, 2010). These abiotic and biotic factors are linked to weather and climate, groundwater interactions (e.g., recharge, discharge), and geomorphology, and can vary by landscape positions which span the wetland to upland transitional gradient. Land use also can have considerable effects on these factors (Euliss and Mushet, 1996; Gleason and Euliss, 1998; van der kamp et al., 2003; Gleason et al., 2009; Liu and Greaver, 2009; Kumar et al., 2014; Serrano-Silva et al., 2014).

Prairie pothole wetlands are interspersed among all of the major land uses of the region, characterized by hydroperiods lasting from a few weeks to an entire season, and typified by seasonally variable soil moisture levels and temperatures. Hence, major factors that affect the processes responsible for regulating soil OC levels and GHG fluxes (redox conditions, methanogenesis, methanotrophy, denitrification) are highly variable, and more often than not, interconnected. For example, water depths and hydroperiods of PPR wetlands are highly dependent on runoff from spring snowmelt and summertime precipitation and evapotranspiration. Further, surface runoff, sedimentation, catchment vegetation composition, and soil chemistry and physical properties (e.g., bulk density) can be greatly influenced by land use (Martin and Hartman, 1987; Euliss and Mushet, 1996; Gleason and Euliss, 1998; van der Kamp et al., 2003; Gleason et al., 2009). Moreover, land-use practices can have opposing effects on the production or consumption of GHGs such as CH_4 and N_2O. For instance, a wetland catchment that is drained and cropped likely would have very little CH_4 production because of prevailing aerobic conditions that do not favor methanogenesis; however, this same catchment would have a greater likelihood of emitting N_2O because of agricultural nitrogen amendments.

The PPR is characterized by a northwest to southeast climate and land-use gradient with precipitation, temperature, and agricultural intensity increasing as you move south and east. Overall, wetland catchments in agricultural lands of the Dakotas and Montana are not drained or drained with moderately-effective surface ditches, and they often are tilled during dry years. Conversely, agricultural catchments in southern Minnesota and Iowa mostly are drained by subsurface and surface drainage systems that allow the lands to be tilled in most years. Thus, it is conceivable that the net carbon balance of PPR wetland catchments could vary along this gradient, and a comprehensive regional study is required to evaluate land-use impacts and assess the GHG mitigation potential of wetland restoration.

Objectives of this study were to 1) provide comprehensive data on GHG fluxes and related soil abiotic parameters for PPR wetland catchments and 2) assess the effects on GHG fluxes and soil parameters of the dominant land-use types of the region, with the purpose of evaluating the overall efficacy of wetland and grassland restoration for sequestering atmospheric carbon. To accomplish these objectives temporally-intensive data collection was performed across a large geographic area and a reference-based approach was applied to compare fluxes from restored grassland catchments to native prairie and cropland reference conditions.

2. Material and methods

2.1. Study sites

Study sites consisted of 59 seasonal (palustrine emergent, seasonally flooded/saturated) and 60 semipermanent (palustrine emergent, semipermanently flooded) wetland catchments (classifications of Stewart and Kantrud, 1971; Cowardin et al., 1979) located throughout the glaciated plains physiographic region in the U.S. part of the PPR (Fig. 1). Seasonal wetlands typically are smaller and shallower than semipermanent wetlands, function as groundwater recharge sites, are characterized by relatively low total dissolved solids (TDS) concentrations (<1000 mg L^{-1}), and often dry completely because of the negative precipitation:evaporation ratio of the region. The comparatively larger semipermanent wetlands often receive groundwater, hence they dry less often than seasonal wetlands and can have much higher concentrations of water-quality constituents such as TDS and sulfate. The water-balance of PPR wetlands is dominated by precipitation and associated runoff; thus, surface-water characteristics of individual wetlands are highly variable temporally (Euliss et al., 2004, 2014). For example, reported sulfate concentrations for PPR wetlands and shallow lakes range from <1 to 87,500 mg L^{-1} depending of factors such as groundwater interaction and seasonal water levels (e.g., Swanson et al., 1988; Tangen et al., 2013; Euliss et al., 2014; Post van der Burg and Tangen, 2015).

For this study, a wetland catchment is defined as the wetland basin and its direct contributing area (Gleason et al., 2008, 2009; Finocchiaro et al., 2014), and data are presented at the subcatchment level consisting of the wetland and upland zones. The fixed wetland-upland transition elevation was delineated based on a combination of spring-time water levels, soils, vegetation, and topography; therefore, the proportion of the wetland zone that was actually inundated varied seasonally and annually. Catchments were selected among three study points that span a large portion of the PPR's climate and land-use gradient. The northernmost group of 41 catchments (GP01) was located near Devils Lake, ND, another group of 40 catchments (GP09) was located near Fergus Falls, MN, and the southernmost group of 38 catchments (GP11) was located near Estherville, IA (Fig. 1; Table 1). Mean (±standard deviation) surface areas for the wetland and upland zones of the catchments were 1.04 (±0.76) and 2.68 (±1.62) ha, respectively (Table 1).

Wetland catchments were selected to span a disturbance gradient characterized by the dominant land-use types of the region: native prairie grassland, restored grassland, and cropland (Gleason et al., 2008). Native prairie catchments are characterized by perennial vegetation and have no history of soil disturbance such as cultivation. Restored catchments were previously in crop production and have been restored by reestablishing perennial vegetation (grasses and forbs) in the uplands, typically through conservation programs (Gleason et al., 2011). Wetland vegetation is established from the existing seed bank or natural seed dispersal; it typically is not seeded during restoration. Wetland restoration also consisted of disrupting any drainage systems (ditches, perforated drainage pipe) associated with the previous cropping practices. Cropland catchments were in fields that were annually tilled for agriculture. Because of differences in disturbance intensity, cropland and restored grassland catchments were divided and categorized as drained or non-drained following Gleason et al. (2008). Cropland catchments with existing surface or subsurface drains were classified as drained cropland, while catchments with no artificial drainage were classified as non-drained cropland. Restored catchments that previously had an artificial drainage system were classified as hydrologically restored, while catchments that did not have a drainage system were classified as non-drained restored (Table 2).

Table 1
Years sampled, mean (standard deviation [sd]) surface areas, and distribution of 119 wetland catchments by study point, catchment classification, and land-use/disturbance category.

			Surface area, ha					Land-use/disturbance category					
Study point	Sample years	Catchment classification	Wetland zone[1]	(sd)	Upland zone	(sd)		Native prairie	Non-drained restored	Hydrologically restored	Non-drained cropland	Drained cropland	Total
GP01	2005–2008	Seasonal	0.21	(0.13)	1.24	(0.85)		4	4	4	4	4	20
		Semipermanent	1.62	(0.77)	4.19	(2.53)		4	4	5	4	4	21
GP09	2005–2006	Seasonal	0.41	(0.23)	1.22	(0.78)		4	4	4	4	4	20
		Semipermanent	1.69	(0.91)	2.93	(1.73)		4	4	4	4	4	20
GP11	2005–2006	Seasonal	0.45	(0.15)	1.52	(0.74)		4	–	11	–	4	19
		Semipermanent	1.88	(1.08)	4.96	(2.92)		4	–	11	–	4	19
		Mean:	1.04	(0.76)	2.68	(1.62)	Total:	24	16	39	16	24	119

[1] Wetland zone surface area represents the maximum extent based on the spill-point elevation. The inundated area of each wetland varies temporally.

The entire area (upland and wetland zones) of drained cropland catchments typically is tilled every year, while the wetland zone of non-drained cropland catchments can only be cropped during extremely dry years when soil conditions are conducive for tillage. The southern-most study point (GP11) included only native prairie, hydrologically restored, and drained cropland catchments because the majority of agricultural lands in southwest Minnesota and northwest Iowa are affected by subsurface drainage and a sufficient number of non-drained catchments could not be identified.

2.2. Gas sampling

Data were collected biweekly (every 2 weeks) between 9:00 and 16:00 h. There were 11 biweekly sample periods during 2005 (June 1–Oct. 31), 13 during 2006 (Apr. 5–Sept. 27), 12 during 2007 (Apr. 11–Sept. 14), and 11 during 2008 (Apr. 2–Aug. 22). Data were collected from all 119 catchments during 2005 and 2006, and from only the 41 catchments at GP01 during 2007 and 2008. A transect was established in each catchment extending from the wetland center to the catchment boundary and catchments were divided into a wetland zone and upland zone as previously described. Each transect included five sampling locations in the wetland zone and three locations in the upland zone. Wetland zone sampling locations were uniformly distributed between the wetland center and the upland transition while upland zone locations were located at the midpoint of the toe-slope, mid-slope, and shoulder-slope landscape positions following Finocchiaro et al. (2014). At each sample location polyvinyl chloride rings (20-cm diameter, 15-cm height) were inserted into the soil approximately 10 cm, and these rings served as bases for gas sampling, which was performed using the static (non-steady state) chamber approach (Coolman and Robarge, 1995; Livingston and Hutchinson, 1995). If water depths at each chamber base exceeded approximately 5 cm, chambers were attached to floats, allowing them to remain on the water surface. Opaque polyvinyl chloride gas-collection chambers (20 cm diameter, 20 cm height) were equipped with a vented gas-impermeable septum to facilitate syringe sampling.

To collect gas samples, chambers were placed onto the base, or attached to a float, for approximately 30 min, and a 50-ml sample of headspace gas was collected with a syringe after mixing through aspiration. Additionally, three ambient air samples were collected to approximate the time-zero (background) concentration of each gas. All samples were transferred to pre-evacuated 10-ml glass bottles fitted with a gas-impermeable septa and a crimp-top retainer. Gas samples were analyzed within 3 weeks of collection using a gas chromatograph. Field and laboratory methods are described in detail by Gleason et al. (2009) and Finocchiaro et al. (2014).

2.3. GHG fluxes

The change in concentration for each gas was determined by subtracting the ambient air concentration collected at the onset of sampling from the concentration withdrawn from the chamber after approximately 30 min. The mass of each element (based on change described above) was determined using the Ideal Gas Law, air temperature, chamber dimensions, and molecular mass. Flux rate was determined by dividing mass by the time the chamber was set. Flux for CH_4 and N_2O (g CH_4 or N_2O m^{-2} day^{-1}) was determined by extrapolating the calculated rate to a daily value. Fluxes for each catchment zone (wetland, upland) were determined by weighting each chamber flux value by the catchment surface area that it represents. The representative surface areas were based on collection-chamber elevations and determined using detailed topographic surveys following Gleason et al. (2009) and Finocchiaro et al. (2014). Similar adjustments were made to the abiotic soil variables (e.g., water-filled pore space) to facilitate comparisons with flux.

Cumulative seasonal fluxes for each land-use/disturbance category (Table 2) were calculated by multiplying the daily flux rates by the time that passed between measurements. The representative time was determined by calculating the number of days between each sample date and summing one-half of the days from the preceding and subsequent time periods. Thus, estimates from the first and last sample dates were multiplied by approximately 7 days while estimates from the remaining dates were multiplied by approximately 14 days. These calculations assume constant fluxes throughout a day and between sample dates and were not extrapolated beyond the range of sample dates to include the entire emission season, which can vary among the

Table 2
Characteristics of the land use/disturbance categories assigned to each wetland catchment. A sufficient number of non-drained catchments (restored and cropland) could not be identified for study point GP11 because of widespread drainage.

					Restoration method	
Land use	Study points	Land use/disturbance category	Agriculture history	Drainage history	Land cover	Drainage
Grassland/perennial vegetation	GP01, GP09, GP11	Native prairie	Never cropped	Never drained	–	–
	GP01, GP09	Non-drained restored	Formerly cropped	Never drained	Perennial vegetation in upland zone	–
	GP01, GP09, GP11	Hydrologically restored	Formerly cropped	Formerly drained	Perennial vegetation in upland zone	Surface and subsurface drains disrupted
Cropland	GP01, GP09	Non-drained cropland	Currently cropped	Never drained	–	–
	GP01, GP09, GP11	Drained cropland	Currently cropped	Currently drained	–	–

study points. The typical growing seasons for the study points range from 88–146, 126–156, and 136–174 days for GP01, GP09, and GP11, respectively (USDA, 2016).

Global warming potential (GWP) for each gas was calculated in carbon dioxide (CO_2) equivalents using 100-year time horizon values of 25 and 298 for CH_4 and N_2O, respectively (Forster et al., 2007). Total GWP was calculated for each catchment (upland and wetland zone combined) by summing values for CH_4 and N_2O and adjusting them by the total catchment surface area to obtain a per-unit-area estimate.

2.4. Abiotic variables and soils

During each biweekly sampling event, air temperature and water depth were measured near each gas-collection chamber. Soil moisture (%) and temperature also were measured in the upper 15 cm of the soil near each collection chamber using a time domain reflectometer (ThetaProbe ML2x, Dynamax Inc., Houston, TX) and a soil thermometer. Water temperature (instead of soil) was measured when water depth was greater than approximately 5 cm. Annual precipitation was obtained from National Oceanic and Atmospheric Administration, National Climatic Data Center. Local precipitation measurements were obtained from four weather stations distributed throughout each study point (12 stations total; Fig. 1).

Soil samples were collected once during the study (Sept.–Dec. of 2005–2006) near each collection chamber location from the approximate center of the 0–15 cm and 15–30 cm depth segments. Soils were assayed for determination of bulk density, OC, inorganic carbon (IC), total nitrogen (N), nitrate (NO_3), ammonium (NH_4), and phosphorus (P) using standard methods (Page et al., 1982; Klute, 1986). For the soil chemistry parameters, values for the 2 depths were summed to estimate concentrations for the upper 30 cm, while a mean of the two depth segments was calculated for bulk density. Particle density and soil porosity were calculated for each sample location using bulk density and organic matter estimates, along with a standard particle density for mineral matter of 2.65 g cm^{-3} and organic carbon/organic matter ratio of 0.58. Water-filled pore space (WFPS) was calculated as soil moisture (%) divided by soil porosity (%).

