1-2012

Greenhouse Gas Fluxes in Southeastern U.S. Coastal Plain Wetlands Under Contrasting Land Uses

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Greenhouse gas fluxes in southeastern U.S. coastal plain wetlands under contrasting land uses

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Abstract. Whether through sea level rise or wetland restoration, agricultural soils in coastal areas will be inundated at increasing rates, renewing connections to sensitive surface waters and raising critical questions about environmental trade-offs. Wetland restoration is often implemented in agricultural catchments to improve water quality through nutrient removal. Yet flooding of soils can also increase production of the greenhouse gases nitrous oxide and methane, representing a potential environmental trade-off. Our study aimed to quantify and compare greenhouse gas emissions from unmanaged and restored forested wetlands, as well as actively managed agricultural fields within the North Carolina coastal plain, USA. In sampling conducted once every two months over a two-year comparative study, we found that soil carbon dioxide flux (range: 8000–64 800 kg $CO_2 \cdot ha^{-1} \cdot yr^{-1}$) comprised 66–100% of total greenhouse gas emissions from all sites and that methane emissions (range: −6.87 to 197 kg $CH_4 \cdot ha^{-1} \cdot yr^{-1}$) were highest from permanently inundated sites, while nitrous oxide fluxes (range: −1.07 to 139 kg $N_2O \cdot ha^{-1} \cdot yr^{-1}$) were highest in sites with lower water tables. Contrary to predictions, greenhouse gas fluxes (as CO_2 equivalents) from the restored wetland were lower than from either agricultural fields or unmanaged forested wetlands. In these acidic coastal freshwater ecosystems, the conversion of agricultural fields to flooded young forested wetlands did not result in increases in greenhouse gas emissions.

Key words: carbon dioxide; denitrification; greenhouse gas; methane; nitrous oxide; North Carolina coastal plain; restoration; soil respiration; wetland.

INTRODUCTION

The extent of wetlands worldwide has been diminished by ~50% through human activities such as clearing, filling, ditching, and drainage (Millennium Ecosystem Assessment 2005). In the United States, the majority of wetland conversions occurred from the 1780s through 1980, primarily driven by agricultural expansion (Dahl 1990). About 27% of active U.S. farmland occurs on former wetland soils (Heimlich et al. 1998, Natural Resources Conservation Service 1999), and this pattern is also seen in many regions of the world (Zedler 2003). In North Carolina, 13% of the state's wetlands were drained and converted to agriculture between 1970 and 1980, particularly in the coastal plain (Dahl 1990, Heimlich et al. 1998). The loss of wetlands has impaired wetland ecosystem services, including wildlife habitat, protection from flooding, carbon (C) storage, and water quality benefits (Zedler and Kercher 2005). On regional and local scales, decreased wetland area and the resulting decreased capacity to retain nutrients in watersheds, along with increased agricultural fertilizer use, contribute to coastal eutrophication and hypoxia (Rönnberg and Bonsdorff 2004, Mitsch et al. 2005, Turner et al. 2008).

The 1989 U.S. policy known as "no net loss" promotes compensatory mitigation to offset future wetland losses through wetland restoration or creation (National Research Council 2001). Wetland restoration efforts are intended to replace habitat and improve water quality (Mitsch 2005, Verhoeven et al. 2006). Marginally productive agricultural areas in former wetlands are often candidates for restoration because of their landscape position, residual organic soils, and poorly drained status, and because economic incentives may exist to promote wetland restoration (Heimlich et al. 1998, Zedler 2003). Restoring forested wetlands in the Mississippi Alluvial Valley can provide net economic benefits to landowners, through governmental Wetlands Reserve Program payments, and to society based on the valuation of ecosystem services provided by the restored wetlands (Jenkins et al. 2010).

Wetland restoration practices in agricultural landscapes generally aim to restore ecosystem functions by re-establishing wetland hydrology and vegetation by recontouring fields, filling ditches, reconnecting wetland areas to surface waters, and planting obligate and facultative wetland species (Zedler and Kercher 2005). Quantification of ecosystem function resulting from

restoration is rarely required or attempted; proxies such as survival of planted trees and mean growing season water table depth (WTD) based on reference wetlands generally are the most commonly mandated metrics for evaluating wetland restoration (e.g., Brinson and Rheinhardt 1996, U.S. Army Corps of Engineers 1997). While wetland restoration ecology aims to predict restoration outcomes and trajectories for multiple ecosystem services (Zedler and Callaway 1999, Zedler 2000), in restoration practice, specific functional goals are rarely set, and the possibility that some ecosystem services may be promoted at the expense of others is seldom addressed (Jackson et al. 2005, Zedler and Kercher 2005). For example, the same conditions that promote nutrient removal from polluted waters may suppress biodiversity or increase greenhouse gas (GHG) emissions (Verhoeven et al. 2006, Wilcock et al. 2008). These potential trade-offs need to be identified and evaluated, so that they can be incorporated into environmental policies, if warranted.

Nutrient removal by wetlands from surface and subsurface waters through sediment deposition, organic matter accumulation, adsorption to particles, and biological uptake is well documented (Richardson 1985, Seitzinger 1988, Johnston 1991). For nitrogen (N), microbial denitrification (DNF) is the main mechanism of permanent removal, as it converts nitrate (NO_3^-) to gaseous N (dinitrogen: N_2 or nitrous oxide [N_2O]). Because it is an anaerobic heterotrophic process, DNF may be stimulated during transient wet events, such as rainstorms (Poe et al. 2003), or when wetlands are restored by re-flooding, if sufficient NO_3^- and labile C are available. It follows that when agricultural wetlands are restored, the cessation of fertilizer inputs and facilitated drainage, coupled with enhanced DNF, could result in lower hydrologic exports of reactive N (Verhoeven et al. 2006, Orr et al. 2007).

Promoting enhanced DNF is not an unequivocal environmental benefit (Schlesinger et al. 2006), since under incomplete anoxia or high NO_3^- availability, DNF can produce N_2O (Davidson et al. 2000), which is a stratospheric ozone-depleting gas with 298 times the global warming potential of carbon dioxide (CO_2, Forster et al. 2007). Agricultural lands, through N fertilization and soil emissions, are currently the largest source of N_2O to the atmosphere (Mosier et al. 1998). Although undisturbed wetlands have not been shown to be major sources of N_2O globally (Bridgham et al. 2006), there are significant concerns that wetland restoration, by combining wetland hydrology with ongoing agricultural N inputs or legacy fertilizer N, could enhance DNF and promote N_2O emissions in agricultural restored wetlands (Verhoeven et al. 2006).

Furthermore, the same flooded soils that promote DNF may also increase the production of methane (CH_4), the GHG with the greatest radiative forcing after CO_2. Emissions from wetlands represent 15–40% of global CH_4 fluxes (Bridgham et al. 2006, Forster et al.

2007). Methane (global warming potential $= 25\times CO_2$) is produced by methanogenic microbes in highly reduced soils or in anoxic microsites and is consumed by methanotrophic microbes in oxic environments. Flooded soils tend to have lower rates of soil respiration, and thus, lower CO_2 emissions from wetland soils could partially offset the increased production of N_2O and CH_4 trace gases (Raich and Schlesinger 1992, Whiting and Chanton 2001).

Our study was designed to evaluate the effect of wetland restoration on multiple ecosystem services in a 440-ha former agricultural field in coastal North Carolina, USA. Our primary objective was to compare the composition and magnitude of GHG fluxes (CO_2, N_2O, and CH_4) throughout the restored wetland with GHG fluxes from adjacent agricultural fields and undrained forested wetlands. Our second objective was to examine whether variation in hydrology across this very large restored wetland led to predictable changes in GHG fluxes. We sampled gas fluxes from 48 permanent sampling stations across the four sites once every two months from July 2007 to June 2009. We hypothesized that hydrologic setting would determine GHG fluxes both within and across the land use types, such that (1) in drier sites, GHG fluxes would be low and dominated by CO_2; (2) in sites with intermittently flooded conditions, nutrients would cycle more rapidly, thus producing more CO_2 and N_2O; and (3) in sites with more permanently flooded conditions, CH_4 would be the dominant GHG. We expected that fertilizer and legacy N would both enhance N_2O fluxes, such that (4) in the agricultural site, N_2O fluxes would be associated with fertilization; (5) that the restored wetland would have the highest annual fluxes of N_2O as a result of legacy fertilizer N and re-flooded conditions; and (6) that forested wetlands would have the highest fluxes of CH_4, based on their relatively undisturbed hydrology, organic soils, and low N inputs.

METHODS

Geographic setting and history

Our study sites are located in the Albemarle Peninsula, in the Outer Coastal Plain of North Carolina, USA (Fig. 1). There is little topographic relief, with >54% of the 5000-km² peninsula under 1 m elevation (Poulter and Halpin 2008). The Albemarle Peninsula is bounded by the Albemarle, Croatan, and Pamlico Sounds. The climate is classified as humid-subtropical, with mean annual precipitation of 1330 mm/yr and temperature of 16.6°C (State Climate Office, Raleigh, North Carolina, USA). Hydrology in this low-relief basin is driven by precipitation, evapotranspiration, and wind tides (Richardson and McCarthy 1994).

