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CARBON DYNAMICS IN A *PHRAGMITES AUSTRALIS* INVADED RIPARIAN
WETLAND

by

Steven G. Walters

A THESIS

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CARBON DYNAMICS IN A *PHRAGMITES AUSTRALIS* INVADED RIPARIAN
WETLAND

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University of Nebraska, 2010

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Invasive plant species are widely recognized as a major threat to biodiversity and
ecosystem stability. Wetland ecosystems tend to be much more susceptible to invasions
because of their location on the landscape where water, nutrients, and the impacts of
disturbances accumulate. Invasive plants have the ability to alter ecosystem processes and
community/population dynamics. The ability of invasive plants to alter these processes
can have profound economic consequences. In the United States, control of invasive
wetland species alone costs approximately 155 million dollars annually. The state of
Nebraska spends 2 million dollars annually controlling invasive plant species in the Platte
River and Republican River basins with *Phragmites australis* being the main focus of
these efforts. *P. australis* can alter ecosystem processes, such as biogeochemical cycling
through its aggressive growth strategy. Our objective was to quantify the effects the *P.
australis* invasion has on biogechemical cycling, specifically the carbon cycle, within an
invaded freshwater, riparian wetland in the Great Plains (Republican River Basin, NE).

This study used a dynamic closed chamber approach to measure carbon dioxide
(CO_2) fluxes and production, and a static chamber to quantify methane (CH_4) emissions.
Measurements were taken 5 times throughout the growing season of 2009 at peak gross
primary production in open water, native vegetation (*Scirpus sp.*), and *P. australis*
habitats. Average rates of net ecosystem exchange of carbon (NEE) were 53 ± 93, 258 ±

186, and 920 ± 752 mg C m^{-2} hr^{-1} for open water, *Scirpus sp.*, and *P. australis* habitats respectively. The study found *P. australis* significantly increased NEE ($F_{8,44} = 11.96$; p <0.001), while methanogenesis was not significantly altered. The invasion of *P. australis* increased aboveground biomass to 5394 ± 1815 g m^{-2} from 564.2 ± 139.2 g m^{-2} in native habitats. The ability of *P. australis* to increase NEE and biomass productions compared to native species at our wetland site results in an increase in carbon sequestration and a decrease in global warming potentials.

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1. Introduction

Over the past ~20 years invasive plant species have been well studied in ecosystems throughout the world including but not limited to wetlands, grasslands, and forests (Vitousek et al. 1987; Belcher and Wilson 1989; Whisenant 1990; Billings 1994; Blossey and Notzold 1995; Lesica and Shelly 1996; Rejamanek and Richardson 1996; Callaway and Aschehoug 2000; Gorchov and Trisel 2003). Across ecosystems, invasive plant species are one of the major threats to biodiversity and ecosystem stability (Wilcove et al. 1998; Mack et al. 2000). Their presence and proliferation lead to the displacement of native plant species (Mack et al. 2000). The ability of invasive plant species to change ecosystem processes was first shown by Vitousek et al. (1987) and summarized by others (Vitousek 1990; Walker and Smith 1997; Gordon 1998). Invasive plant species can alter geomorphology, hydrology, biogeochemistry, and disturbance regimes within the ecosystems they invade (Macdonald et al. 1989). Invasive species can also change community and population dynamics by changing plant stand structure, recruitment of native species, resource competition, and trophic function (Macdonald et al. 1989; Levin et al. 2006).

Invasive plants affect geomorphology through the alteration of erosion rates, sedimentation rates, elevation, and hydrologic flow paths. *Tamarix spp*. can alter erosion rates and stream geomorphology by stabilizing river banks resulting in down cutting of stream channels thereby limiting the river's ability to meander and flood (Graf 1978). *Phalaris arundinacea* has been shown to decrease microtopographic relief in heterogeneous sedge meadows which decreases biodiversity (Wernder and Zedler 2000).

Casuarina equistifloia increases soil erosion and causes shoreline steepening by competively excluding native grass species (Deaton 1994; Johnson 1994). While some species increase erosion many species increase sedimentation thereby stabilizing many of the systems they invade. This has been well documented along the Pacific Coast of the United States where grasses have stabilized sand dunes (Barbour and Johnson 1988; Seabloom and Wideman 1994).