2.5. Analyses

Analysis of variance (ANOVA) was used to test for differences in CH_4 and N_2O fluxes, WFPS, soil temperature, soil bulk density, and soil chemistry parameters among land-use/disturbance categories. Statistical analyses of fluxes, WFPS, and temperature were conducted separately by catchment zone (upland, wetland), study point (GP01, GP09, GP11), and wetland classification (seasonal, semipermanent); independent variables included land-use/disturbance category, sample year, and the interaction between land-use/disturbance category and year. Analyses of soil bulk density and chemical parameters were similar except that year was not considered because soils only were collected once. All analyses were conducted using the PROC MIXED procedure of SAS (version 9.4; SAS Institute Inc., Cary, NC, USA). The level of statistical significance for all tests was 0.05. Linear regressions and qualitative analyses of boxplots also were used to assess general relations between GHG fluxes and soil WFPS and temperature, and soil OC and restoration age. Restoration age is defined as the number of years that a catchment has been restored, and was calculated by subtracting the year that a catchment was restored from the year that soil samples were collected.

3. Results

3.1. Study point conditions

Mean seasonal air temperature for GP11 was approximately 4 °C greater than GP01 and GP09 during 2005. Mean temperatures generally were similar among study points during 2006, and did not differ greatly between 2007 and 2008 for GP01 (Table 3). Mean annual precipitation, however, was greatest in the southern-most point (GP11) during 2005 and 2006. Further, there was a general downward trend in precipitation for all study points from 2005 to 2006 followed by a slight increase for GP01 through 2008 (Table 3).

Mean annual water depths measured at the center of the seasonal and semipermanent wetlands were greatest for GP09, compared to GP01 and GP11. Moreover, mean depths were similar among the wetland classes for GP09, while the semipermanent wetlands were approximately 2.5 times greater than the seasonal wetlands for GP01 and GP11 (Table 4). Yearly mean water depths showed a general decreasing trend throughout the study for GP01 and GP09; mean depths were similar among years for GP11. Mean percent of the wetland zone surface area that was inundated showed trends similar to those for water depths (Table 4). On average, a majority of seasonal wetlands dried during the sample season for GP01 and GP11, while approximately 50% of the GP09 seasonal wetlands dried during the season (Table 4). Approximately 50% of the semipermanent wetlands dried during the season for GP01 and GP11, while 25% of the GP09 semipermanent wetlands dried during the season. All study points had one or two wetlands that were dry for the entire sample season, but this varied by year. The dates that sites dried ranged from April–October and the average date of drying varied by study point and year (Table 4).

3.2. CH_4 flux

3.2.1. Upland zone

Upland zones of catchments generally were characterized by minimal CH_4 flux or uptake (negative flux), and CH_4 flux generally did not differ significantly among land-use/disturbance categories (simply land use hereafter). The lone exception was for semipermanent catchments of GP09, but this effect varied by year (Table 5). Conversely, the difference among years generally was significant for GP01 and GP09. Qualitative assessment of grouped means suggest that upland zone CH_4 fluxes varied among study points and catchment classifications, with the greatest fluxes from GP09, GP01, and GP11, respectively (Table 5).

Two predominant trends were evident when data from all catchments (i.e., all study points, wetland classifications) were combined and presented graphically by yearly sample period (Fig. 2a). First, upland zone CH_4 fluxes were elevated and variable during 2005 compared to fluxes from 2006–2008 (Fig. 2a). Second, the native prairie uplands generally were characterized by greater CH_4 uptake than the other land uses from 2006–2008 (Fig. 2a).

3.2.2. Wetland zone

Wetland zones of catchments were characterized by much greater CH_4 flux than the upland zones (Table 5). Methane flux generally did not differ significantly among land uses, with the exception of semipermanent catchments of GP11 where fluxes of drained cropland

Table 3
Seasonal air temperature and annual precipitation. Temperature is based on data from the biweekly sample events and precipitation is from the twelve National Oceanic and Atmospheric Administration weather stations distributed throughout the study area (Fig. 1). Variation between minimum and maximum values is due to a combination of spatial variability and data availability (i.e., number of days with missing data) among weather stations.

		Annual precipitation, cm			Air temperature, °C		
Point	Year	Mean	Minimum	Maximum	Mean	Minimum	Maximum
GP01	2005	36	16	58	19	4	30
	2006	28	22	39	21	7	30
	2007	29	8	51	20	6	31
	2008	38	9	59	19	8	29
GP09	2005	57	22	87	19	1	30
	2006	36	7	55	21	8	32
GP11	2005	76	60	94	23	9	30
	2006	66	51	75	22	7	33

catchments were lower than the native prairie and hydrologically restored catchments (Table 5). Difference among years was significant for GP01 and GP09. Qualitative assessment of grouped means suggest that wetland zone CH_4 fluxes from semipermanent catchments were greater than those from seasonal catchments, and that the greatest fluxes were observed from GP09, GP01, and GP11, respectively (Table 5).

When data from all catchments were combined it was evident that wetland zone CH_4 flux of drained cropland catchments was minimal and that the native prairie wetlands typically were among the greatest emitters of CH_4 (Fig. 3a). The restored and non-drained cropland catchments were variable and often intermediate for CH_4 flux between the native prairie and drained cropland catchments. Moreover, fluxes where characterized by high seasonal variability (Fig. 3a; Table 5). Methane primarily represents fluxes from the soil or water surface, although samples from the floating chambers located at the water surface could include bubbles from ebullition. Gases transported through arenchymous plant tissue were not specifically accounted for with this study and may represent additional CH_4 flux.

3.3. N_2O flux

3.3.1. Upland zone

Upland zones of drained and non-drained cropland catchments exhibited greater N_2O flux than the native prairie and restored catchments. This trend was highly significant for all study point and catchment classification combinations except for the seasonal catchments of GP11, and this land-use effect varied by year for the semipermanent catchments of GP01 (Table 6). Qualitative assessment of grouped means suggest that upland zone N_2O fluxes from seasonal catchments were greater than those from semipermanent catchments, and that the fluxes from GP11 were greater than from GP01 and GP09, which were similar (Table 6).

Two predominant trends were evident when data from all catchments (i.e., all study points, wetland classifications) were combined and presented graphically by yearly sample period (Fig. 2b). First, upland zone N_2O fluxes of the cropland catchments were consistently greater than the native prairie and restored catchments. Second, upland zones of cropland catchments were characterized by large, periodic N_2O flux events while fluxes from the native prairie and restored catchments were relatively constant over time (Fig. 2b).

3.3.2. Wetland zone

The effect of land use on wetland zone N_2O fluxes was significant for the semipermanent wetlands of GP01 and GP09, where fluxes from the drained cropland catchments were greater than the other land uses (Table 6). Sample year also was significant for the GP09 semipermanent wetlands (Table 6). Qualitative assessment of grouped means suggest that wetland zone N_2O fluxes from seasonal catchments were greater than those from semipermanent catchments, and that the greatest fluxes were observed from GP11, GP01, and GP09, respectively (Table 6). When data from all catchments were combined it was evident that wetland zone N_2O flux was seasonally and annually variable. Moreover, some of the largest emissions were associated with the drained and non-drained cropland catchments (Fig. 3b).

3.4. GWP

Table 7 presents the seasonal mean GWP (based on CH_4 and N_2O) for the entire wetland catchment (upland and wetland zones) by year and land use. Qualitative assessment of these means show that the native prairie catchments had the greatest mean GWP, followed by the non-drained restored, non-drained cropland, hydrologically restored, and drained cropland (Table 7). Based on the 2-year mean from 2005–2006, when all study points were sampled, CH_4 and N_2O accounted for approximately 95% (range 93–97%) and 5% (range 3–7%) of the overall GWP, respectively. Similarly, based on the 2-year mean from 2007–2008 (GP01 only), CH_4 and N_2O accounted for approximately 79% (range 74–83%) and 21% (range 17–26%) of the overall GWP, respectively.

3.5. Cumulative flux

3.5.1. CH_4

Cumulative seasonal CH_4 fluxes from both catchment zones, presented in Table 8, generally reflect the variability and relations (study

Table 4
Mean water depth at center of wetland, mean wetland surface area that was inundated, and characterization of the period of inundation. Dry refers to no ponded water present in the wetland.

					Number of wetlands			Date that wetland dried,[1] month/day/year	
Point	Class	Year	Mean depth, cm	Mean inundated[2] area, %	Inundated entire season	Dry entire season	Dried during season	Mean	Range
GP01	SEAS	2005	22	24	5	–	15	9/11/2005	7/14/2005–10/25/2005
		2006	18	20	1	1	18	7/6/2006	5/19/2006–9/7/2006
		2007	14	14	3	1	16	7/26/2007	6/8/2007–9/14/2007
		2008	8	8	2	1	16	6/9/2008	4/16/2008–8/21/2008
		Mean:	16	17	3	1	16		
	SEMI	2005	55	52	17	–	4	8/26/2005	7/29/2005–9/22/2005
		2006	45	42	7	–	14	8/7/2006	5/18/2006–9/26/2006
		2007	37	31	12	–	9	8/7/2007	5/11/2007–9/14/2007
		2008	24	23	6	1	13	7/22/2008	4/17/2008–8/21/2008
		Mean:	40	37	11	1	10		
GP09	SEAS	2005	60	49	15	–	5	9/4/2005	6/20/2005–10/20/2005
		2006	41	35	4	2	14	8/8/2006	7/17/2006–8/30/2006
		Mean:	50	42	10	2	10		
	SEMI	2005	65	58	16	1	3	7/7/2005	6/20/2005–7/16/2005
		2006	50	45	11	2	7	8/13/2006	5/22/2006–9/23/2006
		Mean:	58	51	14	1.5	5		
GP11	SEAS	2005	15	17	1	2	16	8/20/2005	6/26/2005–10/16/2005
		2006	17	23	–	2	17	6/30/2006	4/20/2006–8/25/2006
		Mean:	16	20	1	2	17		
	SEMI	2005	43	40	11	1	7	9/14/2005	7/8/2005–10/15/2005
		2006	40	39	6	2	11	7/29/2006	4/20/2006–9/21/2006
		Mean:	42	40	9	1.5	9		

[1] Dates based on wetlands that dried during season.
[2] Based on maximum wetland surface area defined by the spill-point elevation.

Table 5

Mean (standard error [se]) methane (CH_4) flux for all catchment zone, study point (point), catchment classification (class), and land use/disturbance category (land use) combinations. Analysis of variance (ANOVA) results are presented for effects of land use, sample year, and their interaction; significant ($P \leq 0.05$) values are bolded. For comparisons where there was a significant land-use effect, mean values with similar letters are not statistically different ($P > 0.05$). Data were collected during 2005–2006 for points GP09 and GP11 and during 2005–2008 for point GP01.

[NP, native prairie; NDR, non-drained restored; HR, hydrologically restored; NDC, non-drained cropland; DC, drained cropland; SEAS, seasonal; SEMI, semipermanent].