The region was historically dominated by pocosin wetlands, with deep Histosol soils, pine forests, and an understory of evergreen shrub–scrub vegetation (Richardson 2003), as well as swamp forests along blackwater creeks. Much of the landscape was logged in the 19th
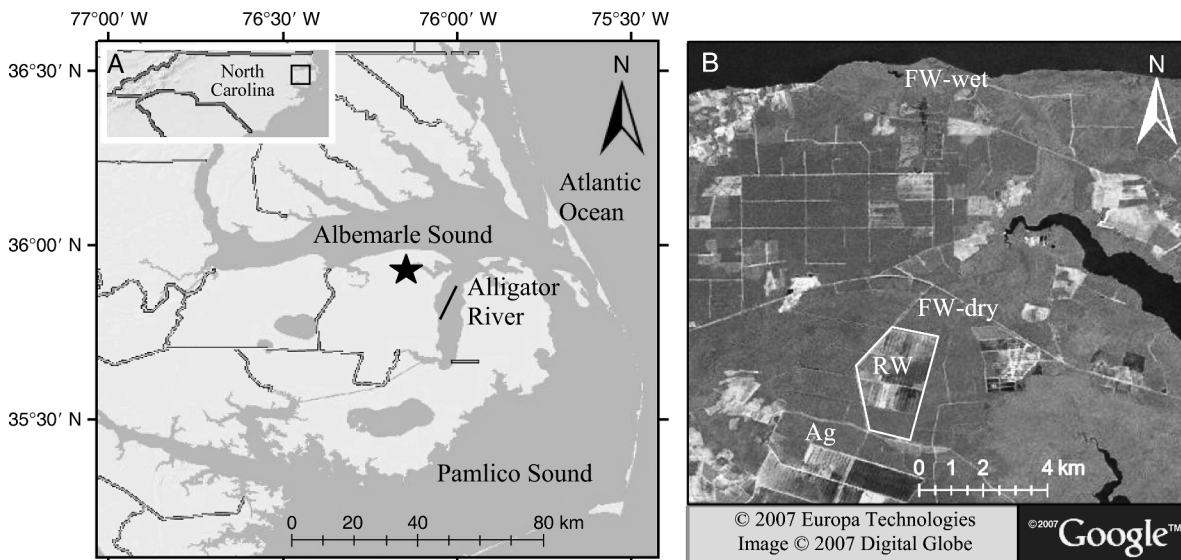
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FIG. 1. Geographic location of the study in North Carolina, USA: (A) overview (with the star indicating the area of the sampling sites) and (B) detailed view of the four sampling sites (agricultural field [Ag], restored wetland [RW], forested wetland in Timberlake Restoration Project preservation area [FW-dry], and Palmetto Peartree Preserve reference forested wetland [FW-wet]). The figure is adapted from Ardón et al. (2010b). Panel B was created using Google Earth under the fair use policy; images and data are copyrighted by Europa Technologies, Digital Globe, and Google (2007).

and 20th centuries; large-scale conversion to agriculture occurred in the 1970–1980s with the construction of large canals and drainage systems (Carter 1975). By 1979, only 9% of historical pocosins remained in the North Carolina coastal plain (Richardson 1983). Much of the Albemarle Peninsula is currently in agriculture (corn–soybean row crops), of which 80% requires active drainage to maintain arable fields (Neely 2008).

Site descriptions

The primary study location is a large compensatory mitigation site (1704 ha; 35°54′22″ N, 76°09′25″ E; Fig. 1), known as the Timberlake Restoration Project (TLRP) and owned by Great Dismal Swamp Mitigation Bank (Chesapeake, Virginia, USA). TLRP drains to the Little Alligator River, which flows into the Alligator River and Albemarle Sound. The elevation in TLRP ranges from −1 m to 2 m above sea level (lidar survey by National Center for Airborne Laser Mapping 2008, Houston, Texas, USA). The TLRP property historically was the headwaters for coastal blackwater streams, with pocosin vegetation in higher elevation areas (Needham 2006). Swamp forests in the site were cleared, drained, and converted to agriculture in the 1970s, while some areas remained forested. The TLRP property currently contains drained shrub–scrub wetlands, restored and selectively timbered forested wetlands, and former agricultural fields undergoing stream and wetland restoration. The former corn and soybean farmland within TLRP (440 ha), last harvested in 2004, is the restored wetland (RW) that is the focus of our study. Restoration of the TLRP agricultural area towards a forested wetland was initiated in 2004 by lowering the

field crowns and filling drainage ditches and then planting 750 000 live saplings. Obligate and facultative wetland tree species were planted, including *Taxodium distichum*, *Nyssa sylvatica*, *Nyssa aquatica*, *Fraxinus pennsylvanica*, *Salix nigra*, *Chamaecyparis thyoides*, *Quercus nigra*, *Quercus michauxii*, *Quercus phellos*, and *Quercus falcata var pagodifolia* (Table 1). In 2007 the former fields were hydrologically connected to both the upstream forest and downstream waters. The two dominant soil series in the RW are very poorly drained hydric soils: Ponzer muck (loamy, mixed, dysic, thermic Terric Haplosaprist) and Hyde loam (fine-silty, mixed, active, thermic Typic Umbraquult; Natural Resources Conservation Service 2009). The site and the restoration practices have been described in detail by Ardón et al. (2010a, b).

The agricultural site (Ag), cropped in a corn and soybean rotation (Table 1), is immediately adjacent to RW and is drained by a system of ditches and pumps, part of which discharges into RW. It is mainly comprised of Weeksville silt loam soils (coarse-silty, mixed, semiactive, thermic Typic Umbraquult; Natural Resources Conservation Service 2009). One of the reference sites is a preservation area (FW-dry) that was established in a minimally impacted forested wetland portion of TLRP, dominated by a mixed hardwood forest (oak–tupelo–cypress; Table 1; Needham 2006). The soils in FW-dry are mapped as Dorovan muck (dysic, thermic Typic Haplosaprist; Natural Resources Conservation Service 2009). The other reference site (FW-wet) is located 8 km away in the Palmetto Peartree Preserve (Fig. 1B), in a swamp hardwood stand of cypress and tupelo (Table 1). Soils

in FW-wet are mapped as Belhaven muck (loamy, mixed, dysic, thermic Terric Haplosaprist; Natural Resources Conservation Service 2009).

Sampling locations

Just prior to hydrologic restoration in 2007, we established two transects with 33 sampling points to capture the expected extent of the flooding gradient. We set up sampling locations ($n = 5$) within each of the three reference sites. At each sampling location, we excavated a soil profile to 50 cm depth, measuring the thickness of the surface organic horizon (where present) and the depth to the relatively impermeable mineral horizon below (except in the Ag site, where we were only able to auger to 15 cm due to soil compaction). We defined our system boundaries as the surface horizon above the mineral confining layer; in all sites, depth to this mineral horizon was at least 15 cm, and was well over 50 cm in the reference forested wetlands.

Environmental variables

Each sampling location was instrumented with five platinum-tipped redox electrodes (Vepraskas and Faulkner 2001). To monitor near-surface and surface waters, we installed slotted polyvinyl chloride (PVC) monitoring wells to just above the mineral horizon layer (or to 45 cm depth, where the mineral horizon was deeper than 45 cm), and programmed a water level recorder (Levelogger Gold or Silver, Solinst Instruments, Ontario, Canada) in each well to record pressure and temperature every 15 min. The slots extended to 10 cm above the ground surface, allowing the Leveloggers to register the pressure of overlying water even when the water table was above the ground surface. Well positions and elevations were professionally surveyed by R. Sanderson (Geodetic Services, Virginia Beach, Virginia, USA) in 2008.

At each sampling location, we collected soil samples from 0–15 cm to determine soil characteristics, including organic carbon content, pH, soil texture, and bulk density. We used a 5 cm diameter soil sampler with a slide hammer attachment (AMS, American Falls, Idaho, USA) for bulk density (BD) sampling without significant compaction in Ag and RW sites. Compaction was a problem in the FW sites; to collect intact samples, we sharpened 10 cm diameter PVC cylinders, pushed them into the soil, and carefully dug around them to remove them. Soil organic C content was determined with a Carlo Erba Elemental Analyzer (Carlo Erba, Milano, Italy). Soil pH was measured on replicate 3-g samples in 5 mL of 0.01 mol/L $CaCl_2$, which is preferable to water when soils have high C content (Hendershot et al. 1993). We extracted inorganic N from duplicate 2.5-g soil samples with 25 mL of 2 mol/L KCl, and analyzed the extracts for NH_4^+ and NO_3^- on a Lachat QuickChem 8000 automated system using the phenate method for NH_4^+ and the hydrazine reduction method for $NO_2^- +$ NO_3^- (Lachat Instruments, Milwaukee, Wisconsin, USA).