Many of the same species that have the ability to change geomorphology can also alter hydrologogy of the system they invade. Hydrologic processes that can be altered include decreases in water table depth, surface flow patterns, and rainfall interception. Tree species invading herbaceous areas provide some of the best examples of hydrologic changes. For example, *Melaleuca quiquenervia* can increase rainfall interception, increase evapotransipration (ET) rates, and reduce surface water flows (Versefeld and van Wilgen 1986; Vitousek 1986). In Florida, aquatic species *Pistia striates* and *Echhornia crassipes* ET rates exceed open-water ET by 3 to 10 times (Schimtz et al. 1993) and *Hydrilla verticillata* impedes water flow in canals (Duever et al. 1986). *Tamarix spp.* can increase flooding severity, decrease flows through enhanced ET rates, and lower the water table by exploiting deep water resources (Everit 1980; Davenport et al. 1982; Brotherson and Field 1987; Great Western Research 1989; Frasier and Johnson 1991; Friederici 1995).

Invasive plants alter biogeochemical cycles by changing nutrient mineralization rates, soil and water chemistry, and nutrient immobilization. Impacts on C and N cycling have been the main focus, although other elemental cycles are impacted (e.g., phosphorus

and mercury). A well studied impact of invasive species on biogeochemistry is the introduction of N fixing species into the N limited soils of Hawaii (Vitousek 1987; Mack et al. 2001; Mack and D'Antonio 2003; Hughes and Denslow 2005). Aquatic species (e.g., *E. crassipes, H verticllata, P. straiodes*) have been shown to modify water quality by decreasing dissolved oxygen, pH, and phosphorus and increasing dissolved carbon dioxide, turbidity, and water color (Schmitz et al. 1993). Invasive plants also tend to increase above ground biomass and decrease litter quality, which leads to an increase in net soil C pools and N mineralization within the invaded system (Evans et al. 2001; Drenovsky and Batten 2007; Mack et al. 2001; Agren and Knecht 2001). Other species including *Berberis thunbergii*, *Microstegium vimineum*, and *Phragmites australis* have been shown to alter N mineralization, nitrification, and aboveground biomass (Windham and Lathrop 1999; Ehrenfeld et al. 2001).

Alteration of geomorphology, hydrology, and biogeochemical processes can also impact the disturbance regimes of invaded ecosystems. Most of the research on altered disturbance regimes has focused on how the invasion alters fire regimes, specifically the change in the intensity, frequency, and duration of fires (van Wilgen and Richardson 1985; Whisenant 1990; Hughes et al. 1991; D'Antonio and Vitousek 1992; Busch 1995; Lippincourt 2000; Tunnison et al. 2001). For example, the increase in biomass production can result in more frequent, longer duration, and more intense fires.

Wetland ecosystems tend to be more susceptible to invasions of grasses, graminoids, shrubs, forbs, and trees due to the location on the landscape where nutrients, the impacts of disturbances, and moisture accumulate (Zedler and Kercher 2004). The

impacts of invasive plants on wetland ecosystems includes altering habitat structure, decreasing biodiversity of both plant and animal species, alteration of biogeochemical cycles, changing hydrologic regimes, and an increase in microtopography (Able et al. 2003; Ehrendeld 2003; Zedler and Kercher 2004). One of the most widely recognized and distributed wetland invasive species in the United States, Purple loosestrife (*Lythrum salicaria*) has been shown to increase hydrologic flux, nutrient cycling, organic matter distribution, decomposition rates, and reduce species richness in wetland systems (Emery and Perry 1996; Gabor et al. 1996; Mitsch and Gooselink 2000; Blossey et al. 2001).

Invasive plants may have a much greater effect on soil nutrient dynamics than suggested by previous studies (Ehrenfeld 2001). Ehrenfeld (2001) further concluded that numerous plant characteristics can affect biogeochemical processes such as plant structure, life history, tissue type, photosynthetic pathway, physiology, symbiotic relationships, vegetative spread, root structure and morphology, and tissue chemistry. Examples of changes to C and N biogeochemical cycling include decreasing litter quality and increasing decomposition rates, fine sediment accumulation, increasing aboveground and belowground pools of C and N,. and increasing net ecosystem exchange (NEE) (Tilman et al. 1997; Hooper and Vitousek 1998; Baruch and Goldstein 1999; Hector et al. 1999; Chapin et al. 2000; Evans et al. 2001; Fickbohm and Zhu 2003; Allison and Vitousek 2004; Ashton et al. 2005).