ANOVA results					Mean (se) CH_4 Flux, g CH_4 m^{-2} day^{-1}										
					Land use										
Point	Class	Land use	Year	Interaction	NP	(se)	NDR	(se)	HR	(se)	NDC	(se)	DC	(se)	Grouped land use means:
Upland zone															
GP01	SEAS	$F_{4,15} = 1.44$; $P = 0.27$	$F_{3,44} = 2.76$; $P =$ **0.05**	$F_{12,44} = 1.82$; $P = 0.07$	0.0108	(0.0123)	0.0012	(0.0016)	0.0006	(0.0009)	−0.0001	(0.0001)	−0.0003	(0.0001)	0.0024
	SEMI	$F_{4,16} = 0.79$; $P = 0.55$	$F_{3,47} = 4.72$; $P =$ **0.01**	$F_{12,47} = 0.88$; $P = 0.57$	0.0033	(0.0042)	0.0067	(0.0069)	0.0019	(0.0022)	0.0008	(0.0007)	−0.0001	(<0.0001)	0.0025
GP09	SEAS	$F_{4,15} = 0.62$; $P = 0.66$	$F_{1,15} = 8.82$; $P =$ **0.01**	$F_{4,15} = 0.61$; $P = 0.66$	0.0059	(0.0058)	0.0023	(0.0021)	0.0009	(0.0010)	0.0049	(0.0040)	0.0063	(0.0061)	0.0041
	SEMI	$F_{4,15} = 3.07$; $P =$ **0.05**	$F_{1,15} = 10.78$; $P =$ **0.01**	$F_{4,15} = 3.29$; $P =$ **0.04**	0.0053	(0.0048)	0.0022	(0.0024)	0.0022	(0.0025)	0.0168	(0.0162)	−0.0001	(<0.0001)	0.0053
GP11	SEAS	$F_{2,16} = 1.28$; $P = 0.31$	$F_{1,16} = 0.76$; $P = 0.4$	$F_{2,16} = 0.77$; $P = 0.48$	−0.0005	(0.0004)	–	–	0.0019	(0.0017)	–	–	<0.0001	(0.0002)	0.0004
	SEMI	$F_{2,16} = 1.33$; $P = 0.29$	$F_{1,16} = 3.95$; $P = 0.06$	$F_{2,16} = 1.23$; $P = 0.32$	0.0017	(0.0024)	–	–	0.0024	(0.0016)	–	–	<0.0001	(0.0002)	0.0014
				Grouped means:											
				SEAS:	0.0054		0.0017		0.0011		0.0024		0.0020		0.0025
				SEMI:	0.0034		0.0044		0.0022		0.0088		−0.0001		0.0038
				GP01:	0.0071		0.0039		0.0013		0.0003		−0.0002		0.0025
				GP09:	0.0056		0.0023		0.0015		0.0108		0.0031		0.0047
				GP11:	0.0006		–		0.0021		–		<0.0001		0.0009
Wetland zone															
GP01	SEAS	$F_{4,15} = 1.65$; $P = 0.21$	$F_{3,44} = 5.08$; $P =$ **0.004**	$F_{12,44} = 0.94$; $P = 0.52$	0.7219	(0.1625)	0.2244	(0.1724)	0.2606	(0.1307)	0.0256	(0.0116)	0.0010	(0.0008)	0.2467
	SEMI	$F_{4,16} = 1.28$; $P = 0.32$	$F_{3,47} = 8.53$; $P =$ **0.0001**	$F_{12,47} = 1.61$; $P = 0.12$	2.6360	(0.5948)	0.9305	(0.3803)	0.2643	(0.1165)	0.6751	(0.2215)	0.0180	(0.0109)	0.9048
GP09	SEAS	$F_{4,15} = 1.2$; $P = 0.35$	$F_{1,15} = 10.44$; $P =$ **0.01**	$F_{4,15} = 0.64$; $P = 0.64$	3.1297	(1.3077)	2.1650	(1.1598)	1.3639	(0.3249)	2.6735	(0.6702)	0.7552	(0.4520)	2.0175
	SEMI	$F_{4,15} = 2.1$; $P = 0.13$	$F_{1,15} = 7.36$; $P =$ **0.02**	$F_{4,15} = 0.9$; $P = 0.49$	3.9083	(0.9220)	2.3214	(0.2197)	3.1410	(0.6898)	3.6881	(1.0457)	0.0049	(0.0041)	2.6127
GP11	SEAS	$F_{2,16} = 2.15$; $P = 0.15$	$F_{1,16} = 0.69$; $P = 0.42$	$F_{2,16} = 0.45$; $P = 0.64$	0.2054	(0.0298)	–	–	0.4147	(0.1158)	–	–	0.0014	(0.0010)	0.2072
	SEMI	$F_{2,16} = 5.02$; $P =$ **0.02**	$F_{1,16} = 0.33$; $P = 0.57$	$F_{2,16} = 0.09$; $P = 0.92$	1.1273^{a}	(0.0750)	–	–	0.9385^{a}	(0.0916)	–	–	$<0.0001^{b}$	(0.0002)	0.6886
				Grouped means:											
				SEAS:	1.3523		1.1947		0.6797		1.3496		0.2526		0.9658
				SEMI:	2.5572		1.6260		1.4479		2.1816		0.0076		1.5641
				GP01:	1.6789		0.5775		0.2624		0.3504		0.0095		0.5757
				GP09:	3.5190		2.2432		2.2524		3.1808		0.3801		2.3151
				GP11:	0.6664		–		0.6766		–		0.0007		0.4479

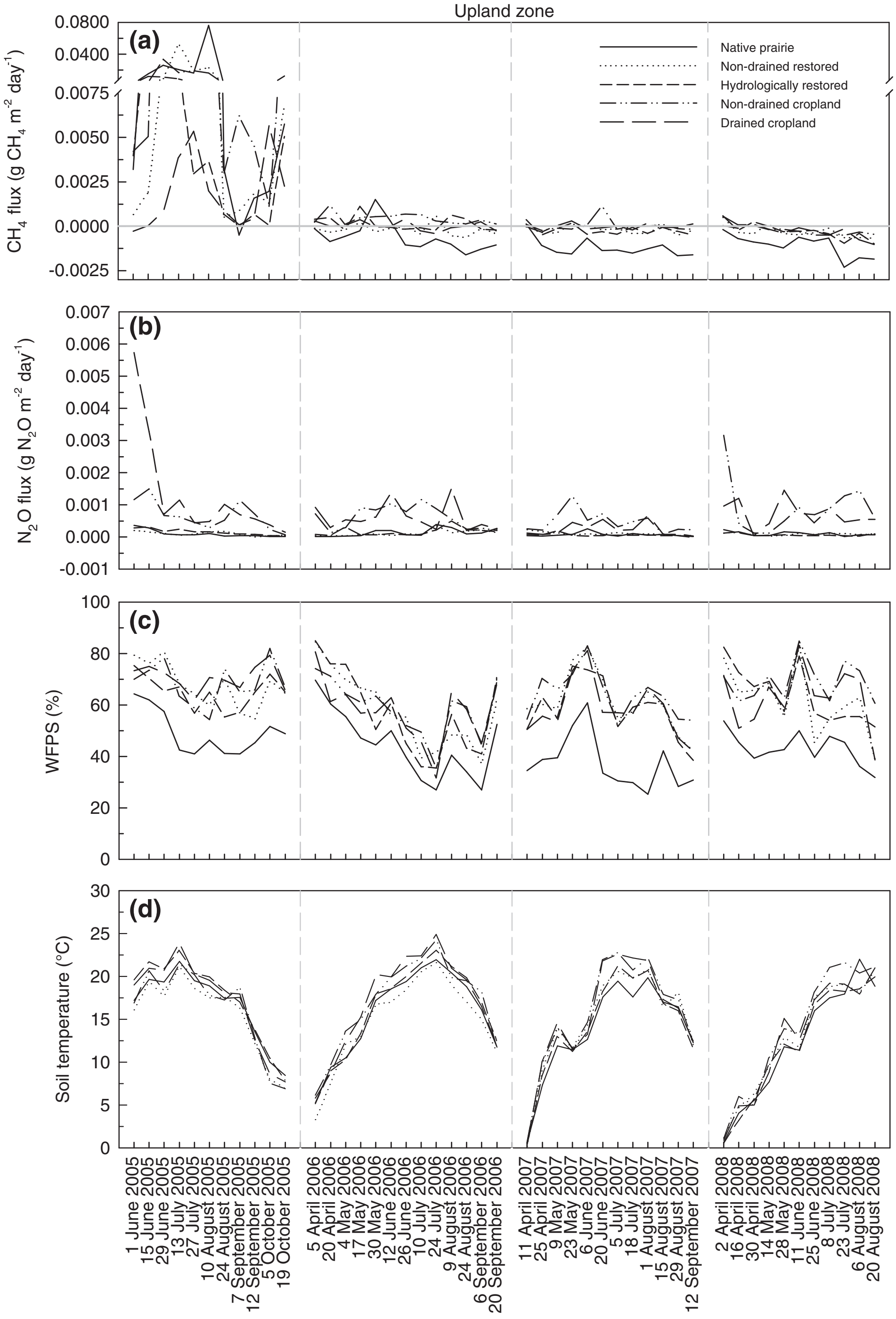

Fig. 2. Mean upland zone a) methane (CH_4) flux, b) nitrous oxide (N_2O) flux, c) soil water-filled pore space (WFPS), and d) soil temperature for each land-use/disturbance category by sample date. Data from 2005 and 2006 represent wetland catchments from all study points (GP01, GP09, GP11), while data from 2007 and 2008 represent only GP01.

point, class, land use) demonstrated by the overall mean fluxes (Table 5). Overall, cumulative upland zone CH_4 fluxes were negligible, while cumulative wetland zone fluxes were extremely high in some instances. The notable exception was the wetland zones of the drained cropland catchments, which were characterized by minimal cumulative CH_4 fluxes (Table 8).

3.5.2. N_2O

Similar to CH_4, cumulative seasonal N_2O fluxes from both catchment zones (Table 8) generally reflected the variability and relations demonstrated by the overall mean fluxes (Table 7). Cumulative N_2O fluxes from the wetland zones were slightly higher than for the upland zones; however, overall fluxes from both zones were low (Table 8).

3.6. Soil WFPS and temperature

The effects of land use on soil WFPS were significant for seven of the 12 comparisons, and all but two of the significant effects varied by year (Table 9). Differences among sample years were significant for 11 of the 12 comparisons (Table 9). When data from all catchments (i.e., all study points, wetland classifications) were combined and presented graphically by yearly sample period, it was evident that the native prairie catchments consistently exhibited the lowest WFPS for the upland

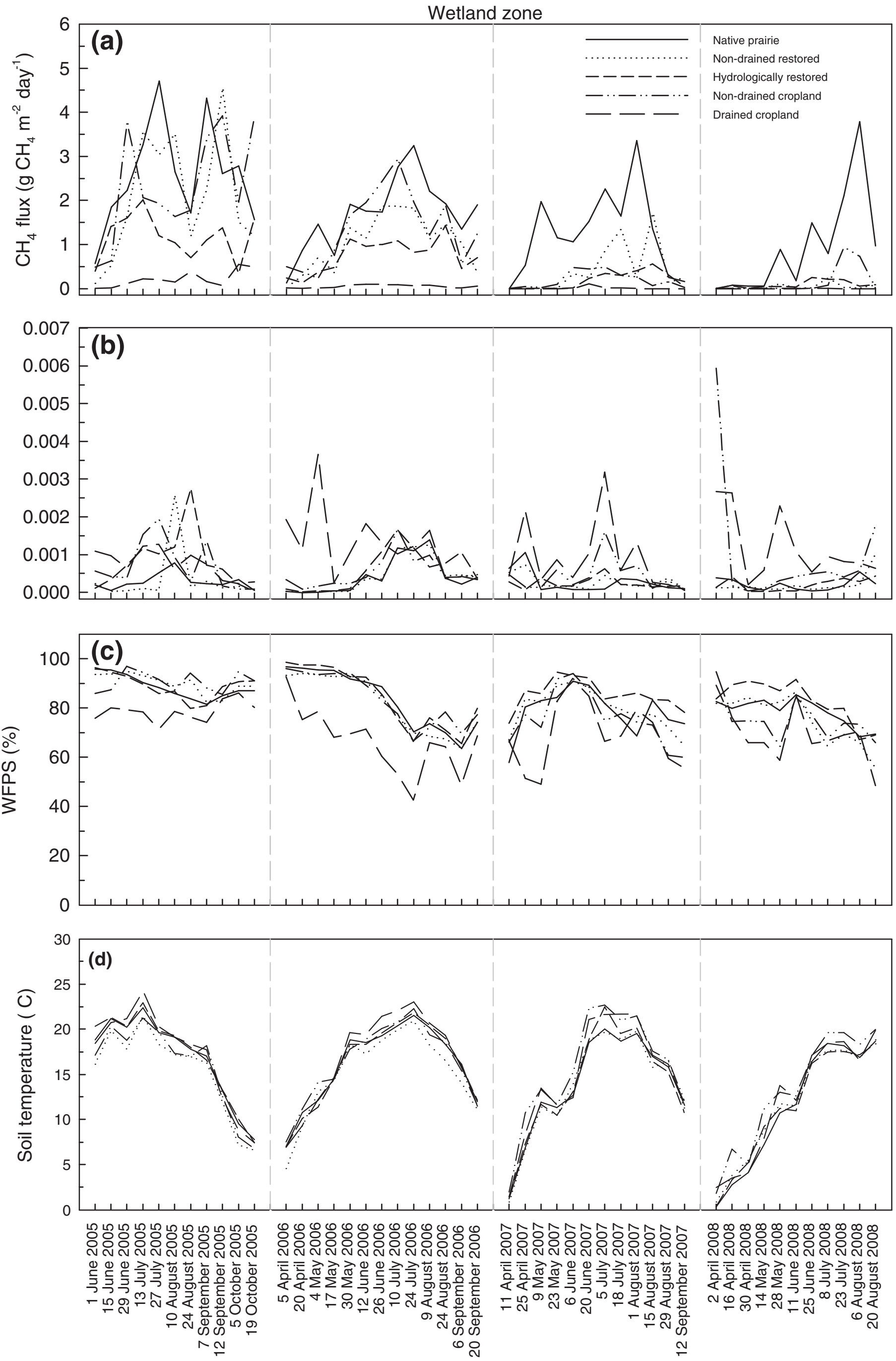

Fig. 3. Mean wetland zone a) methane (CH_4) flux, b) nitrous oxide (N_2O) flux, c) soil water-filled pore space (WFPS), and d) soil temperature for each land-use/disturbance category by sample date. Data from 2005 and 2006 represent wetland catchments from all study points (GP01, GP09, GP11), while data from 2007 and 2008 represent only GP01.

zones; the restored and cropland catchments generally were similar to each other (Fig. 2c). Mean upland zone WFPS for the native prairie catchments, based on these combined data, was 44%; the restored grassland and cropland catchments ranged from 61–65%. Conversely, mean WFPS in the wetland zone was lowest in the drained cropland catchments, while the native prairie, restored, and non-drained cropland catchments generally were similar (Fig. 3c). Mean wetland zone WFPS for the drained cropland catchments, based on the combined data, was 71%; the native prairie, restored grassland, and non-drained cropland catchments ranged from 81–85%. Mean upland and wetland zone WFPS values for the semipermanent catchments were 60.31 and 83.81%, respectively; respective mean upland and wetland zone values for the seasonal catchments were 57.47 and 76.67%.

The effects of land use and sample year on soil temperature were significant for two and eight of the 12 comparisons, respectively (Table 9). When data from all catchments (i.e., all study points, wetland classifications) were combined and presented graphically by yearly sample period, it was evident that the cropland sites often exhibited slightly greater soil temperatures for both catchment zones than the native prairie and restored sites, but this trend was variable (Figs. 2d, 3d; Table 8). Further, soil temperatures were temporally variable, with consistent seasonal trends showing the greatest temperatures during mid-summer. Mean upland zone soil temperatures for the non-drained and drained cropland catchments were 15.61 and 15.62 °C, respectively; respective overall values for the native prairie, non-drained restored, and hydrologically restored were 14.54, 14.45, and 15.04 °C. Mean wetland zone

Table 6

Mean (standard error [se]) nitrous oxide (N_2O) flux for all catchment zone, study point (point), catchment classification (class), and land use/disturbance category (land use) combinations. Analysis of variance (ANOVA) results are presented for effects of land use, sample year, and their interaction; significant ($P \leq 0.05$) values are bolded. For comparisons where there was a significant land-use effect, mean values with similar letters are not statistically different ($P > 0.05$). Data were collected during 2005–2006 for points GP09 and GP11 and during 2005–2008 for point GP01.