Gas flux measurements

We applied the static chamber approach (Livingston and Hutchinson 1995) to measure soil–atmosphere and water–atmosphere gas fluxes, and therefore positioned the enclosures to avoid large plants and trees. As a result, our CO_2 flux measurements do not encompass photosynthetic uptake and should be interpreted as soil fluxes. At each sampling location, we installed a soil collar (15 cm tall × 20 cm diameter PVC pipe) to a depth of ~5 cm in the soil. Chamber tops were built from opaque 20-cm molded PVC caps with gas-tight rubber gaskets by adding a 0.6 cm (one-quarter inch) Swagelok brass sampling port with rubber septum, vent tube, internal fan (0.003 m^3/s [7 cubic feet per minute]; Jameco Electronics, Belmont, California, USA) to each cap (adapted from Livingston and Hutchinson 1995 and McLain et al. 2002). Litter was not removed from inside the soil collar, but herbaceous vegetation (if present) inside the collar was clipped to 10 cm to place the chamber top on the collar. Clipping or removal of emergent wetland plants has been shown to substantially decrease methane emissions in some natural wetlands (Laanbroek 2010), but not in others (Kelker and Chanton 1997, Altor and Mitsch 2006, Laanbroek 2010). Given that trees were the dominant vegetation in all of our sites except for the agricultural field, we were constrained in our ability to enclose the vegetation in any realistic way. Our measures of soil effluxes allow comparison across sites.

Gas samples were collected once every two months from July 2007 to June 2009 ($n = 11$; November 2008 was not sampled), with all sites and sampling points visited during three consecutive sampling days. We collected 10-mL headspace samples with a glass syringe immediately following cap placement and after each of two intervals of 30–40 min. Gas samples were collected in triplicate and injected into 9-mL pre-evacuated glass vials (Teledyne Tekmar, Mason, Ohio, USA). A total of 5165 gas samples were collected during the two-year study. Air temperature, barometric pressure, and soil temperature at 5 cm were recorded at the beginning of each sampling interval. Chamber height, water depth, and redox potentials were recorded once for each location on each sampling date. Redox potentials were measured using the installed platinum redox probes, a voltmeter, and a calomel reference electrode (Fisher Scientific, Pittsburgh, Pennsylvania, USA), and values were corrected by adding 241 mV (Vepraskas and Faulkner 2001). The median value of the five redox probes was used in subsequent data analyses. Piezometers (wetter locations) and lysimeters (drier conditions) installed at a depth of 15 cm were sampled in conjunction with gas flux measurements to determine soil water chemistry. Samples were analyzed for sulfate

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TABLE 1. General soil characteristics (0–15 cm depth) of the study site in North Carolina, USA.

Site name and dominant vegetation	Group†	WTD < 10 cm (%)‡	BD (g/cm^3)	Soil organic C (%)	Soil total N (%)
Agricultural field					
Corn–soybean	Ag	<1	1.31^a ± 0.02	3.8^c ± 0.6	0.19^b ± 0.04
Timberlake Restored Wetland					
Cypress–oak–tupelo¶	RW (all)	58	0.70 ± 0.06	17.5 ± 2.4	0.67 ± 0.09
Cypress–oak–tupelo¶	RW-dry	5	0.98^{ab} ± 0.09	8.7^{bc} ± 2.3	0.37^{ab} ± 0.08
Cypress–oak–tupelo¶	RW-int	24	0.87^{ab} ± 0.14	11.8^{bc} ± 4.7	0.46^{ab} ± 0.16
Cypress–oak–tupelo¶	RW-wet	82	0.34^{bc} ± 0.06	32.2^b ± 4.8	1.11^a ± 0.14
Timberlake Preservation Area					
Oak–tupelo–cypress	FW-dry	4	0.17^{bc} ± 0.04	39.4^{ab} ± 3.4	2.27^a ± 0.32
Palmetto Peartree Preserve					
Cypress–tupelo	FW-wet	11	0.06^c ± 0.01	47.2^a ± 0.6	2.57^a ± 0.03

Note: Means (±SE) were compared for six groups (including the three RW subgroups); different letters indicate differences at $P < 0.10$. Groups are agricultural field (Ag), restored wetland (RW) with three hydrologic classes (dry, intermittent, wet), and two forested wetland sites (FW-dry, FW-wet). Abbreviations are: WTD, water table depth; and BD, bulk density.

† Five sampling points per group, except for RW (all), in which 33 were sampled.

‡ Proportion of the time during which the water table was within 10 cm of the surface.

‡ Soil water was never sufficient for sampling.

¶ Planted in 2004.

(SO_4) concentrations by ion chromatography (for an in-depth description, see Ardón et al. 2010*a*).

When surface water was above 10 cm, we used a similar approach, except that a floating PVC collar imbedded in a polystyrene platform was used to capture water–air gas exchange. For floating collar samples, water samples for determination of dissolved gas concentrations were collected in 120-mL pre-evacuated glass bottles during each incubation, and headspace equilibration techniques were used to extract a 10-mL gas sample for analysis (Hudson 2004). Water temperature and volume of the water sample were also measured.

Gas samples were analyzed for CO_2, N_2O, and CH_4 concentrations injected by a Tekmar 7050 Headspace Autosampler to a Shimadzu 17A gas chromatograph with electron capture detector (ECD) and flame ionization detector (FID; Shimadzu Scientific Instruments, Columbia, Maryland, USA), retrofitted with six-port valves and a methanizer to allow the determination of the three gases from the same sample. Ultra-high purity N_2 was used as the carrier gas, and a P5 mixture served as the make-up gas for the ECD. A Nafion tube (Perma Pure, Toms River, New Jersey, USA) and counter-current medical breathing air were used to remove water vapor from the sample stream. Samples were analyzed as soon as feasible after collection, and always within two weeks (sample holding time was determined to be at least two weeks during laboratory testing). Peak areas of samples and known standards were determined with GCsolution software version 2.3 (Shimadzu Scientific Instruments 2004) and exported to a Microsoft Access database for data storage. Gas concentrations in vials were calculated from linear regression ($r^2 > 0.95$) of concentrations of certified primary standards (Airgas, Morrisville, North Carolina,

USA) against peak areas; concentrations of field samples were obtained by averaging values from duplicate samples analyzed in the same analytical batch, unless the relative percent difference exceeded 20%, in which case the maximum value was used (assuming that a vial had leaked since field sampling).

Under ideal conditions, gases accumulate (or are consumed) linearly over time during static chamber incubations, and the slope of the concentration vs. incubation time is used to estimate the flux. Static chambers are sensitive to disturbance and chamber effects; gas fluxes can be underestimated due to chamber effects if high concentrations in the chamber limit the diffusion of gases from soil to atmosphere (Livingston and Hutchinson 1995). Therefore, we excluded incubations with elevated initial concentrations (attributed to disturbance). From replicate determinations of known standards for each gas, we calculated the minimum detectable concentration difference for each sampling date (MDCD; Yates et al. 2006, Matson et al. 2009). To estimate gas flux, the slope of the concentration vs. time line was used when $r^2 > 0.90$. When the accumulation rate was nonlinear, and the change in concentration during the first interval was greater than MDCD, we used the rate during the first interval; when a longer incubation was needed to exceed MDCD, we used the rate calculated from the initial to the final sample. Incubations in which the concentration increased significantly then decreased significantly, or vice versa, were excluded from the data set as failed incubations (see Appendix: Table A1), while incubations during which there was no detectable concentration change were set to zero. Gas concentrations (g/cm^3) were multiplied by chamber height to report flux rates by surface area.

TABLE 1.   Extended.

C:N	NH_4-N (mg N/kg)	NO_3-N (mg N/kg)	pH	Redox potential (mV)	Soil water SO_4 (mg/L)
$19.5^b \pm 0.5$	$0.698^b \pm 0.006$	$71.1^c \pm 5.07$	5.53^a	$367^a \pm 30.4$	NA§
25.0 ± 0.7	14.4 ± 5.98	54.9 ± 7.14	3.84	-1.61 ± 14.8	20.3 ± 2.1
$22.5^{ab} \pm 1.3$	$1.63^b \pm 0.854$	$49.1^c \pm 5.61$	4.40^{ab}	$89.3^b \pm 36.6$	$40.7^b \pm 7.7$
$23.5^{ab} \pm 1.6$	$4.47^b \pm 3.74$	$42.1^c \pm 4.24$	4.29^b	$5.27^b \pm 34.4$	$46.5^b \pm 8.5$
$28.7^a \pm 1.5$	$49.6^a \pm 19.7$	$22.3^c \pm 14.6$	3.75^b	$-100^c \pm 36.6$	$18.7^c \pm 3.6$
$17.2^b \pm 0.2$	$42.3^a \pm 8.85$	$171^b \pm 27.1$	4.03^b	$12.1^b \pm 19.7$	$36.6^b \pm 4.5$
$18.4^b \pm 0.2$	$36.5^a \pm 5.54$	$367^a \pm 14.4$	4.78^a	$-180^c \pm 19.8$	$156.8^a \pm 19.7$

To estimate water–atmosphere gas exchange, we determined the concentration of gases dissolved in the water samples (Hudson 2004), the gas transfer velocity using water temperature and the Bunsen coefficient for each gas (Fogg and Sangster 2003), and the change in gas concentrations in the chamber volume during the first time interval of the incubations (Conrad and Seiler 1988, MacIntyre et al. 1995).