[NP, native prairie; NDR, non-drained restored; HR, hydrologically restored; NDC, non-drained cropland; DC, drained cropland; SEAS, seasonal; SEMI, semipermanent].

ANOVA results					Mean (se) N_2O Flux, g N_2O m^{-2} day^{-1}										
					Land use										
Point	Class	Land use	Year	Interaction	NP	(se)	NDR	(se)	HR	(se)	NDC	(se)	DC	(se)	Grouped land use means:
Upland zone															
GP01	SEAS	$F_{4,15} = 12.35$; P = **0.0001**	$F_{3,44} = 1.53$; P = 0.22	$F_{12,44} = 0.58$; P = 0.85	0.00009^{a}	(0.00001)	0.00012^{a}	(0.00002)	0.00011^{a}	(0.00003)	0.00055^{b}	(0.00009)	0.00049^{b}	(0.00009)	0.00027
	SEMI	$F_{4,16} = 12.53$; P = **0.0001**	$F_{3,47} = 6.96$; P = **0.001**	$F_{12,47} = 3.12$; P = **0.003**	0.00014	(0.00004)	0.00009	(0.00001)	0.00011	(0.00003)	0.00072	(0.00017)	0.00065	(0.00016)	0.00034
GP09	SEAS	$F_{4,15} = 9.64$; P = **0.0005**	$F_{1,15} = 1.03$; P = 0.33	$F_{4,15} = 1.14$; P = 0.38	0.00010^{a}	(0.00003)	0.00011^{a}	(0.00001)	0.00011^{a}	(0.00001)	0.00081^{b}	(0.00020)	0.00079^{b}	(0.00005)	0.00038
	SEMI	$F_{4,15} = 12.21$; P = **0.0001**	$F_{1,15} = 0.3$; P = 0.59	$F_{4,15} = 0.29$; P = 0.88	0.00009^{a}	(0.00001)	0.00010^{a}	(0.00005)	0.00005^{a}	(0.00001)	0.00058^{b}	(0.00001)	0.00046^{b}	(0.00003)	0.00026
GP11	SEAS	$F_{2,16} = 3.54$; P = 0.053	$F_{1,16} = 4.03$; P = 0.06	$F_{2,16} = 3.18$; P = 0.07	0.00013	(0.00004)	–	–	0.00019	(0.00005)	–	–	0.00232	(0.00150)	0.00088
	SEMI	$F_{2,16} = 13.79$; P = **0.0003**	$F_{1,16} = 0.72$; P = 0.41	$F_{2,16} = 3.28$; P = 0.06	0.00013^{a}	(0.00002)	–	–	0.00019^{a}	(0.00006)	–	–	0.00080^{b}	(0.00018)	0.00037
				Grouped means:											
				SEAS:	0.00011		0.00011		0.00014		0.00068		0.00120		0.00045
				SEMI:	0.00012		0.00010		0.00012		0.00065		0.00064		0.00032
				GP01:	0.00011		0.00010		0.00011		0.00064		0.00057		0.00031
				GP09:	0.00009		0.00010		0.00008		0.00069		0.00062		0.00032
				GP11:	0.00013		–		0.00019		–		0.00156		0.00063
Wetland zone															
GP01	SEAS	$F_{4,15} = 1.54$; P = 0.2415	$F_{3,44} = 0.82$; P = 0.49	$F_{12,44} = 0.75$; P = 0.7	0.00039	(0.00011)	0.00042	(0.00009)	0.00031	(0.00005)	0.00105	(0.00023)	0.00093	(0.00034)	0.00062
	SEMI	$F_{4,16} = 5.74$; P = **0.0046**	$F_{3,47} = 2.9$; P = **0.04**	$F_{12,47} = 0.88$; P = 0.57	0.00038^{a}	(0.00020)	0.00026^{a}	(0.00013)	0.00031^{a}	(0.00006)	0.00040^{a}	(0.00005)	0.00121^{b}	(0.00019)	0.00051
GP09	SEAS	$F_{4,15} = 1.7$; P = 0.202	$F_{1,15} = 0.05$; P = 0.82	$F_{4,15} = 0.93$; P = 0.47	0.00008	(0.00006)	0.00049	(0.00019)	0.00024	(0.00013)	0.00073	(0.00009)	0.00074	(0.00018)	0.00046
	SEMI	$F_{4,15} = 5.04$; P = **0.0089**	$F_{1,15} = 0.71$; P = 0.41	$F_{4,15} = 0.3$; P = 0.87	0.00004^{a}	(0.00005)	0.00013^{a}	(0.00008)	0.00017^{a}	(0.00001)	0.00029^{a}	(0.00002)	0.00090^{b}	(0.00018)	0.00030
GP11	SEAS	$F_{2,16} = 0.21$; P = 0.8091	$F_{1,16} = 0.002$; P = 0.96	$F_{2,16} = 0.15$; P = 0.86	0.00076	(<0.00001)	–	–	0.00100	(0.00010)	–	–	0.00101	(0.00007)	0.00092
	SEMI	$F_{2,16} = 1.52$; P = 0.2493	$F_{1,16} = 0.45$; P = 0.51	$F_{2,16} = 1.13$; P = 0.35	0.00019	(0.00005)	–	–	0.00108	(0.00041)	–	–	0.00123	(0.00004)	0.00083
				Grouped means:											
				SEAS:	0.00041		0.00045		0.00051		0.00089		0.00089		0.00063
				SEMI:	0.00020		0.00019		0.00052		0.00034		0.00111		0.00047
				GP01:	0.00039		0.00034		0.00031		0.00073		0.00107		0.00057
				GP09:	0.00006		0.00031		0.00020		0.00051		0.00082		0.00038
				GP11:	0.00047		–		0.00104		–		0.00112		0.00088

Table 7
Mean (standard deviation [sd]) global warming potential (GWP), in carbon dioxide equivalents, based on seasonal fluxes of methane and nitrous oxide from all wetland catchments (upland and wetland zones combined). Data were collected during 2005–2006 for points GP09 and GP11 and during 2005–2008 for point GP01.

	GWP, g CO_2 m^{-2} day^{-1}									
Year	Native prairie	(sd)	Non-drained restored	(sd)	Hydrologically restored	(sd)	Non-drained cropland	(sd)	Drained cropland	(sd)
2005	24	(26)	22	(21)	12	(22)	20	(18)	2	(10)
2006	16	(21)	12	(15)	8	(15)	12	(11)	1	(2)
2007	9	(20)	5	(8)	1	(1)	2	(4)	<1	(<1)
2008	7	(15)	1	(1)	1	(1)	2	(5)	<1	(<1)
Mean:	14		10		5		9		1	

soil temperatures for the non-drained and drained cropland catchments were 15.28 and 15.20 °C, respectively; respective overall values for the native prairie, non-drained restored, and hydrologically restored were 14.56, 14.00, and 14.70 °C. Mean temperatures did not vary greatly among wetland classifications for either catchment zone, with values ranging from 14.39–15.13 °C.

Table 8
Mean cumulative methane (CH_4) and nitrous oxide (N_2O) fluxes, and the duration of each sample season (days), for all catchment zone, study point (point), catchment classification (class), year, and land use/disturbance category (land use) combinations. Cumulative fluxes represent only the period of time between the first and last sample periods. Data were collected during 2005–2006 for points GP09 and GP11 and during 2005–2008 for point GP01.
[NP, native prairie; NDR, non-drained restored; HR, hydrologically restored; NDC, non-drained cropland; DC, drained cropland; SEAS, seasonal; SEMI, semipermanent].

				Cumulative CH_4 flux, g CH_4 m^{-2}						Cumulative N_2O flux, g N_2O m^{-2}					
				Land use						Land use					
Point	Class	Year	Days	NP	NDR	HR	NDC	DC	Grouped land use means:	NP	NDR	HR	NDC	DC	Grouped land use means:
Upland zone															
GP01	SEAS	2005	144	7.34	0.88	0.47	−0.03	−0.07	1.72	0.01	0.02	0.02	0.06	0.09	0.04
		2006	168	−0.29	−0.08	−0.05	0.01	−0.04	−0.09	0.02	0.02	0.03	0.13	0.09	0.06
		2007	154	−0.22	−0.04	−0.05	0.00	−0.01	−0.06	0.01	0.02	0.01	0.08	0.04	0.03
		2008	140	−0.20	−0.06	−0.04	−0.06	−0.05	−0.08	0.01	0.01	0.01	0.08	0.06	0.03
	SEMI	2005	144	2.42	4.10	1.56	0.43	−0.01	1.70	0.02	0.01	0.03	0.09	0.12	0.05
		2006	168	−0.19	−0.06	−0.08	0.02	−0.03	−0.07	0.04	0.02	0.02	0.09	0.08	0.05
		2007	154	−0.17	−0.03	−0.03	0.01	0.00	−0.04	0.01	0.01	0.01	0.08	0.04	0.03
		2008	140	−0.11	−0.04	−0.04	−0.02	−0.02	−0.05	0.02	0.01	0.01	0.15	0.14	0.06
GP09	SEAS	2005	136	1.67	0.68	0.20	1.26	1.77	1.12	0.01	0.02	0.01	0.14	0.12	0.06
		2006	171	0.02	0.03	−0.02	0.15	0.03	0.04	0.02	0.02	0.02	0.11	0.14	0.06
	SEMI	2005	136	1.45	0.75	0.69	4.70	−0.04	1.51	0.01	0.01	0.01	0.07	0.07	0.03
		2006	171	0.09	−0.02	−0.04	0.12	−0.02	0.03	0.02	0.03	0.01	0.10	0.08	0.05
GP11	SEAS	2005	142	−0.02	–	0.48	–	−0.03	0.14	0.02	–	0.03	–	0.46	0.17
		2006	166	−0.15	–	0.03	–	0.03	−0.03	0.02	–	0.02	–	0.14	0.06
	SEMI	2005	142	0.62	–	0.57	–	−0.03	0.39	0.01	–	0.02	–	0.13	0.05
		2006	166	−0.11	–	0.14	–	0.05	0.03	0.03	–	0.04	–	0.11	0.06
			Grouped means:												
			SEAS:	1.02	0.23	0.13	0.22	0.20	0.36	0.02	0.02	0.02	0.10	0.14	0.06
			SEMI:	0.50	0.79	0.35	0.88	−0.01	0.50	0.02	0.02	0.02	0.10	0.09	0.05
			GP01:	1.07	0.58	0.22	0.05	−0.03	0.38	0.02	0.02	0.02	0.09	0.08	0.05
			GP09:	0.81	0.36	0.21	1.56	0.44	0.67	0.01	0.02	0.01	0.11	0.10	0.05
			GP11:	0.08	–	0.31	–	0.00	0.13	0.02	–	0.03	–	0.21	0.09
Wetland zone															
GP01	SEAS	2005	144	183	114	102	3	0.2	80.40	0.10	0.07	0.05	0.21	0.06	0.10
		2006	168	90	14	13	9	−0.02	25.22	0.07	0.12	0.08	0.14	0.32	0.14
		2007	154	113	13	45	5	0.5	35.30	0.03	0.06	0.05	0.08	0.09	0.06
		2008	140	72	0.01	10	0.03	−0.02	16.48	0.03	0.03	0.02	0.14	0.11	0.07
	SEMI	2005	144	568	284	107	191	7.6	231.39	0.01	0.00	0.06	0.04	0.11	0.04
		2006	168	614	157	41	127	0.7	187.98	0.17	0.12	0.07	0.08	0.16	0.12
		2007	154	312	126	19	60	3.2	104.28	0.05	0.02	0.03	0.06	0.21	0.07
		2008	140	205	13	16	49	0.1	56.71	0.03	0.02	0.03	0.05	0.21	0.07
GP09	SEAS	2005	136	631	482	219	450	160	388.52	0.00	0.13	0.02	0.12	0.08	0.07
		2006	171	318	184	186	364	52	221.11	0.02	0.05	0.07	0.11	0.17	0.08
	SEMI	2005	136	659	357	498	626	1	428.28	0.00	0.01	0.03	0.05	0.10	0.04
		2006	171	509	373	417	451	0.1	350.01	0.01	0.04	0.03	0.04	0.20	0.06
GP11	SEAS	2005	142	34	–	73	–	0.4	35.88	0.11	–	0.15	–	0.13	0.13
		2006	166	31	–	54	–	0.1	28.45	0.13	–	0.16	–	0.19	0.16
	SEMI	2005	142	180	–	149	–	−0.03	109.89	0.02	–	0.22	–	0.16	0.13
		2006	166	189	–	151	–	0.04	113.29	0.04	–	0.12	–	0.22	0.13
			Grouped means:												
			SEAS:	184.13	134.66	87.77	138.53	26.73	114.36	0.06	0.08	0.07	0.13	0.14	0.10
			SEMI:	404.53	218.19	174.87	250.90	1.64	210.03	0.04	0.03	0.07	0.05	0.17	0.07
			GP01:	269.71	90.13	44.19	55.53	1.54	92.22	0.06	0.05	0.05	0.10	0.16	0.08
			GP09:	529.26	349.03	330.00	473.08	53.54	346.98	0.01	0.06	0.03	0.08	0.14	0.06
			GP11:	108.62		106.90		0.12	71.88	0.08		0.16		0.18	0.14

Table 9
Results of analyses of variance (ANOVA) testing for effects of land use/disturbance category (land use), sample year, and their interaction on soil water-filled pore space and temperature. ANOVA results values are presented by catchment zone, study point, and catchment classification; significant ($P < 0.05$) values are bolded.
[SEAS, seasonal; SEMI, semipermanent].

ANOVA results							
		Water-filled pore space			Temperature		
Point	Class	Land use	Year	Interaction	Land use	Year	Interaction
Upland zone							
GP01	SEAS	$F_{4,15} = 8.04$; $P =$ **0.001**	$F_{3,44} = 28.08$; $P <$ **0.0001**	$F_{12,44} = 0.72$; $P = 0.73$	$F_{4,15} = 2.04$; $P = 0.14$	$F_{3,44} = 6.02$; $P =$ **0.002**	$F_{12,44} = 0.5$; $P = 0.9$
	SEMI	$F_{4,16} = 3.71$; $P =$ **0.03**	$F_{3,47} = 17.79$; $P <$ **0.0001**	$F_{12,47} = 2.49$; $P =$ **0.01**	$F_{4,16} = 2.83$; $P = 0.06$	$F_{3,47} = 7.15$; $P =$ **0.0005**	$F_{12,47} = 0.39$; $P = 0.96$
GP09	SEAS	$F_{4,15} = 1.57$; $P = 0.23$	$F_{1,15} = 52.77$; $P <$ **0.0001**	$F_{4,15} = 0.63$; $P = 0.65$	$F_{4,15} = 3.22$; $P =$ **0.04**	$F_{1,15} = 0.66$; $P = 0.43$	$F_{4,15} = 1.09$; $P = 0.4$
	SEMI	$F_{4,15} = 0.61$; $P = 0.66$	$F_{1,15} = 49.81$; $P <$ **0.0001**	$F_{4,15} = 4.08$; $P =$ **0.02**	$F_{4,15} = 1.4$; $P = 0.28$	$F_{1,15} = 2.93$; $P = 0.11$	$F_{4,15} = 0.05$; $P = 0.99$
GP11	SEAS	$F_{2,16} = 4.44$; $P =$ **0.03**	$F_{1,16} = 11.68$; $P =$ **0.004**	$F_{2,16} = 5.25$; $P =$ **0.02**	$F_{2,16} = 0.77$; $P = 0.48$	$F_{1,16} = 6.84$; $P =$ **0.02**	$F_{2,16} = 1.28$; $P = 0.3$
	SEMI	$F_{2,16} = 1.51$; $P = 0.25$	$F_{1,16} = 17.37$; $P =$ **0.0007**	$F_{2,16} = 1.37$; $P = 0.28$	$F_{2,16} = 0.53$; $P = 0.6$	$F_{1,16} = 9.22$; $P =$ **0.01**	$F_{2,16} = 1.3$; $P = 0.3$
Wetland zone							
GP01	SEAS	$F_{4,15} = 2.09$; $P = 0.13$	$F_{3,44} = 26.02$; $P <$ **0.0001**	$F_{12,44} = 0.93$; $P = 0.53$	$F_{4,15} = 4.99$; $P =$ **0.01**	$F_{3,44} = 13.02$; $P <$ **0.0001**	$F_{12,44} = 0.72$; $P = 0.73$
	SEMI	$F_{4,16} = 5.6$; $P =$ **0.01**	$F_{3,47} = 51.3$; $P <$ **0.0001**	$F_{12,47} = 1.24$; $P = 0.29$	$F_{4,16} = 0.48$; $P = 0.75$	$F_{3,47} = 16.27$; $P <$ **0.0001**	$F_{12,47} = 0.36$; $P = 0.97$
GP09	SEAS	$F_{4,15} = 1.39$; $P = 0.29$	$F_{1,15} = 18.25$; $P =$ **0.0007**	$F_{4,15} = 0.08$; $P = 0.99$	$F_{4,15} = 2.3$; $P = 0.11$	$F_{1,15} = 3.88$; $P = 0.07$	$F_{4,15} = 0.27$; $P = 0.89$
	SEMI	$F_{4,15} = 9.42$; $P =$ **0.001**	$F_{1,15} = 37.94$; $P <$ **0.0001**	$F_{4,15} = 4.63$; $P =$ **0.01**	$F_{4,15} = 1.15$; $P = 0.37$	$F_{1,15} = 2.24$; $P = 0.15$	$F_{4,15} = 0.15$; $P = 0.96$
GP11	SEAS	$F_{2,16} = 4.64$; $P =$ **0.03**	$F_{1,16} = 4.14$; $P = 0.06$	$F_{2,16} = 3.85$; $P =$ **0.04**	$F_{2,16} = 0.72$; $P = 0.5$	$F_{1,16} = 9.59$; $P =$ **0.01**	$F_{2,16} = 0.5$; $P = 0.61$
	SEMI	$F_{2,16} = 32.74$; $P <$ **0.0001**	$F_{1,16} = 9.96$; $P =$ **0.006**	$F_{2,16} = 3.36$; $P = 0.06$	$F_{2,16} = 0.54$; $P = 0.59$	$F_{1,16} = 8.53$; $P =$ **0.01**	$F_{2,16} = 1.4$; $P = 0.28$

3.7. Soil bulk density and chemistry

The effect of land use was significant for 100% ($P_s < 0.005$) and 50% ($P_s < 0.025$) of upland and wetland zone bulk density comparisons, respectively (Tables 10, 11). Native prairie and cropland catchments typically exhibited the lowest and highest soil bulk densities, respectively. The restored catchments were equivalent to, or intermediate among, the native prairie and cropland catchments (Tables 10, 11).

The effect of land use on the six soil chemistry parameters was significant for 53% and 50% of upland ($P_s < 0.05$) and wetland ($P_s < 0.03$) zone comparisons, respectively (Tables 10, 11). Relations among the land uses for all soil chemistry parameters varied by study point and wetland classification (Tables 10, 11). In general, upland zone OC and N were greatest in the native prairie catchments and lowest in the cropland catchments; restored catchments were equivalent to, or intermediate among, the native prairie and cropland catchments. Wetland zone OC and N were less variable among the land uses, and the restored catchments tended to have the lowest values overall. Concentrations of IC were variable and were not significantly different among land uses. In most instances, upland and wetland zone NO_3 concentrations were greatest in the cropland catchments, while the native prairie and restored catchments were equivalent. Conversely, NH_4 concentrations for both catchment zones were variable, with no consistent trends among study points and wetland classifications. Concentrations of P were greatest in the drained cropland catchments in most instances; non-drained cropland catchments were variable while the native prairie and restored catchments typically were equivalent (Tables 10, 11).

Linear regressions (not shown) suggested a weak positive correlation between the number of years that a catchment was restored (restoration age) and upland ($P = 0.06$, $r^2 = 0.07$) and wetland ($P = 0.02$, $r^2 = 0.10$) zone OC in the upper 30 cm of the soil profile. However, when catchments with similar restoration ages were grouped, boxplots displayed an increasing trend of OC with restoration age. This trend, however, was associated with high variability (Figs. 4a, b).

3.8. Relations between GHG fluxes and abiotic factors

Qualitative graphical analyses showed a strong relation between mean wetland zone CH_4 flux and WFPS, with minimal fluxes when WFPS was <60% and the greatest fluxes occurring where WFPS exceeded 80% (Fig. 5c). Wetland zone CH_4 flux also displayed a positive relation with soil temperature (Fig. 6c). Fluxes were minimal when temperatures were below approximately 5 °C and were the greatest when temperature exceeded approximately 15 °C. Variability in fluxes also increased with WFPS and temperature (Figs. 5c, 6c). Upland zone CH_4 fluxes were minimal regardless of WFPS or soil temperature (Figs. 5a, 6a).

Median upland zone N_2O fluxes were similar regardless of WFPS, but the mean displayed an increasing trend with WFPS (Fig. 5b). Variability in fluxes also increased with WFPS. Soil temperature did not appear to have a strong influence on upland zone N_2O flux, although the greatest mean values were observed when temperature was >20 °C (Fig. 6b). Wetland zone N_2O fluxes displayed similar relations to WFPS and temperature as the upland zone, with the exception of lower emissions when WFPS exceeded approximately 80% (Figs. 5d, 6d).

4. Discussion

Methane and N_2O fluxes from the 119 catchments monitored during this study were temporally and spatially variable at multiple scales. Fluxes displayed high seasonal and annual variability and often differed between the upland and wetland catchment zones, geographically-distributed study points, and to a lesser extent wetland classifications. Similar variability was evident for the abiotic and soil chemistry parameters, and although inconsistent and complex, all study parameters displayed some relations with land use. The observed variability and patterns are consistent with findings of other wetland studies representing the PPR (Phillips and Beeri, 2008; Gleason et al., 2009; Pennock et al., 2010; Badiou et al., 2011; Finocchiaro et al., 2014), and underscore the difficulty in quantifying or modeling the GHG balance of wetland systems.

The low upland zone CH_4 fluxes from this study (<0.02 g CH_4 m^{-2} day^{-1}) were similar to values reported for other PPR wetland catchments. Conversely, mean wetland zone CH_4 fluxes from this study, which in certain instances approached 4.0 g CH_4 m^{-2} day^{-1}, were much greater than the maximum values of <1 g CH_4 m^{-2} day^{-1} reported elsewhere (Phillips and Beeri, 2008; Gleason et al., 2009; Pennock et al., 2010; Badiou et al., 2011; Finocchiaro et al., 2014). This discrepancy in wetland zone CH_4 flux likely is related to the diverse characteristics (e.g., period of inundation, sulfate concentrations) of wetlands considered, as well as geographic location, weather, and timing and intensity of sampling.

In their meta-analysis on the carbon balance of North American wetlands, Bridgham et al. (2006) reported a mean estimated cumulative annual CH_4 flux for freshwater wetlands of 7.1 g CH_4 m^{-2} $year^{-1}$, with a maximum reported value of 227.1 g CH_4 m^{-2} $year^{-1}$. Recent studies from the PPR of the U.S. and Canada reported ranges of cumulative seasonal or annual CH_4 fluxes from the wetland landscape elements (i.e., basin center, open water, wetland zone) of 0.01–138 g CH_4 m^{-2} (Pennock et al., 2010) and −0.2–136 g CH_4 m^{-2} $year^{-1}$ (Finocchiaro et al., 2014). Mean cumulative CH_4 fluxes from this study ranged from roughly 0–650 g CH_4 m^{-2}, with an overall mean of approximately 160 g CH_4 m^{-2} (Table 8). The maximum values from this study are nearly 3 times as high as the maximum value from North American wetlands presented by Bridgham et al. (2006), suggesting that PPR wetlands have the potential to be significant sources of CH_4. However, CH_4 fluxes from PPR wetlands are seasonally and annually variable and can differ among geographic locations, wetland types, and land uses.

Throughout this study, N_2O flux events occurred periodically throughout the seasons, with some of the largest episodes taking place during spring and early summer. High temporal variability of N_2O flux has been well documented for all types of systems (e.g., Mosier et al., 1996; Izaurralde et al., 2004; Venterea et al., 2005; Hernandez and Mitsch, 2006; Hyde et al., 2006) and the overall magnitude and variability of fluxes from this study (<0.0001–0.0023 g N_2O m^{-2} day^{-1}) were comparable to reported values of similar PPR wetland catchments (Phillips and Beeri, 2008; Gleason et al., 2009; Pennock et al., 2010; Badiou et al., 2011; Finocchiaro et al., 2014).

4.1. Abiotic factors

Wetland zone CH_4 flux showed a positive relation with WFPS that is consistent with the process-based models and ecosystem literature (e.g., Segers, 1998; Le Mer and Roger, 2001; Gleason et al., 2009; Finocchiaro et al., 2014). Accordingly, CH_4 fluxes of the non-inundated upland zones were minimal, and upland soils often were a slight CH_4 sink. The exception to this was the noticeably greater upland zone CH_4 fluxes during 2005. These fluxes were most likely due to weather conditions (e.g., precipitation, snowmelt runoff) which resulted in high surface-water levels and greater fluxes from the toe-slope area of the upland zone, which is dry during most years. Wetland zone CH_4 fluxes also showed a positive relation to soil temperature, and fluxes generally were greatest during late spring and summer when these abiotic conditions were most conducive for methane production and flux. However, there were inconsistent flux events that did not appear to be related to changes in soil WFPS or temperature. Although many of the semipermanent catchments contained water throughout the study, water depths and ponded surface areas of all study wetlands generally decrease throughout the summer because of the region's negative precipitation:evaporation ratio. These changes could result in periodic

Table 10
Mean (standard error [se]) upland zone soil bulk density (BD, g cm^{-3}), organic carbon (OC, Mg ha^{-1}), inorganic carbon (IC, Mg ha^{-1}), total nitrogen (N, Mg ha^{-1}), nitrate (NO_3, Mg ha^{-1}), ammonium (NH_4, Mg ha^{-1}), and total phosphorus (P, Mg ha^{-1}). Analysis of variance (ANOVA) results are presented for effects of land use/disturbance category (land use); significant ($P \le 0.05$) values are bolded. For comparisons where there was a significant land-use effect, mean values with similar letters are not statistically different ($P > 0.05$).
[NP, native prairie; NDR, non-drained restored; HR, hydrologically restored; NDC, non-drained cropland; DC, drained cropland; SEAS, seasonal; SEMI, semipermanent].