Data analysis

Field and analytical data files were assimilated and manipulated within a relational database in Microsoft Access. Data files were extracted for flux calculations and statistical analyses using the R programming language (R Development Core Team 2009) and its RODBC package (Ripley and Lapsley 2009). In order to compare across sites for which we had differential sampling intensity, ($n = 5$ at each reference site vs. $n = 33$ in RW), we created three post hoc groupings of sampling points in RW, choosing sites with (1) the fewest missing values for GHG fluxes; and (2) daily mean water table depth (WTD), such that $n = 5$ for each group: typically dry, RW-dry (WTD < -20 cm); intermittently wetted, RW-int (WTD between -15 and -5 cm); and typically flooded, RW-wet (WTD > 10 cm).

For statistical comparisons, performing parametric tests such as ANOVA to detect group differences was not appropriate because results were not normally distributed. Instead of relying on a theoretical normal probability distribution, we used a resampling approach that essentially exchanges the group labels (Ag, RW-dry, RW-int, RW-wet, FW-dry, FW-wet) attached to observations and generates a distribution of test statistics by Monte Carlo sampling (Good 2000). Specifically, we used permutation one-way tests with adjusted P values for multiple comparisons between groups (oneway_test and Nemenyi-Damico-Wolfe-Dunn test, R package coin; Hothorn et al. 2008). This method was used to determine whether gas fluxes and soil properties differed between groups. Tests on pH data were conducted on hydrogen ion concentrations, before transforming results back to pH notation. We converted N_2O and CH_4

to CO_2 equivalents by multiplying by 298 and 25, respectively, based on the 100-year time horizon estimates in the IPCC's Fourth Assessment Report (Forster et al. 2007). To estimate cumulative annual fluxes, we calculated the areas under each curve (minimum, mean, and maximum) over the two-year period using the trapezoidal rule (trap.rule, R package Hmisc; Harrell 2009).

RESULTS

Environmental variables as potential drivers of GHG fluxes

During the two years of this study, data from air temperature loggers did not differ among sites (Fig. 2). Daily mean air temperature during the study was 16.0°C, with an overall range of $-14°$ to 41°C. Seasonal patterns in water table depth were similar across the restored (RW) and forested (FW) wetland sites, differing only in the amplitude of seasonal variation, while the water table was below our shallow leveloggers for most of the year in the agricultural site (Ag; Fig. 2). In the wetlands, water levels were low in the mid- to late-growing season, began rising during October through May, and fell again in the early summer. This pattern did not closely track air temperature trends, especially during the warming season when temperatures and water levels both tended to rise. Average daily mean soil temperatures at 15 cm were higher in the driest sites (17°C in Ag and 15°C in RW-dry) and intermittently flooded sites (14.1°C in RW-int and 12.7°C in FW-dry), compared to the two wettest sites (11.0°C in both RW-wet and FW-wet; $P < 0.001$; data not shown).

Sites within all three wetlands exhibited marked overall differences in water table depth and variation. The daily mean WTD was within 10 cm of the surface less than 1% of the time in the actively drained Ag field, 4% in FW-dry, and 11% of the time in FW-wet (Fig. 2). The 15 cm depth of wells in Ag was too shallow to record many valid measurements of WTD, as active drainage maintained low water tables for agricultural purposes (Fig. 2). The RW was much wetter overall,
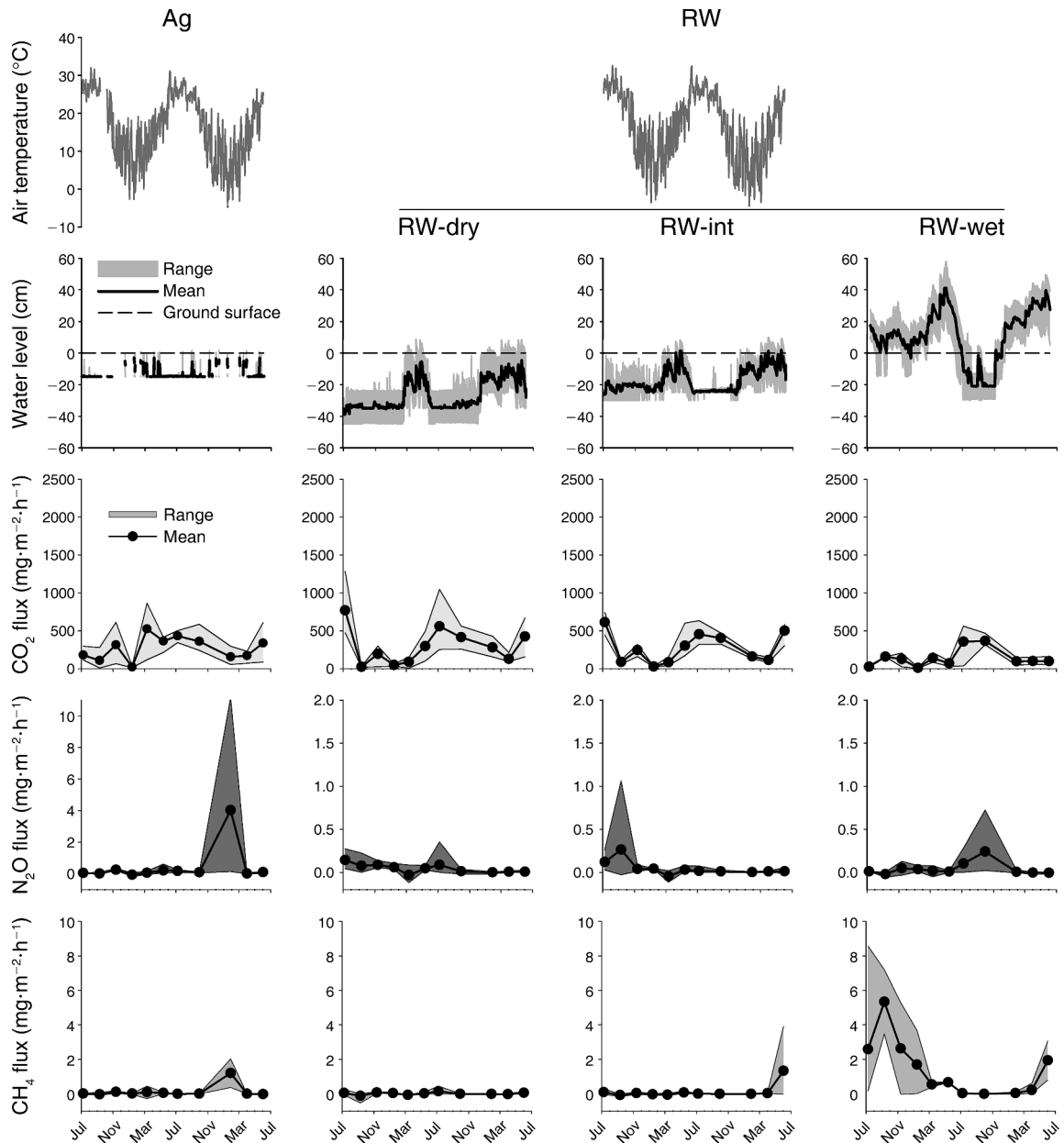
FIG. 2. Temporal and spatial patterns in environmental variables and greenhouse gas (GHG) fluxes (July 2007–June 2009) by site: agricultural field (Ag), restored wetland (RW) with three hydrologic classes (dry, intermittent, wet), and two forested wetland sites (FW-dry, FW-wet). Data are presented for air temperature, water level (daily mean and range), soil CO_2 flux, N_2O fluxes, and CH_4 fluxes.

with WTD within 10 cm of the surface 58% of the time; surface water was recorded 27% of the time. Within RW, water table was within 10 cm of the surface 5% of the time in the dry subgroup (RW-dry), 24% of the time in the intermittent subgroup (RW-int), and 82% of the time in the wet subgroup (RW-wet; Fig. 2).