Point	Class	Soil constituent	ANOVA results	Land use									
				NP	(se)	NDR	(se)	HR	(se)	NDC	(se)	DC	(se)
GP01	SEAS	BD	$F_{4,15} = 10.11; P = \mathbf{0.0004}$	1.14^{b}	(0.03)	1.39^{a}	(0.03)	1.45^{a}	(0.03)	1.39^{a}	(0.02)	1.39^{a}	(0.06)
		OC	$F_{4,15} = 6.45; P = \mathbf{0.003}$	137.11^{a}	(3.94)	117.61^{b}	(5.38)	107.31^{b}	(8.08)	105.70^{b}	(5.41)	102.78^{b}	(3.68)
		IC	$F_{4,15} = 1.46; P = 0.26$	6.38	(5.10)	18.13	(3.73)	21.03	(7.43)	22.55	(4.95)	28.04	(10.08)
		N	$F_{4,15} = 2.54; P = 0.08$	12.38	(0.29)	11.01	(0.47)	10.16	(0.86)	10.47	(0.49)	10.50	(0.50)
		NO_3	$F_{4,15} = 4.17; P = \mathbf{0.02}$	0.02^{b}	(<0.01)	0.02^{b}	(<0.01)	0.02^{b}	(<0.01)	0.07^{a}	(0.01)	0.08^{a}	(0.03)
		NH_4	$F_{4,15} = 2.97; P = 0.054$	0.03	(0.01)	0.02	(<0.01)	0.01	(<0.01)	0.01	(<0.01)	0.01	(<0.01)
		P	$F_{4,15} = 0.06; P = 0.99$	0.07	(0.01)	0.07	(0.01)	0.07	(0.01)	0.07	(0.01)	0.07	(<0.01)
	SEMI	BD	$F_{4,16} = 5.7; P = \mathbf{0.005}$	1.14^{b}	(0.06)	1.46^{a}	(0.05)	1.44^{a}	(0.04)	1.49^{a}	(0.04)	1.40^{a}	(0.09)
		OC	$F_{4,16} = 12.67; P = \mathbf{0.0001}$	145.20^{a}	(5.06)	110.87^{b}	(5.83)	104.81^{bc}	(4.34)	94.53^{c}	(6.38)	107.48^{bc}	(5.04)
		IC	$F_{4,16} = 1.77; P = 0.18$	8.21	(4.90)	17.81	(3.93)	41.43	(10.98)	30.11	(15.80)	38.74	(11.98)
		N	$F_{4,16} = 6.51; P = \mathbf{0.003}$	13.17^{a}	(0.65)	10.45^{b}	(0.55)	9.99^{b}	(0.49)	9.44^{b}	(0.69)	11.04^{b}	(0.37)
		NO_3	$F_{4,16} = 21.61; P < \mathbf{0.0001}$	0.02^{c}	(0.01)	0.02^{c}	(0.01)	0.02^{c}	(<0.01)	0.04^{b}	(<0.01)	0.09^{a}	(0.01)
		NH_4	$F_{4,16} = 3.1; P = \mathbf{0.05}$	0.03^{a}	(0.01)	0.02^{ab}	(<0.01)	0.01^{b}	(<0.01)	0.02^{ab}	(0.01)	0.01^{b}	(<0.01)
		P	$F_{4,16} = 3.08; P = \mathbf{0.05}$	0.07^{ab}	(0.01)	0.06^{b}	(<0.01)	0.05^{b}	(0.01)	0.06^{b}	(0.01)	0.09^{a}	(0.01)
GP09	SEAS	BD	$F_{4,15} = 8.16; P = \mathbf{0.001}$	0.97^{b}	(0.05)	1.16^{b}	(0.07)	1.16^{b}	(0.08)	1.45^{a}	(0.09)	1.43^{a}	(0.07)
		OC	$F_{4,15} = 4.02; P = \mathbf{0.02}$	141.62^{a}	(14.81)	124.01^{ab}	(12.00)	114.63^{ab}	(17.81)	69.25^{c}	(9.65)	96.08^{bc}	(13.45)
		IC	$F_{4,15} = 0.52; P = 0.72$	21.40	(10.71)	34.71	(7.35)	14.15	(4.34)	23.91	(13.72)	24.98	(12.27)
		N	$F_{4,15} = 3.26; P = \mathbf{0.04}$	12.89^{a}	(1.61)	11.39^{ab}	(1.59)	10.58^{abc}	(1.56)	6.45^{c}	(0.89)	8.62^{bc}	(1.14)
		NO_3	$F_{4,15} = 1.72; P = 0.2$	0.03	(<0.01)	0.02	(<0.01)	0.02	(<0.01)	0.03	(0.01)	0.04	(0.01)
		NH_4	$F_{4,15} = 0.29; P = 0.88$	0.02	(<0.01)	0.01	(<0.01)	0.01	(<0.01)	0.01	(<0.01)	0.01	(<0.01)
		P	$F_{4,15} = 2.08; P = 0.13$	0.05	(<0.01)	0.05	(0.01)	0.06	(0.01)	0.09	(0.02)	0.07	(0.01)
	SEMI	BD	$F_{4,15} = 9.39; P = \mathbf{0.001}$	0.86^{c}	(0.04)	1.16^{b}	(0.08)	1.19^{b}	(0.11)	1.39^{a}	(0.04)	1.31^{a}	(0.02)
		OC	$F_{4,15} = 2.73; P = 0.07$	136.14	(15.82)	110.22	(14.62)	130.07	(21.44)	74.36	(5.91)	94.06	(15.34)
		IC	$F_{4,15} = 0.67; P = 0.62$	32.44	(11.61)	18.86	(7.82)	44.95	(15.98)	46.16	(20.21)	53.55	(23.12)
		N	$F_{4,15} = 2.77; P = 0.07$	12.57	(1.46)	10.05	(1.18)	12.39	(2.25)	6.85	(0.42)	8.77	(1.38)
		NO_3	$F_{4,15} = 4.64; P = \mathbf{0.01}$	0.02^{bc}	(0.01)	0.02^{bc}	(<0.01)	0.02^{bc}	(<0.01)	0.03^{ab}	(<0.01)	0.04^{a}	(0.01)
		NH_4	$F_{4,15} = 0.97; P = 0.45$	0.01	(<0.01)	0.01	(<0.01)	0.02	(<0.01)	0.02	(<0.01)	0.01	(<0.01)
		P	$F_{4,15} = 2.19; P = 0.12$	0.04	(0.01)	0.05	(0.01)	0.06	(<0.01)	0.07	(0.01)	0.05	(0.01)
GP11	SEAS	BD	$F_{2,16} = 10.94; P = \mathbf{0.001}$	1.13^{b}	(0.02)	–	–	1.37^{a}	(0.03)	–	–	1.29^{a}	(0.03)
		OC	$F_{2,16} = 6.44; P = \mathbf{0.01}$	118.27^{a}	(3.81)	–	–	92.49^{b}	(4.32)	–	–	112.07^{a}	(8.31)
		IC	$F_{2,12} = 1.64; P = 0.23$	1.42	(0.98)	–	–	5.93	(2.63)	–	–	9.82	(3.04)
		N	$F_{2,16} = 6.3; P = \mathbf{0.01}$	10.43^{a}	(0.34)	–	–	8.13^{b}	(0.37)	–	–	9.87^{a}	(0.84)
		NO_3	$F_{2,16} = 18.46; P = \mathbf{0.0001}$	0.02^{b}	(<0.01)	–	–	0.01^{b}	(<0.01)	–	–	0.03^{a}	(<0.01)
		NH_4	$F_{2,16} = 7.73; P = \mathbf{0.004}$	0.01^{b}	(<0.01)	–	–	0.02^{b}	(<0.01)	–	–	0.03^{a}	(<0.01)
		P	$F_{2,16} = 0.51; P = 0.61$	0.06	(0.01)	–	–	0.07	(<0.01)	–	–	0.07	(0.01)
	SEMI	BD	$F_{2,16} = 13.9; P = \mathbf{0.0003}$	1.04^{b}	(0.03)	–	–	1.37^{a}	(0.02)	–	–	1.32^{a}	(0.09)
		OC	$F_{2,16} = 9.68; P = \mathbf{0.002}$	136.50^{a}	(5.49)	–	–	89.97^{b}	(5.32)	–	–	114.51^{a}	(13.40)
		IC	$F_{2,15} = 1.46; P = 0.26$	14.88	(11.59)	–	–	4.62	(1.63)	–	–	6.53	(3.87)
		N	$F_{2,16} = 10.2; P = \mathbf{0.001}$	12.05^{a}	(0.48)	–	–	7.94^{b}	(0.47)	–	–	10.37^{a}	(1.16)
		NO_3	$F_{2,16} = 17.29; P = \mathbf{0.0001}$	0.02^{b}	(<0.01)	–	–	0.01^{b}	(<0.01)	–	–	0.05^{a}	(<0.01)
		NH_4	$F_{2,16} = 4.26; P = \mathbf{0.03}$	0.01^{b}	(<0.01)	–	–	0.02^{a}	(<0.01)	–	–	0.02^{a}	(<0.01)
		P	$F_{2,16} = 8.91; P = \mathbf{0.003}$	0.05^{b}	(<0.01)	–	–	0.06^{b}	(0.01)	–	–	0.11^{a}	(0.02)

Table 11

Mean (standard error [se]) wetland zone soil bulk density (BD, g cm^{-3}), organic carbon (OC, Mg ha^{-1}), inorganic carbon (IC, Mg ha^{-1}), total nitrogen (N, Mg ha^{-1}), nitrate (NO_3, Mg ha^{-1}), ammonium (NH_4, Mg ha^{-1}), and total phosphorus (P, Mg ha^{-1}). Analysis of variance (ANOVA) results are presented for effects of land use/disturbance category (land use); significant ($P \leq 0.05$) values are bolded. For comparisons where there was a significant land-use effect, mean values with similar letters are not statistically different ($P > 0.05$). [NP, native prairie; NDR, non-drained restored; HR, hydrologically restored; NDC, non-drained cropland; DC, drained cropland; SEAS, seasonal; SEMI, semipermanent].

				Land use									
Point	Class	Soil constituent	ANOVA results	NP	(se)	NDR	(se)	HR	(se)	NDC	(se)	DC	(se)
GP01	SEAS	BD	F4,15 = 3.81; P = **0.025**	0.94^{b}	(0.10)	1.18^{a}	(0.12)	1.20^{a}	(0.03)	1.25^{a}	(0.02)	1.34^{a}	(0.05)
		OC	F4,15 = 1.01; P = 0.43	137.02	(6.67)	121.79	(7.47)	116.68	(6.82)	129.73	(8.89)	129.97	(9.18)
		IC	F4,15 = 0.06; P = 0.99	29.40	(20.47)	27.75	(14.04)	23.34	(9.53)	21.44	(9.73)	25.38	(7.74)
		N	F4,15 = 1.27; P = 0.32	12.56	(0.53)	11.48	(0.72)	11.09	(0.67)	12.61	(0.77)	13.11	(0.99)
		NO_3	F4,15 = 6.16; P = **0.004**	0.02^{b}	(0.01)	0.02^{bc}	(0.01)	0.02^{bc}	(0.01)	0.07^{a}	(0.02)	0.05^{ab}	(0.01)
		NH_4	F4,15 = 2.37; P = 0.1	0.02	(<0.01)	0.02	(<0.01)	0.02	(0.01)	0.01	(<0.01)	0.01	(<0.01)
		P	F4,15 = 2.26; P = 0.11	0.06	(0.01)	0.11	(0.04)	0.11	(0.03)	0.18	(0.03)	0.15	(0.03)
	SEMI	BD	F4,16 = 2.08; P = 0.13	0.84	(0.12)	1.12	(0.09)	1.04	(0.05)	1.14	(0.10)	1.11	(0.07)
		OC	F4,16 = 3.32; P = **0.04**	133.35^{ab}	(10.89)	115.95^{b}	(4.45)	110.30^{b}	(8.48)	121.62^{b}	(16.79)	155.85^{a}	(3.31)
		IC	F4,16 = 2.07; P = 0.13	6.35	(4.58)	27.02	(5.26)	42.30	(11.37)	36.45	(15.70)	17.72	(8.15)
		N	F4,16 = 5.68; P = **0.005**	12.44^{b}	(0.97)	11.13^{b}	(0.50)	10.60^{b}	(0.80)	12.27^{b}	(1.51)	16.23^{a}	(0.50)
		NO_3	F4,16 = 3.74; P = **0.02**	0.01^{b}	(<0.01)	0.01^{b}	(<0.01)	0.01^{b}	(<0.01)	0.01^{b}	(<0.01)	0.04^{a}	(0.02)
		NH_4	F4,16 = 3.95; P = **0.02**	0.06^{abc}	(0.01)	0.06^{ab}	(0.01)	0.05^{bc}	(0.01)	0.08^{a}	(0.01)	0.02^{c}	(<0.01)
		P	F4,16 = 3.89; P = **0.02**	0.06^{b}	(0.01)	0.08^{b}	(<0.01)	0.07^{b}	(0.02)	0.08^{b}	(0.01)	0.15^{a}	(0.02)
GP09	SEAS	BD	F4,15 = 6.72; P = **0.003**	0.82^{c}	(0.07)	0.87^{bc}	(0.05)	1.03^{b}	(0.03)	1.02^{b}	(0.07)	1.22^{a}	(0.06)
		OC	F4,15 = 0.69; P = 0.61	133.89	(9.61)	143.00	(9.88)	147.87	(23.97)	120.01	(1.93)	134.42	(6.85)
		IC	F4,15 = 0.94; P = 0.47	8.85	(5.12)	11.63	(3.57)	15.77	(3.56)	7.73	(4.64)	5.59	(2.94)
		N	F4,15 = 0.05; P = 0.995	9.13	(1.26)	9.09	(0.92)	8.69	(1.76)	9.10	(1.23)	9.45	(0.68)
		NO_3	F4,15 = 1.5; P = 0.25	0.01	(<0.01)	0.02	(0.01)	0.01	(<0.01)	0.02	(0.01)	0.03	(0.01)
		NH_4	F4,15 = 0.51; P = 0.73	0.03	(0.01)	0.01	(<0.01)	0.01	(<0.01)	0.03	(0.01)	0.04	(0.02)
		P	F4,15 = 4.63; P = **0.01**	0.05^{b}	(0.02)	0.04^{b}	(0.01)	0.04^{b}	(<0.01)	0.11^{a}	(0.01)	0.13^{a}	(0.04)
	SEMI	BD	F4,15 = 3.01; P = 0.052	0.84	(0.13)	0.84	(0.03)	1.06	(0.11)	1.07	(0.03)	1.16	(0.06)
		OC	F4,15 = 0.86; P = 0.51	121.43	(9.15)	118.28	(10.82)	151.05	(23.63)	123.43	(3.49)	129.11	(15.02)
		IC	F4,15 = 0.42; P = 0.79	21.72	(6.92)	15.83	(7.17)	12.23	(1.65)	14.26	(7.12)	13.28	(3.64)
		N	F4,15 = 1.36; P = 0.29	9.40	(1.52)	9.34	(1.52)	7.95	(0.68)	11.50	(0.67)	8.40	(1.16)
		NO_3	F4,15 = 5.3; P = **0.01**	0.00^{b}	(<0.01)	0.01^{b}	(<0.01)	0.01^{b}	(<0.01)	0.01^{ab}	(0.01)	0.03^{a}	(0.01)
		NH_4	F4,15 = 4.21; P = **0.02**	0.02^{bc}	(<0.01)	0.05^{ab}	(0.02)	0.03^{abc}	(0.01)	0.06^{a}	(0.01)	0.01^{c}	(<0.01)
		P	F4,15 = 10.74; P = **0.0003**	0.03^{b}	(0.01)	0.05^{b}	(0.01)	0.05^{b}	(0.01)	0.12^{a}	(0.02)	0.06^{b}	(0.01)
GP11	SEAS	BD	F2,16 = 2.99; P = 0.08	1.03	(0.12)	–	–	1.23	(0.04)	–	–	1.23	(0.03)
		OC	F2,16 = 7.6; P = **0.005**	142.06^{a}	(13.16)	–	–	103.71^{b}	(5.91)	–	–	136.34^{a}	(4.83)
		IC	F2,13 = 1.65; P = 0.23	5.65	(4.89)	–	–	0.94	(0.40)	–	–	6.92	(5.11)
		N	F2,16 = 9.16; P = **0.002**	8.46^{a}	(0.82)	–	–	5.73^{b}	(0.34)	–	–	7.81^{a}	(0.50)
		NO_3	F2,16 = 4.24; P = **0.03**	0.01^{ab}	(<0.01)	–	–	0.01^{b}	(<0.01)	–	–	0.02^{a}	(<0.01)
		NH_4	F2,16 = 5.2; P = **0.02**	0.01^{b}	(<0.01)	–	–	0.01^{ab}	(<0.01)	–	–	0.02^{a}	(<0.01)
		P	F2,16 = 0.91; P = 0.42	0.07	(0.03)	–	–	0.06	(0.01)	–	–	0.09	(0.03)
	SEMI	BD	F2,16 = 21.27; P < **0.0001**	0.69^{b}	(0.05)	–	–	1.24^{a}	(0.04)	–	–	1.09^{a}	(0.11)
		OC	F2,16 = 17.09; P = **0.0001**	169.38^{a}	(10.17)	–	–	96.22^{b}	(5.70)	–	–	155.37^{a}	(20.10)
		IC	F2,15 = 1.48; P = 0.26	10.37	(3.77)	–	–	6.22	(2.60)	–	–	0.81	(0.50)
		N	F2,16 = 12.45; P = **0.001**	9.09^{a}	(0.88)	–	–	5.36^{b}	(0.50)	–	–	9.94^{a}	(1.12)
		NO_3	F2,16 = 15.25; P = **0.0002**	0.01^{b}	(<0.01)	–	–	0.01^{b}	(<0.01)	–	–	0.05^{a}	(0.01)
		NH_4	F2,16 = 1.08; P = 0.36	0.01	(<0.01)	–	–	0.03	(0.01)	–	–	0.02	(<0.01)
		P	F2,16 = 11.5; P = **0.001**	0.03^{b}	(0.01)	–	–	0.05^{b}	(0.01)	–	–	0.12^{a}	(0.02)

CH_4 releases from saturated soils or areas of reduced water depths as water levels decline.

Mean wetland zone CH_4 fluxes of the semipermanent catchments generally were greater than fluxes of the seasonal catchments. Semipermanent catchments often are larger and deeper than seasonal catchments, receive groundwater, and have longer hydroperiods; thus, conditions that favor methanogenesis likely are more prevalent in the semipermanent catchments. However, this pattern of greater fluxes from the semipermanent catchments likely will vary in areas where inputs of sulfate-rich groundwater to these wetlands could inhibit CH_4 production and flux (Martens and Berner, 1974; Segers, 1998; Le Mer and Roger, 2001; Gauci et al., 2004; Pennock et al., 2010).

Results of this study showed a general relation between WFPS and N_2O flux that was consistent with process-based models and field studies (Davidson et al., 2000; Gleason et al., 2009; Pennock et al., 2010; Finocchiaro et al., 2014). Optimal soil moisture conditions for the flux of N_2O occur near field capacity (approximately 60% WFPS), and fluxes from wetland catchments have been related to soil conditions where WFPS transitions from nearly or completely saturated to values <60% (Davidson et al., 2000; Gleason et al., 2009; Pennock et al., 2010). The irregular seasonal N_2O fluxes did not show a strong relation with soil temperature, although the greatest mean fluxes generally were associated with the warmest temperatures. On the basis of general relations between soil WFPS and N_2O flux, the observed variability likely is linked to fluctuating soil moisture levels associated with precipitation and water-level changes. Depending on duration and intensity, precipitation events could result in short-term conditions favorable for N_2O flux in the upland zones, and precipitation runoff can affect wetland water levels. Further, seasonal water-level declines, which are characteristic of PPR wetlands, could result in optimal conditions for N_2O flux along the wetland-upland transition zone, resulting in sporadic and localized flux events. However, results of this study suggest that N_2O fluxes of the cropland catchments were greater and more variable than the grassland catchments; thus, relations between flux and abiotic factors likely are confounded by land use and are discussed below.

4.2. Land use effects

Land use affected CH_4 fluxes and associated abiotic properties for both catchment zones. Excluding the anomalous year of 2005, upland zones of the native prairie catchments generally exhibited the greatest CH_4 uptake compared to the other land uses. This observation likely was associated with lower soil bulk densities and WFPS values that are characteristic of undisturbed grasslands with well-established root

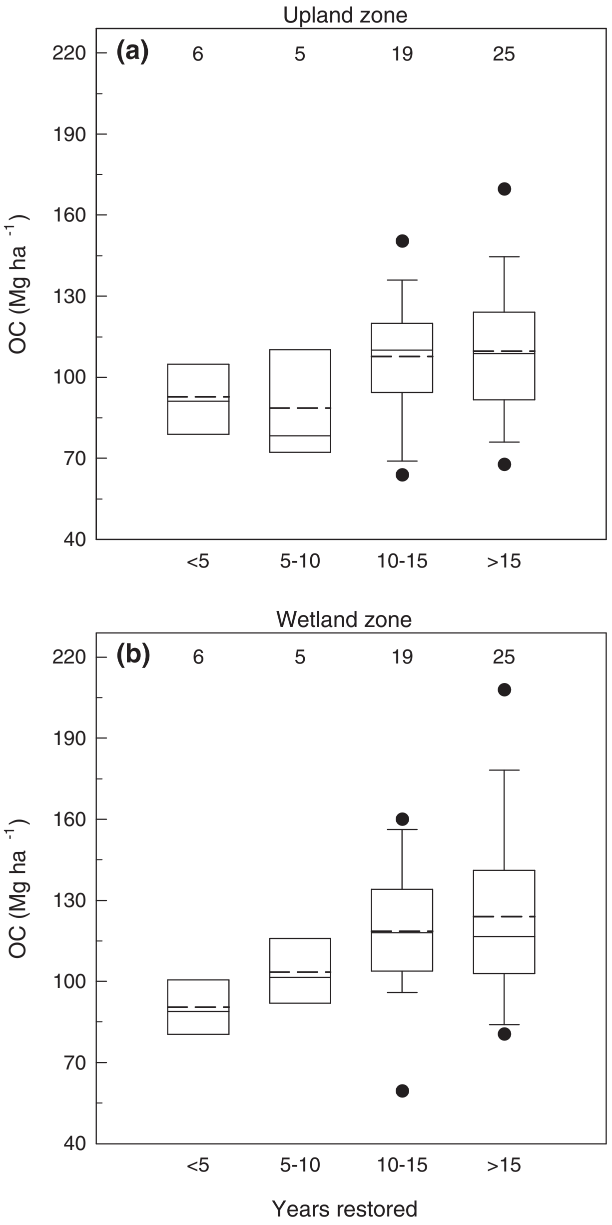

Fig. 4. Boxplots showing soil organic carbon (OC) concentrations for the a) upland zone and b) wetland zone, by number of years restored, for all restored catchments combined. Boxes define the 25th and 75th percentiles, error bars define 10th and 90th percentiles, dots show 5th and 95th percentiles, and the solid and dashed lines show the median and mean, respectively. The number of observations for each boxplot is shown at the top of the graph.

systems, greater water infiltration, and well-aerated soils. Differences among microbial and plant communities also could be a factor. Excluding the native prairie catchments, land-use effects on upland zone WFPS and soil temperature were marginal, and associated fluxes of restored catchments generally were similar to the pre-restoration baselines (i.e., cropland catchments).

Wetland zones of the drained cropland catchments, where ponded water typically does not persist, exhibited low WFPS values and minimal CH_4 fluxes relative to the other land uses. These observations can be directly attributed to the artificial drainage of these catchments, which results in enhanced removal of surface and soil pore water. Kumar et al. (2014) reported similar differences among drained and non-drained soil conditions. Conversely, wetland zones of the native prairie catchments consistently exhibited some of the highest CH_4 fluxes. Wetland zone WFPS was similar among land uses, excluding drained cropland catchments, so these relatively high fluxes likely were associated with other factors such as, microbial and plant communities, available organic carbon, water table elevation, pH, and soils (Segers, 1998; Le mer and Roger, 2001; Whalen, 2005; Kayranli et al., 2010; Laanbroek, 2010; Bridgham et al., 2013; Serrano-Silva et al., 2014).

Land use affected N_2O fluxes and associated soil properties for both catchment zones, and these effects were most evident when land uses were lumped into active croplands (drained, non-drained) and grasslands (native prairie, hydrologically restored, non-drained restored). Cropland catchments, especially the upland zones, generally were characterized by greater and more variable N_2O fluxes, NO_3 concentrations, and to a lesser extent P concentrations and mean soil temperatures. There also were land-use effects on WFPS, with wetland zones of drained cropland catchments exhibiting much lower values than the other land uses. Differences in soil properties can be attributed to the addition of agricultural soil amendments and greater exposure of bare soil to sunlight in the cropland catchments, and these factors have been linked to N_2O fluxes (Bremner and Blackmer, 1978; Burke et al., 2002; Izaurralde et al., 2004; Venterea et al., 2005; Hyde et al., 2006; Liu and Greaver, 2009).

Precipitation and associated runoff can cause abrupt changes in WFPS and water levels of cropland catchments compared to grassland catchments (Euliss and Mushet, 1996; van der kamp et al., 2003; Gleason et al., 2009), and the margins of wetlands can be associated with rapidly changing redox conditions as water levels fluctuate. Additionally, the relatively low wetland zone WFPS values of drained cropland catchments often were in the ranges optimal for N_2O fluxes, and this likely contributed to the relatively high fluxes of cropland catchments. The increased nutrient concentrations, combined with greater soil temperatures and the relatively dynamic nature (e.g., water-level fluctuations) of cropland catchments relative to grassland catchments, likely are responsible not only for the greater overall N_2O fluxes, but the sporadic nature of these fluxes. Periodic application of nitrogen-based agricultural amendments also could contribute to the irregular flux patterns. Ultimately, the relatively high N_2O fluxes from the cropland catchments cannot be attributed to a single variable; instead, these fluxes likely are associated with a combination of factors including NO_3 concentration, soil temperature, WFPS, and water-level fluctuations.

4.3. Carbon sequestration

Sequestration of atmospheric carbon has been documented in upland soils under conditions where land-use practices have been altered to maximize sequestration (Gebhart et al., 1994; Conant et al., 2001; Follet et al., 2001, 2012; Nelson et al., 2008). The carbon sequestration potential of mineral soil wetlands has been demonstrated, but the dynamic nature of these systems adds a great deal of uncertainty in terms of measuring changes in soil OC and determining representative sequestration rates (Euliss et al., 2006; Gleason et al., 2008, 2009; Badiou et al., 2011; Finocchiaro et al., 2014). Moreover, the relations between land use and OC concentrations can be highly variable and they often deviate from expectations (Euliss et al., 2006; Gleason et al., 2008; Badiou et al., 2011). A common approach for assessing carbon sequestration potential in the PPR is to compare restored grassland catchments to native prairie and cropland baselines with the assumption that, over time, restored catchments are capable of accumulating soil OC to a level similar to that of the native prairie catchments. Further, sequestration rates often are determined by comparing restored catchments of difference ages (i.e., length of time since restoration) to a pre-restoration baseline (Euliss et al., 2006; Gleason et al., 2008).