We examined soil properties by group based on the three reference sites and the three hydrologic subgroups in RW. For most soil characteristics (bulk density, soil organic C, total N, KCl-extractable N, and redox

potential), the clearest differences among sites were seen between the agricultural field and the forested wetlands, with areas within the restored wetland generally in the middle along the dry-to-wet gradient (Table 1). Ag had higher bulk density ($P < 0.038$) and lower soil organic carbon ($P < 0.080$) and total N ($P < 0.010$) compared to the three wetter sites (two forested wetlands and RW-wet). Portions of the restored wetland that were rarely or intermittently flooded (RW-dry and RW-int) had statistically higher BD and lower SOC only compared
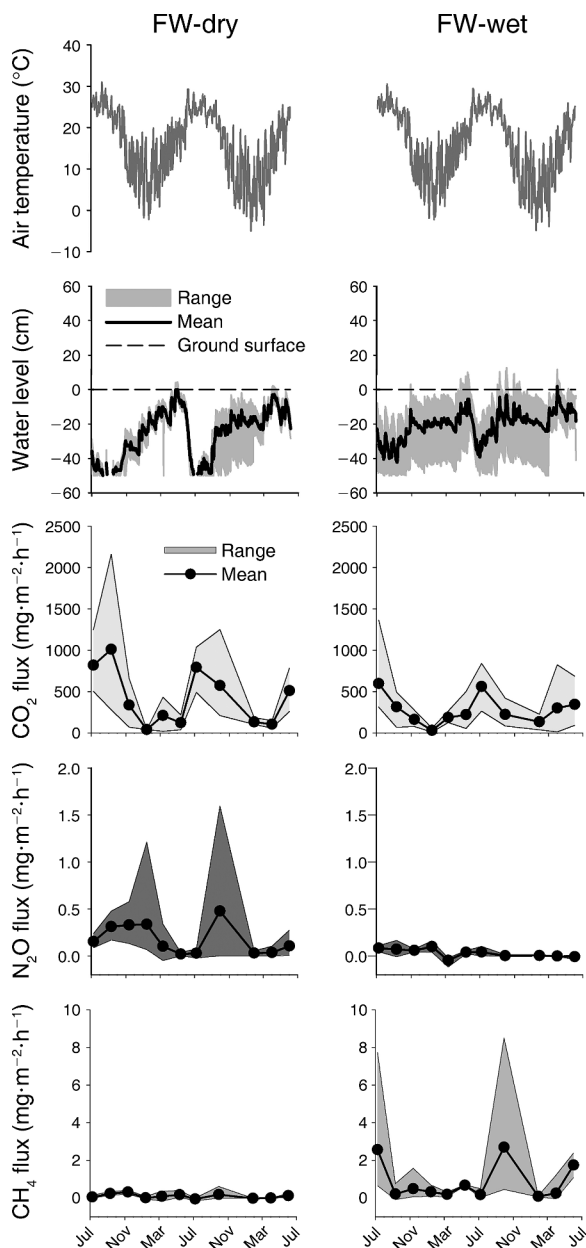
FIG. 2. Continued.

to FW-wet ($P < 0.009$ and $P < 0.032$, respectively; Table 1). KCl-extractable NH_4-N was significantly lower in the three driest sites compared to the three wettest sites (0.7 to 4.5 vs. 42.3 to 49.6 mg N/kg; $P < 0.08$; Table 1). Redox potential measurements showed three clear groupings: Ag soils were generally oxic (367 mV), the three sites with intermediate hydrology were similar (5.27–89.3 mV at RW-int, FW-dry, and RW-dry), and the two wettest sites had reducing environments (−100 and −180 at RW-wet and FW-dry, respectively; Table 1).

Soil variables that did not follow the dry-to-wet gradient were soil C:N, soil pH, and KCl-extractable

NO_3^-. Soil C:N ratios were highest in the typically flooded portions of the restored wetland (28.7 in RW-wet), compared to the three reference sites (17.2 to 19.5; $P < 0.07$). The Ag and FW-wet sites had higher pH than RW-wet, FW-dry, and RW-int sites (5.53 and 4.78 vs. 3.75 to 4.29; $P < 0.096$). The two forested wetlands were significantly higher than the other sites in KCl-extractable NO_3-N ($P < 0.001$; Table 1). Over the entire sampling period, mean SO_4 concentrations in soil solution were highest in FW-wet (156.8 mg/L; $P < 0.001$), while in FW-dry and RW values ranged from 18.7 to 46.5 mg/L (Table 1). Efforts to produce simple multiple linear regressions to explain GHG flux based on environmental variables across all observations were unsuccessful.

Greenhouse gas fluxes: temporal and spatial patterns

Soil CO_2 fluxes were strongly seasonal throughout the RW sites and the adjacent forested wetland (FW-dry), with high measured rates during the warmest months (maximum at FW-dry in September 2007; 2160 mg $CO_2 \cdot m^{-2} \cdot h^{-1}$) and very low rates during the coldest months (<20 mg $CO_2 \cdot m^{-2} \cdot h^{-1}$). In contrast, soil CO_2 fluxes measured in the Ag site were generally lower and did not track changes in temperature (Fig. 2). Mean soil CO_2 fluxes were not statistically different between Ag, RW-dry, RW-int, FW-dry, and FW-wet, ranging from 290 mg $CO_2 \cdot m^{-2} \cdot h^{-1}$ in Ag to 472 mg $CO_2 \cdot m^{-2} \cdot h^{-1}$ in FW-dry (Fig. 3; Appendix: Table A1), but were significantly lower in RW-wet (150 mg $CO_2 \cdot m^{-2} \cdot h^{-1}$; $P < 0.046$) compared to all other sites.

Soil N_2O fluxes were also seasonal throughout the restored wetland and adjacent forested wetland (RW and FW-dry); however, the magnitude of these seasonal changes in the restored wetland and forested wetlands was dwarfed by very high fluxes measured in the Ag site in January 2009 (11.2 mg $N_2O \cdot m^{-2} \cdot h^{-1}$; Fig. 2). N_2O fluxes in FW-wet were uniformly low throughout the study period. Mean N_2O fluxes were very low across the three RW groups and FW-wet (0.030–0.065 mg $N_2O \cdot m^{-2} \cdot h^{-1}$; $P < 0.027$), while the highest average N_2O flux, as well as the greatest temporal variation in N_2O fluxes, were measured in the Ag site (0.46 ± 0.27 mg $N_2O \cdot m^{-2} \cdot h^{-1}$; Fig. 3B; Appendix: Table A1).

Methane fluxes were occasionally high, and highly variable over time, in both RW and FW-wet, with high fluxes measured during warm months (8.50 and 8.58 mg $CH_4 \cdot m^{-2} \cdot h^{-1}$; Fig. 2). This pattern was not consistent across all sites, nor in all warm months; for example, the largest CH_4 fluxes in the Ag site were measured in January 2009, while CH_4 fluxes in FW-dry were consistently low (Fig. 2). Mean CH_4 fluxes differed across the sites, with significantly higher fluxes at the two wettest sites (FW-wet and RW-wet) compared to the other sites (0.94 and 1.2 mg $CH_4 \cdot m^{-2} \cdot h^{-1}$, respectively; $P < 0.012$; Fig. 3C; Appendix: Table A1).

Soil CO_2 fluxes tended to show similar qualitative changes between dates across all sites (Fig. 2). In
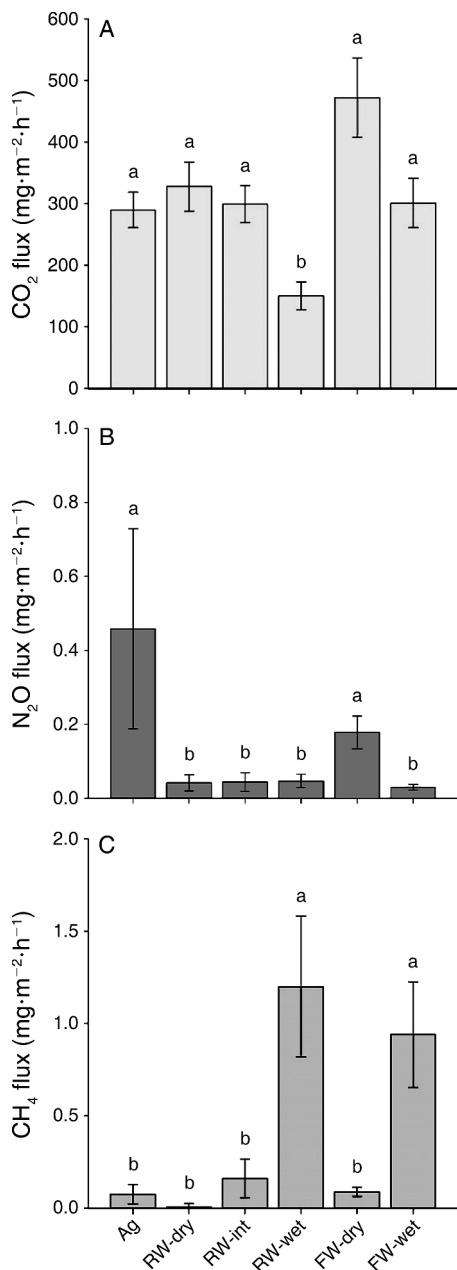
FIG. 3.   Mean ($\pm$SE) greenhouse gas (GHG) fluxes over two years by site: agricultural field (Ag), restored wetland (RW) with three hydrologic classes (dry, intermittent, wet), and two forested wetland sites (FW-dry, FW-wet). (A) soil CO_2 flux, (B) N_2O fluxes, and (C) CH_4 fluxes. Different letters indicate statistical differences between sites ($P < 0.1$).

contrast, the highest and lowest fluxes of N_2O and CH_4 did not occur on the same sampling date across sites (Fig. 2). Within the Ag site, temporal variability was very high and driven by observations in January 2009, when the range of measured N_2O fluxes was over 10 times larger than the range of values measured there during the rest of the study (Fig. 2).

Greenhouse gas fluxes: cumulative annual fluxes

We integrated the curves describing variation in the minimum, mean, and maximum GHG fluxes measured on each sampling date to estimate annual fluxes for each gas at each of the six sites (Fig. 2; Appendix: Table A2). We used the ratio of the range to the mean (Levins and Lopez 1999) of the annual fluxes to describe the variability of our estimates. We found that the overall range to mean ratio for CO_2 was 150%, compared to 450% for N_2O and 557% for CH_4, and that the variability for CO_2 and N_2O was more consistent across sites than it was for CH_4 (Appendix: Table A2). The variability of cumulative CO_2 flux ranged from 62% to 110% within the restored wetland, while in the reference sites the variability of cumulative CO_2 fluxes ranged from 110% to 155%. The pattern of variability in estimated cumulative fluxes was reversed for N_2O and CH_4: Variability was greater within the restored wetland than in the reference sites (N_2O, 302–378% in RW vs. 224–264% in reference sites; CH_4: 145–2740% in RW vs. 192–248% in reference sites; Appendix: Table A2).

The flooded portions of the restored wetland had low CO_2 fluxes (1.3×10^4 kg $CO_2 \cdot ha^{-1} \cdot yr^{-1}$), while the adjacent forested wetland (FW-dry) had three times higher cumulative soil CO_2 flux (4.3×10^4 kg $CO_2 \cdot ha^{-1} \cdot yr^{-1}$). High cumulative N_2O fluxes were measured in the agricultural field (51 kg $N_2O \cdot ha^{-1} \cdot yr^{-1}$), with the cumulative mean estimate strongly driven by fluxes measured on a single date (Appendix: Table A2). The adjacent forested wetland (FW-dry) also had high cumulative N_2O fluxes, due to more consistent elevated N_2O fluxes (16.2 kg $N_2O \cdot ha^{-1} \cdot yr^{-1}$). In contrast, all three hydrologic subgroups within the restored wetland had low mean annual N_2O fluxes (3.37–4.52 kg $N_2O \cdot ha^{-1} \cdot yr^{-1}$; Appendix: Table A2). Relatively high CH_4 mean annual fluxes were calculated for the two wettest sites (the flooded portions of the restored wetland [RW-wet] and the more frequently inundated forested wetland [FW-wet]) as 107 and 71.6 kg $CH_4 \cdot ha^{-1} \cdot yr^{-1}$ (respectively), while values from the other sites were much lower (0.53–14.3 kg $CH_4 \cdot ha^{-1} \cdot yr^{-1}$; Appendix: Table A2).

We converted mean annual rates of N_2O and CH_4 emissions into CO_2 equivalents to compare their cumulative contributions to global radiative balance (Fig. 4A; Bridgham et al. 2006). For all groups, the main component of GHG fluxes was soil CO_2 flux. The FW-dry site had relatively high radiative balance overall (527 mg CO_2 equivalents$\cdot m^{-2} \cdot h^{-1}$), but was only statistically distinguishable from RW-wet ($P = 0.037$; Fig. 4A). Because we estimated net fluxes of N_2O and CH_4, but not of CO_2 (photosynthesis was not measured), we also show the comparison of CO_2 equivalents for N_2O and CH_4 only (Fig. 4B). In this scenario, N_2O is the most important contributor to the radiative balance, except in FW-wet and RW-wet, in which CH_4 was the largest source. Based on N_2O and CH_4, the two drier hydrologic classes in RW are statistically lower in CO_2

equivalents compared to Ag, FW-dry, and FW-wet ($P <$ 0.01; Fig. 4B).

DISCUSSION

GHG fluxes as a function of land use and environmental variables

Our primary motivation for this research effort was to determine whether reinstating wetland hydrology in former agricultural fields would result in enhanced production of N_2O and CH_4 (as suggested by Verhoeven et al. 2006). We found that N_2O fluxes were lower across this restored forested wetland than in nearby managed agricultural fields and one of two unmanaged forested wetlands. Methane emissions were enhanced in permanently flooded areas of the restored wetland; however, in the flooded soils (RW-wet and FW-wet) where CH_4 fluxes were highest, soil respiration was low enough that differences in total GHG emissions (CO_2, N_2O, and CH_4) were not significantly different among the contrasting land uses (agriculture, restored wetland, forested wetland; Fig. 4A).

Since we did not estimate rates of photosynthesis, our CO_2 fluxes cannot be considered net ecosystem fluxes. Soil CO_2 fluxes have been shown to be negatively correlated with aboveground biomass (Tyree et al. 2006), so the restored wetland's long-term potential as a CO_2 sink is strong, given that our CO_2 flux estimates included root respiration. In the southeast United States, young oak–gum–cypress stands are estimated to accumulate live biomass at a mean rate of 1.78×10^3 kg C·ha^{-1}·yr^{-1} in the first 50 years of establishment (Smith et al. 2006). Since this restored wetland is a young, aggrading forest, compared to the conventionally managed Ag site and the two mature forested wetlands (FW-dry and FW-wet), the restored wetland undoubtedly represents a stronger CO_2 sink in soils and plant biomass (Odum 1969, Pregitzer and Euskirchen 2004, Peng et al. 2008). Furthermore, if we only consider N_2O and CH_4 fluxes, the drier areas of the restored wetland produced significantly less trace gas CO_2 equivalents than either the agricultural field or the forested wetlands (Fig. 4B). Collectively, this evidence would support the idea that the restored wetland did not have higher overall GHG fluxes compared to the reference sites.

We had expected that soil respiration in both reference forested wetlands would be lower than in the Ag site, as is typically the case for reducing environments (Schlesinger 1997, Peng et al. 2008), but we found no differences. A drought during the first year of the study period likely suppressed soil respiration in the drier Ag soils and increased soil respiration in the reference forested wetlands, but patterns were not markedly different in the second year, when precipitation patterns were closer to normal (Fig. 2).

We had expected to find relatively higher N_2O emissions in intermittently flooded sites, resulting from enhanced decomposition and N mineralization, which in
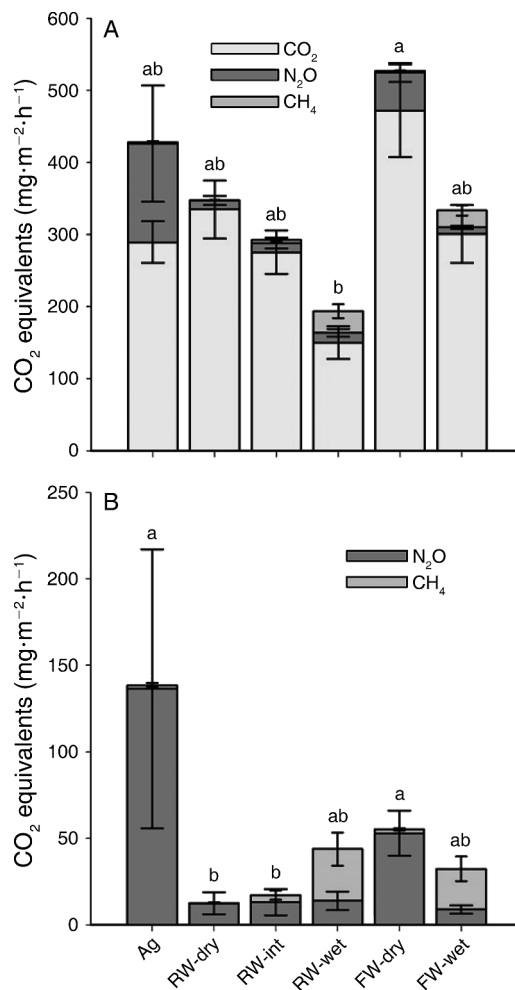

FIG. 4. CO_2 equivalents (two-year means) by site: agricultural field (Ag), restored wetland (RW) with three hydrologic classes (dry, intermittent, wet), and two forested wetland sites (FW-dry, FW-wet). (A) Soil respiration (CO_2) + 298× N_2O + 25× CH_4; (B) N_2O and CH_4 only. Different letters indicate statistical differences between sites ($P < 0.1$).

turn would stimulate nitrification and denitrification while suppressing methanogenesis (Reddy and Patrick 1984, Hernandez and Mitsch 2006). We observed this pattern in the drier of the two forested wetlands (FW-dry), but not within the restored wetland, where fluxes of N_2O were low regardless of flooding dynamics. Indeed, the highest N_2O fluxes were measured in the Ag site, which had the driest soil conditions, suggesting that hydrological regime was not the only driver (Fig. 2).

Correlations between denitrification and a number of environmental factors are well described, including soil redox potential (optimal at 200 mV) and soil C:N ratio (low C:N can promote denitrification; Hume et al. 2002, 2007). Based on mean redox potentials of the bulk soil in the intermittently flooded forested wetland (FW-dry; 12 mV) and in the rarely and intermittently flooded portions of the restored wetland (RW-dry and RW-int;

89 and 5.3 mV, respectively), we would expect that denitrification would be a dominant process in those sites, representing an important source of N_2O (Megonigal et al. 2004). Of those three sites, soils in FW-dry had much higher N availability compared to RW-dry and RW-int (based on low soil C:N and KCl-extractable N concentrations; Table 1), which is consistent with the high N_2O fluxes measured in that site. Nitrification, an aerobic chemolithotrophic microbial process that converts NH_4^+ to NO_3^-, is another N_2O-generating process that may be significant in sites with intermittent hydrology. Although nitrification is generally thought to be less important than denitrification in contributing to N_2O fluxes from wetlands (Davidson et al. 2000), it can be a substantial pathway for N_2O flux in acid-organic wetland soils (De Boer and Kowalchuk 2001, Morse 2010).