Soil organic carbon levels of wetland catchments from this study (96–170 Mg ha^{-1} in the upper 30 cm) were within ranges reported for other PPR wetland catchments (Euliss et al., 2006; Gleason et al., 2008). Comparisons of OC among land uses also were similar to other

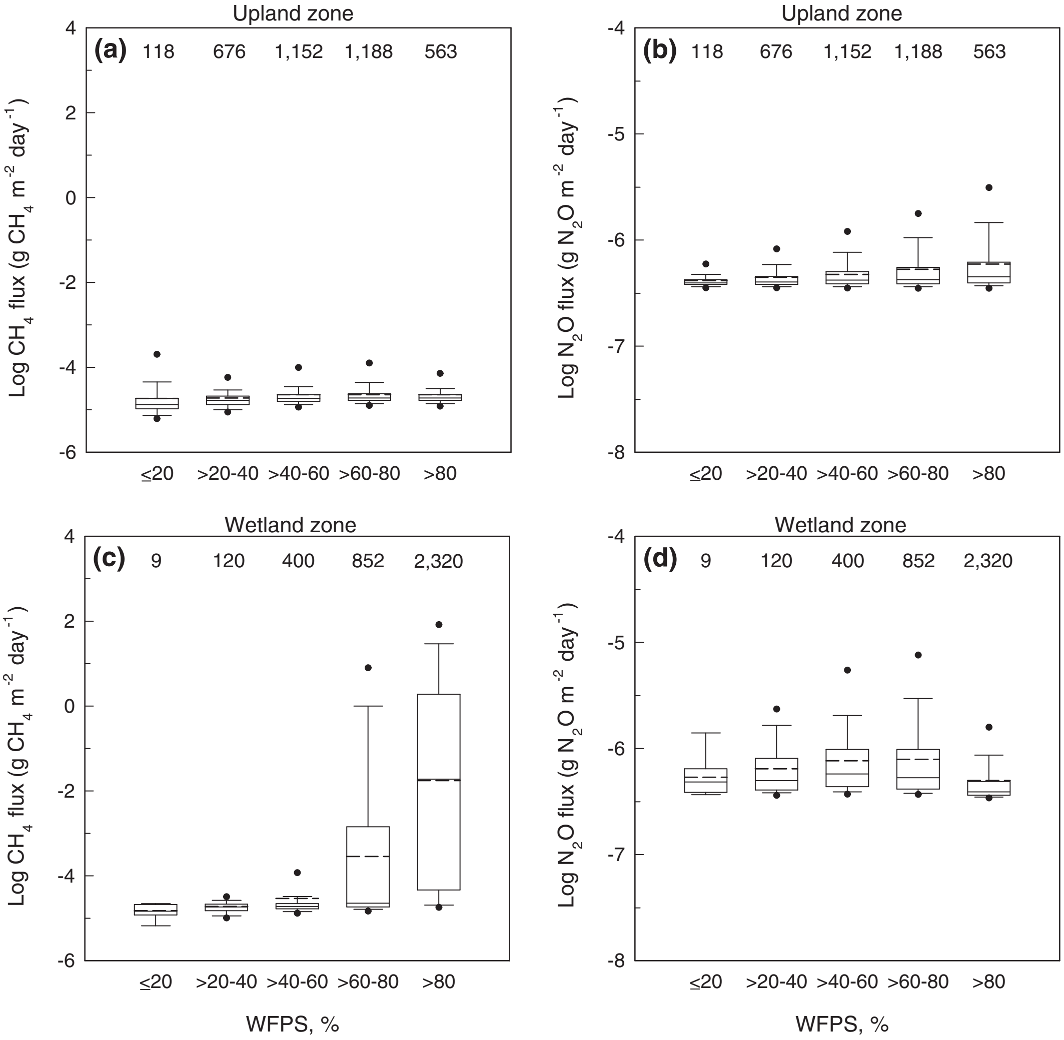

Fig. 5. Boxplots showing the natural log a) upland zone methane (CH_4) flux, b) upland zone nitrous oxide (N_2O) flux, c) wetland zone CH_4 flux, and d) wetland zone N_2O flux across the range of soil water-filled pore space (WFPS) values for all catchments combined. Boxes define the 25th and 75th percentiles, error bars define 10th and 90th percentiles, dots show 5th and 95th percentiles, and the solid and dashed lines show the median and mean, respectively. The number of observations for each boxplot is shown at the top of the graph.

studies in that the minimally disturbed reference catchments, particularly the upland zones, often displayed greater concentrations while the restored and cropland catchments displayed variable relations to each other (Euliss et al., 2006; Gleason et al., 2008; Gleason et al., 2009; Badiou et al., 2011; Finocchiaro et al., 2014). Gleason et al. (2008, 2009) reported that OC often was similar between cropland and restored catchments, and in some instances cropland catchments had significantly more OC. Euliss et al. (2006) identified soil depth and wetland classification as important factors in determining sequestration rates and Badiou et al. (2011) showed that OC varies among landscape elements (e.g., upper slope, lower slope, wet edge) within catchments.

Based on results of this and other studies it is evident that OC is lost when undisturbed, native prairie catchments are converted for agriculture. Further, it has been shown that ceasing agriculture and restoring grasses does result in increased OC. However, the high degree of observed variability (biotic and abiotic) associated with PPR wetland catchments, combined with the long-term prerequisite of OC sequestration, makes it extremely difficult to quantify sequestration associated with land-use changes. This variability can be especially problematic over large geographic areas that differ in terms of climate and agricultural and restoration practices. These observations suggest that further research and intensive monitoring (e.g., GHG fluxes, net primary production) will be required to accurately assess carbon sequestration potential and rates, and that future research must consider factors that contribute variability, such as landscape position, hydrologic characteristics, soils, restoration methods and age, post-restoration vegetation characteristics, weather, and land-use history (e.g., cropping practices).

4.4. GHG mitigation potential of wetland restoration

Assessing whether the practice of restoring wetland catchments contributes to the overall mitigation of atmospheric carbon emissions requires estimates of the effects of restoration on GHG fluxes and carbon sequestration, as well as the ability to determine the long-term balance between the two. Results of this study suggest that the effects of restoration on CH_4 fluxes are variable and depend on the type of catchment restored. Restoring drained cropland catchments could result in greater CH_4 fluxes while restoring non-drained cropland catchments may not greatly affect CH_4 fluxes, but this would depend on various catchment characteristics such as period of inundation. Conversely, restoring wetland catchments would reduce overall N_2O emissions in most instances. However, since CH_4 accounts for a large majority of the overall GWP compared to N_2O, it should be considered more prominently when assessing restoration. The effects of restoration on soil OC were inconsistent and suggest that sequestration rates are variable and affected by site-specific biotic and abiotic conditions.

Results of this and other studies suggest that GHG fluxes from wetlands are irregular and temporally variable (Gleason et al., 2009;

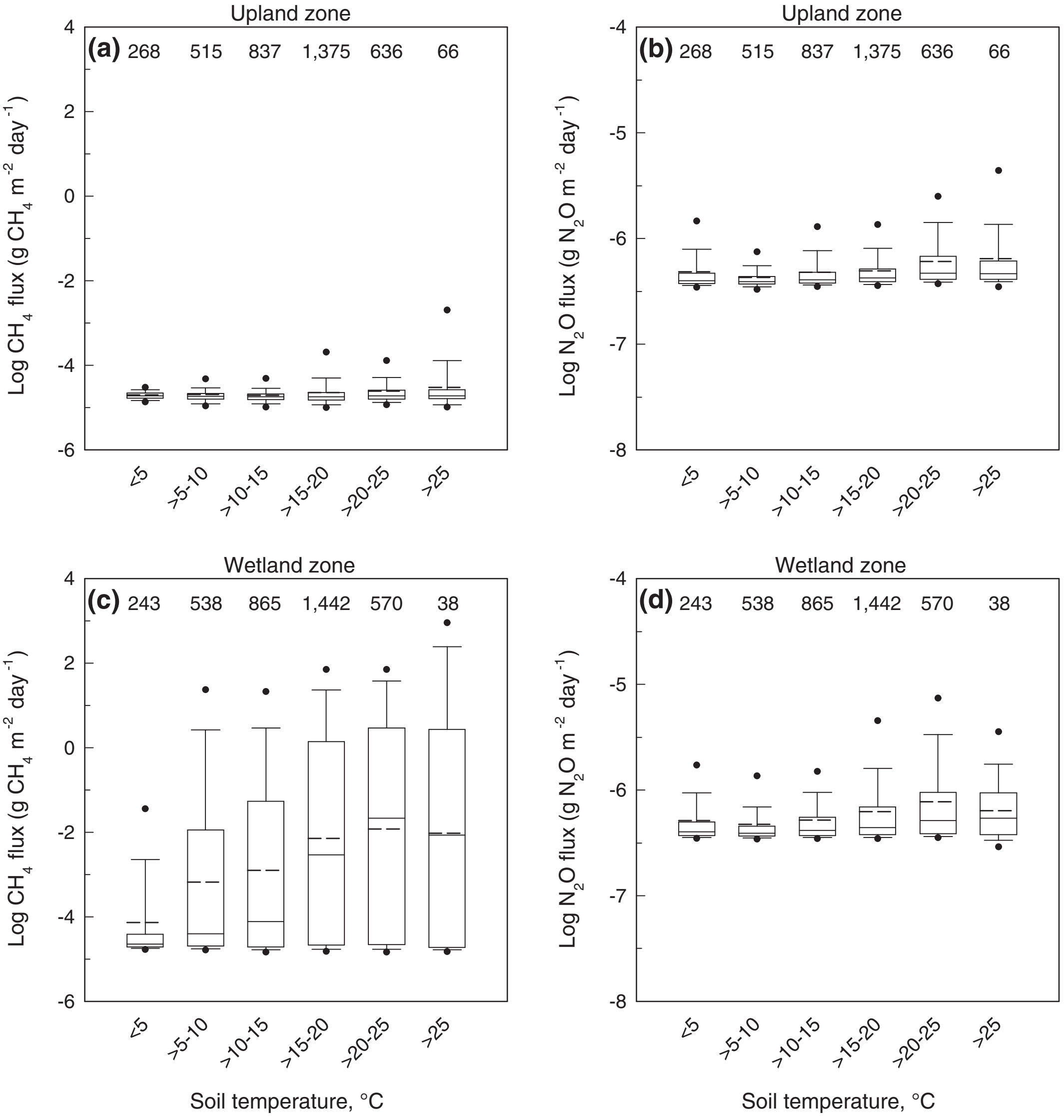

Fig. 6. Boxplots showing the natural log a) upland zone methane (CH_4) flux, b) upland zone nitrous oxide (N_2O) flux, c) wetland zone CH_4 flux, and d) wetland zone N_2O flux across the range of soil temperature values for all catchments combined. Boxes define the 25th and 75th percentiles, error bars define 10th and 90th percentiles, dots show 5th and 95th percentiles, and the solid and dashed lines show the median and mean, respectively. The number of observations for each boxplot is shown at the top of the graph.

Pennock et al., 2010; Badiou et al., 2011; Finocchiaro et al., 2014). Research also has shown that that estimating carbon sequestration rates for wetland catchments can be difficult, and published rates are highly variable and associated with a great deal of uncertainty (Euliss et al., 2006; Gleason et al., 2008; Kayranli et al., 2010; Badiou et al., 2011; Bernal and Mitsch, 2012; Mitsch et al., 2013). Gleason et al. (2008) suggested that in addition to factors such as land-use history, restoration methods, soils, and time, carbon sequestration rates of restored PPR wetlands could be affected by climate. The PPR is characterized by relatively wet and dry periods which have a great effect on wetland water levels, and consequently abiotic factors that regulate carbon sequestration and GHG fluxes. Thus, it is likely that carbon sequestration rates and GHG fluxes would differ greatly between wet and dry periods when wetlands could be filled to capacity or completely dry, and this variability could be exacerbated by land use. Thus, the overall net carbon balance of wetland catchments, and strength of the carbon sink or source, likely would fluctuate with time (i.e., climate patterns). As an example, Table 7 demonstrates that mean GWP for a given land use can vary greatly from year to year in response to weather and other factors. Consequently, estimates of the overall net carbon balance for these catchments would vary from year to year. Compounding the uncertainty around field-based estimates of carbon sequestration and GHG fluxes is the fact that studies of OC sequestration typically rely on soil samples collected once during a study, and annual GHG flux estimates often are extrapolated from a small number of point-in-time (e.g., midday) measurements. These types of estimates often do not accurately account for diurnal and temporal variability of fluxes or sequestration rates, and do not represent the dynamic nature of wetland catchments (e.g., Pennock et al., 2010; Finocchiaro et al., 2014).

With this study cumulative fluxes were not extrapolated beyond the sample-collection periods because of the observed variability and inherent uncertainty. Further, carbon sequestration rates were not calculated because there were weak relations between soil OC and restoration age and no consistent differences between the restored catchments and the cropland baselines. However, general inferences made using a referenced-based approach to compare restored catchments to a cropland baseline suggest that restoring drained cropland catchments would result in increased CH_4 fluxes, while restoring non-drained cropland catchments would not greatly affect CH_4 fluxes. Similarly, it is apparent that restoring all cropland catchments to more natural grasslands would result in decreased N_2O emissions. Conversely, generalizations regarding the effects of restoration on OC cannot be made because relations between land uses differ.

Hydrological characteristics and nutrient cycling of PPR wetland catchments are inherently variable, both temporally and spatially. Results of this and other studies suggest that temporally-intensive data collection is required to reduce the uncertainty around GHG fluxes and carbon sequestration rates based on point-in-time measurements, and long-term studies may be required to determine if GHG fluxes from restored catchments will eventually approach those of the native prairie baseline. Moreover, results suggest that it is important to consider wetland type (drained, non-drained) when assessing whether restoration will result in increased GHG fluxes that could outweigh potential benefits of increased soil OC sequestration. Lastly, it is apparent that to accurately assess whether wetlands are long-term sinks or sources of atmospheric carbon, research should focus on developing and validating models of wetland hydrology (e.g., hydroperiods, water-level changes) and the associated GHG fluxes across climate and land use scenarios to reduce uncertainties.

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