In the agricultural site, human manipulations (efficient drainage and fertilization), rather than intermittent flooding, were the likely cause of high N_2O fluxes we measured there. Soils in the Ag site were very oxic (Table 1), resulting from a system of vee-ditches, canals, and pumps for drainage that maintained the water table >1 m below the soil surface. In the absence of intermittent flooding, and with low soil organic matter, the stimulation of nitrification and denitrification of mineralized N from soil organic matter that would be expected from intermittent flooding was less likely in this site.

The very high measured N_2O fluxes in January 2009 suggested that N fertilization might be involved. Based on personal communication with the farm manager, we learned that the Ag site was generally fertilized in early winter (December/January) and early spring (March), in advance of that year's corn crop. Water samples collected from the farm's drainage canal during January 2009 had mean NO_3-N concentrations two orders of magnitude higher than what was measured in May–November 2008 (1.68 vs. 0.052 mg NO_3-N/L; Ardón et al. 2010b). Other periods of high NO_3^- concentrations in Ag drainage water did occur during our study, but were not associated with high N_2O fluxes, perhaps due to lags in gas sampling following fertilization, differences in soil moisture and temperature that might have suppressed N_2O fluxes, or different fertilization practices for other crops. Because temperatures were around 8°C during the week prior to and the day of sampling in January 2009, it is unlikely that the high N_2O flux was the result of freeze–thawing, a pathway that has been shown to be important for northern forests in winter and spring (Papen and Butterbach-Bahl 1999, Groffman et al. 2009, Eberling et al. 2010). This N_2O pulse was not seen in our other sites on this date, supporting this conclusion.

Our hypotheses for CH_4 were that continuously flooded sites would have the highest fluxes; according to our soil redox measurements, methanogenesis (optimal at −400mV; Megonigal et al. 2004) would be likely to dominate in the wetter forested wetland (FW-wet)

and the flooded portions of the restored wetland (RW-wet; mean of −180 mV and −100 mV, respectively). We did find that CH_4 fluxes were highest in these two sites. In the Ag site, the highest CH_4 flux was also measured during January 2009, which could be the result of wetter soils or reduced CH_4 consumption with higher N availability: NH_4^+ can suppress CH_4 consumption by CH_4 oxidizers, while NO_3^- can raise the redox potential of soils (Le Mer and Roger 2001, Liu and Greaver 2009).

While sulfate in soil or surface water is another factor that can suppress methanogenesis, because sulfate reduction is more thermodynamically favorable than methanogenesis (Megonigal et al. 2004), the presence of sulfate is unlikely to have limited CH_4 production in the drier sites. In the more flooded areas, sulfate concentrations were clearly not high enough to suppress CH_4 production altogether, as is commonly seen in brackish waters (e.g., Neubauer et al. 2005). For 97% of our CH_4 flux measurements, water tables were too low to be sampled or sulfate concentrations were below 100 ppm. When no soil water could be sampled (79% of CH_4 observations), CH_4 fluxes averaged 215 ± 3.0 $\mu g \cdot m^{-2} \cdot h^{-1}$.(means $\pm$ SE) When SO_4 concentrations were below 100 ppm, mean CH_4 flux was 850 ± 29 $\mu g \cdot m^{-2} \cdot h^{-1}$, while when SO_4 concentrations were above 100 ppm (3% of the CH_4 data set), mean CH_4 flux was somewhat lower (515 ± 62 $\mu g \cdot m^{-2} \cdot h^{-1}$). This suggests that, while CH_4 flux in wetter sites may be periodically depressed by the availability of sulfate for anaerobes during saltwater intrusion or drought-induced concentration of SO_4 (M. Ardón, J. L. Morse, and E. S. Bernhardt, unpublished manuscript), this factor did not dominate our CH_4 flux estimates (Table 1).

GHG fluxes in context

Our study is one of the first to estimate soil fluxes of CO_2, CH_4, and N_2O in the southeast USA, and additionally provides a perspective on wetland restoration. While this restored wetland (440 ha) is one of the largest wetland restoration projects in the eastern USA, it represents only 0.4% of the total land area of organic soils converted to drained agriculture in North Carolina alone (92 000 ha; C. J. Richardson, *personal communication*). The opportunity for large-scale wetland restoration in similar coastal plain agricultural lands on former wetlands in North Carolina and other states in the southeast USA is therefore extensive. To put our results in context, we compiled a selection of published studies of GHG fluxes, ranging from northern peatlands and constructed wetlands to tropical forests and agricultural fields; we found few studies that report flux estimates for all three biogenic greenhouse gases (Table 2). We found no clear pattern of GHG flux by latitude, ecosystem, or land use.

Given this context, our CH_4 flux rates (mean of 0.53–107 kg·ha^{-1}·yr^{-1}; Appendix: Table A2) are especially low for wetlands, compared to the overall mean of 1030

kg·ha^{-1}·yr^{-1}. The highest annual estimate of CH$_4$ flux in our study was in RW-wet, with 259 kg·ha^{-1}·yr^{-1}, still far below the mean CH$_4$ flux. While we may have underestimated CH$_4$ fluxes in permanently flooded areas by not specifically measuring ebullition fluxes (MacIntyre et al. 1995), even doubling our estimates would still result in relatively low fluxes. Factors that can suppress CH$_4$ flux to the atmosphere include (1) lack of reducing conditions in soils (lower CH$_4$ production); (2) CH$_4$ consumption in oxic surface soils; and (3) low substrate availability for methanogens (Bridgham and Richardson 1992, Megonigal et al. 2004). The first two factors are most likely to apply to the restored wetland, in which areas with saturated soils might be less reducing (due to more mineral soils with larger pools of reducible iron [Ardón et al. 2010a] or due to high sulfate concentrations [another competing electron acceptor; Megonigal et al. 2004, Neubauer et al. 2005]) and areas with unsaturated surface soils could oxidize CH$_4$ (Le Mer and Roger 2001).

Compiled values for N$_2$O fluxes from natural wetlands and other undisturbed ecosystems were relatively low (0–16 kg·ha^{-1}·yr^{-1}, except for a Louisiana swamp with 85.6 kg·ha^{-1}·yr^{-1}) compared to the restored and forested wetlands in our study (5.90 and 8.35 kg·ha^{-1}·yr^{-1}, respectively; Table 2). Elevated values were reported in nutrient-rich systems such as constructed wetlands, rice paddies, and especially in agricultural watersheds (up to 946 kg·ha^{-1}·yr^{-1}; Table 2). Hydrologic status and N availability in our study sites together could explain high N$_2$O fluxes and low CH$_4$ fluxes in our study relative to natural wetlands, through intermittent flooding that could increase aeration and greater N mineralization in soils, which would promote N$_2$O production from nitrification and denitrification, while lowering net CH$_4$ emissions (Reddy and Patrick 1984, Davidson et al. 2000).

We can also view our N$_2$O flux estimates in the context of other N fluxes we have measured in TLRP. We measured N inputs from wet deposition during the study period of 6.45 kg N·ha^{-1}·yr^{-1}; Ardón et al. 2010b); with a mean estimated N$_2$O-N flux across the RW of 2.43 kg N·ha^{-1}·yr^{-1}, this yields an emission factor of 0.38 in RW. However, if we assume a typical N$_2$O mole fraction (N$_2$O-N/[N$_2$O-N + N$_2$-N]) reported for denitrification in freshwater wetlands and agricultural fields (0.08–0.37; Schlesinger 2009), our estimated N-gas fluxes (6.57–30.4 kg N·ha^{-1}·yr^{-1}) would be up to 4.7 times higher than atmospheric N inputs. Assuming our estimates of N-gas flux and atmospheric N deposition are reasonably accurate, this would imply that (1) there is excess N available in RW soils (despite lower inorganic N pools in the restored wetland compared to the other sites), either from legacy N fertilizers or N mineralization of soil organic matter; (2) N fixation is contributing substantially to the N budget of TLRP; or (3) surface water N inputs are fueling denitrification. Results from water monitoring show that NO$_3$-N inputs

to the site in surface water (mean of 126.5 kg N/yr) exceed NO$_3$-N outputs in surface water (mean of 29.9 kg N/yr; Ardón et al. 2010b). While denitrification is likely to contribute to this observed NO$_3$-N retention for the site, it would account for only 0.22 kg N·ha^{-1}·yr^{-1} of our estimated N-gas emissions, which suggests that contributions from N fixation or soil N pools must be substantial.

Implications for restoration

The large extent (440 ha) and hydrologic variability of TLRP are not typical of conventional restored wetlands, which tend to be much smaller in area (Wagner et al. 2008). The extent of TLRP, along with its hydrologic regime (driven by precipitation and evapotranspiration) and low relief, allowed us to identify patterns of GHG fluxes within the RW that were associated with hydrological variables. Such relationships could help us understand the consequences of restoration for the many similar low-lying forested wetlands and peatlands in the Mid-Atlantic region that were converted to drained agriculture (Carter 1975, Dahl 1990), including at least 92 000 ha in coastal North Carolina, and lands surrounding the Chesapeake Bay.

Forested wetlands and peatlands commonly feature acidic soils, and this acidity in TLRP persisted despite 20–30 years of agriculture that included liming, among other management practices (R. Needham, *personal communication*). Although we expected to find large pools of legacy N two years after the last crop harvest, based on fertilization history, we found lower soil N content in the restored wetland compared to forested wetland reference sites. If soil N pools and N$_2$O fluxes in the restored wetland were enhanced by fertilizer-derived N, it is possible that these pools were depleted during the major soil movement to recontour the site and fill drainage ditches, or within the initial two years following cessation of farming.

Contemporary elevated N inputs to TLRP are therefore external to the system. Based on other work at we conducted at TLRP (Ardón et al. 2010b), inputs of N to the restored wetland from surface water, rain, and drainage from the Ag site are equal parts NH$_4$-N, NO$_3$-N, and dissolved organic N. The restored wetland retained 70% of total N inputs (retaining 98% of NO$_3$-N and 25% of NH$_4$-N), while acting as a net source of dissolved organic N. The dominance of NH$_4$-N over NO$_3$-N suggests that denitrification rates are high enough to remove available NO$_3^-$ and that nitrification could be limited by high acidity or by high organic C (Davidsson and Stahl 2000). In other work at TLRP, we have found that soil denitrification potential is relatively low compared to other wetlands (Reddy and Delaune 2008, Morse 2010), which suggests that nitrification could be a major determinant of denitrification by limiting NO$_3^-$ supply. The role of nitrification in controlling denitrification rates in restored wetlands is not frequently discussed when considering the impor-

TABLE 2. Reported non-CO_2 greenhouse gas (GHG) fluxes (N_2O and CH_4) and CO_2 equivalents for selected freshwater wetlands (WL), forests, and agricultural systems, by approximate latitude and land use (A, agricultural; D, drained; R, restored; U, unmanaged).

Source	Ecosystem	Latitude (°)	Land use	N_2O (kg·ha^{-1}·yr^{-1})	CH_4 (kg·ha^{-1}·yr^{-1})	CO_2 equivalents (kg·ha^{-1}·yr^{-1})
Zona et al. (2009)	boreal peatland, tundra	71	D	⋯	0–175	⋯
Liikanen et al. (2009)	temperate marshes, Baltic Sea	64	U	−0.1 to 0.24	631 to 883	15800 to 22100
Sovik and Klove (2007)	temperate constructed WL, Norway	59	R	−2.81 to 631	−5.84 to 9250	−984 to 419 000
Mander et al. (2008)	temperate constructed WL, Estonia	58	DR	7.46 to 23.5	6.81 to 204	2390 to 12100
Dinsmore et al. (2009)	temperate peat bog, Scotland	56	U	0.01	1.41	38.3
Stadmark and Leonardson (2005)	temperate constructed WL, Sweden	55	R	0	70.1 to 6310	79 700
Matson et al. (2009)	boreal forests, Canada	53	U	0	−0.63	−15.8
Hefting et al. (2003)	temperate riparian forest, Netherlands	52	A	31.43	⋯	⋯
Hefting et al. (2003)	temperate riparian grass, Netherlands	52	A	1.57 to 3.14	⋯	⋯
Hendriks et al. (2007)	temperate peatlands, Netherlands	52	ADR	−13.8 to 13.8	145 to 689	−479 to 21 300
Freeman et al. (1993)	temperate peat monolith, Wales	51	AD	0.4 to 4.16	164 to 2190	4230 to 56000
Brumme et al. (1999)	temperate forested WL, Germany	50	U	0.19 to 1.04	⋯	⋯
Schmidt et al. (1988)	temperate forests, Germany	50	U	0.41 to 1.51	⋯	⋯
Brumme et al. (1999)	temperate forest, Germany	49	U	11.47	⋯	⋯
Butterbach-Bahl et al. (2002)	temperate forests, Germany	48	U	1.54 to 10.1	⋯	⋯
Oorts et al. (2007)	temperate croplands, conventional, corn/soy, France	48	A	1.02 to 1.49	⋯	⋯
Oorts et al. (2007)	temperate croplands, no-till, corn/soy, France	48	A	1.26 to 2.89	⋯	⋯
Gleason et al. (2009)	temperate croplands, North Dakota, USA	47	AD	0.46 to 7.51	−1.17 to 1310	108 to 35100
Gleason et al. (2009)	temperate wet meadow, North Dakota, USA	47	ADR	0.17 to 9.46	−6.18 to 1080	−103 to 29 900
Brumme et al. (1999)	temperate pine forest, Wisconsin, USA	44	U	1.56	⋯	⋯
Altor and Mitsch (2006)	temperate riparian marshes, Ohio, USA	40	R	⋯	307 to 934	⋯
Altor and Mitsch (2008)	riparian mesocosms, Ohio, USA	40	R	⋯	48.5 to 91.7	⋯
Hernandez and Mitsch (2006)	riparian marshes, Ohio, USA	40	R	0.31 to 0.95	⋯	⋯
Mosier et al. (1986)	croplands, barley/corn, Colorado, USA	39	A	34.4 to103	⋯	⋯
Rolston et al. (1978)	croplands, ryegrass, California, USA	38	A	57.4 to 1840	⋯	⋯
This study	cropland, corn/soy, North Carolina, USA	36	AD	3.0 to 139	−0.65 to 28.0	910 to 42100
This study	forested wetlands, North Carolina, USA	36	U	−1.1 to 14.1	−6.9 to 194	−500 to 9050
This study	restored agricultural wetland, North Carolina, USA	36	ADR	−0.2 to 44	0.7 to 197	−42.1 to 18 000
Pulliam (1993)	forested wetland, Georgia, USA	32	U	⋯	228	⋯
Zou et al. (2005)	subtropical rice paddies, China	32	AD	0.17 to 51.4	124 to 907	3140 to 38000
Xiong et al. (2007)	subtropical rice paddies, China	31	AD	16.9 to 21.2	0 to 11100	5030 to 284000
Yu et al. 2008)	subtropical forested wetland, Louisiana, USA	31	U	−2.19 to 173	−2.63 to 249	−718 to 114 000
Liu et al. (2008)	subtropical plantations, China	22	A	4.76 to 13.6	−3.48 to −3.43	⋯

TABLE 2. Continued.

Source	Ecosystem	Latitude (°)	Land use	N$_2$O (kg·ha^{-1}·yr^{-1})	CH$_4$ (kg·ha^{-1}·yr^{-1})	CO$_2$ equivalents (kg·ha^{-1}·yr^{-1})
Brumme et al. (1999)	tropical wet forest, Brazil	10	U	9.27	⋯	1330 to 3960
Brumme et al. (1999)	tropical wet forest, Brazil	−3	U	2.99	⋯	⋯
Bartlett et al. (1988)	tropical forested WL, Amazon	−3	U	⋯	603 to 799	⋯
Livingston et al. (1988)	tropical forests, Amazon	−10	U	1.79	⋯	⋯
Brumme et al. (1999)	tropical wet forest, Costa Rica	−15	U	3.82	⋯	⋯
Weier et al. (1996)	croplands, sugarcane, Australia	−19	A	34.4 to 516	⋯	⋯

Note: Ellipses indicate that no data was available.

tance of denitrification to wetland restoration and ecosystem services (e.g., Schlesinger et al. 2006, Verhoeven et al. 2006), yet it is likely to be an important constraint on the ability of acidic wetlands to provide water quality benefits and an important determinant of N$_2$O fluxes (Reddy and Patrick 1984).

Conclusions

Over the two years of our study, when considering the net radiative balance of the three GHGs, we found that CO$_2$ was the largest component (66–100% of total GHGs) and did not differ between land uses in our study. This is an important reminder that soil respiration must be accounted for when drawing conclusions about the GHG consequences of converting wetlands to farmlands or vice-versa (contra Huang et al. 2010). If we exclude soil CO$_2$ flux, the wet portions of the restored wetland were greater sources of GHG, but not higher than the reference sites, while drier and intermittent areas within RW were significantly lower. Restoring wetland hydrology to TLRP has led to significant NO$_3$ retention or removal (Ardón et al. 2010b), but does not appear to have significantly increased GHG emissions (contra Verhoeven et al. 2006). This conclusion has been reached in a few other studies in constructed wetlands in Estonia (Mander et al. 2005) and restored prairie wetlands in South Dakota (Gleason et al. 2009). The current study, by presenting data for acidic coastal freshwater wetlands in a humid-subtropical climate, provides a regional and biogeochemical perspective that has not been presented to date.

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SUPPLEMENTAL MATERIAL

Appendix

Tables summarizing greenhouse gas flux statistics and cumulative annual fluxes for each study site from July 2007 to June 2009 (*Ecological Archives* A022-017-A1).