The impact of invasive species on the structure and function of ecosystems in the United States also has profound economic consequences (Pimentel et al. 2000). The cost of controlling the 25,000 invasive plants species has been estimated at over $34 billion

annually with aquatic and wetland species control costing nearly $155 million annually (Pimentel et al. 2005). This is of particular interest in Nebraska, where concerns about the impact on ecotourism, threatened and endangered species, and water availability have led the state to spend approximately $2 million annually to control invasive plant species in the riparian corridors of the Republican and Platte Rivers. The targeted invasive plant species include *Tamarix sp.*, *Elaeagnus angustifolia*, and *Phragmites australis*, but *P. australis* appears to be the major invader along both river systems. Although *P.australis* was initially a native species within North America, the recent expansion over the past 75 years in the north-eastern and central United States is thought to be from an introduced haplotype (Saltonstall 2002). The introduced haplotype is considered invasive and has not only displaced most native populations of *P.australis*, but also out-competes other native species within aquatic ecosystems as well (Saltonstall 2002; Catling et al. 2003).

The dense and aggressive growth of *P.australis* creates monoculture stands and significantly alters the system it invades by changing the availability of resources for native species (Meyerson et al. 2000). *P.australis*'s dense growth, tall plant height, and high detrital accumulation combine to reduce light availability at the soil surface and reduce air temperature within the canopy (Meyerson et al. 2000) The reduced light availability and lower air temperatures inhibit seed germination and the successful colonization of other plant species (Meyerson et al. 2000). One study found that the invasion of *P.australis* increased siltation rates and the accumulation of organic matter, which could lead to the filling in of small waterways (Lathrop et al. 2003). Further, research studies have documented a decrease in plant diversity after the invasion of

P.australis, particularly in freshwater wetlands where diversity tends to be much higher than tidal and brackish wetlands (Odum et al. 1984; Chambers et al. 1999; Meyerson et al. 2000).

The impacts of *P.australis* have been well documented in the tidal and freshwater marshes of the North-Eastern United States; however, little work has been done in inland, freshwater wetlands within the Great Plains Region. Our study focused on the Republican River Basin in Nebraska where *P.australis* has invaded aquatic habitats (e.g. wetlands, river bars, and ponds). Specifically, the study examined how *P. australis* affected C dynamics in a freshwater, riparian wetland characteristic of this region. The three main objectives of the study were: 1) Assess the interhabitat differences in net ecosystem exchange of the carbon (NEE) and its associated components (soil respiration, methanogenesis, and gross primary production) during peak photosynthetic periods between *P.australis*, *Scirpus sp.*(the native species); and open water habitats; 2) Document how rates of NEE and its components change throughout the growing season; and 3) Examine the diurnal change in NEE rates in *P.australis* and native habitats. Based on these objectives I had the following hypotheses: 1) *P.australis* would have significantly higher rates of C exchange throughout the growing season; 2) Seasonally, *P.australis* would have significantly higher rates at peak growth compared to the native habitat, while open water would remain a relatively neutral source of carbon; and 3) *P.australis* and native habitats would display similar daily changes in C dynamics with *P.australis* having higher peak NEE rates and higher nighttime respiration rates.

2. Methods

2.1 Site Description

The site used in this study was a riparian wetland in south-central Nebraska located in the Republican River Basin (40° 17.9' N, 99° 58.1' W, elevation 665 m). The wetland is located in a remnant stream channel and was approximately 36,000 m^2 (700 m by 60 m, Figure 1). The riparian zone at our site is dominated by a mature stand of Eastern cottonwoods (*Populus deltoides*). The vegetation distribution at our site was dominated by *P.australis* (53% aerial coverage), followed by a native species mixture of *Scirpus sp.*, *Carex sp.*, and *Typha sp.* (37% aerial coverage), and the remaining 10% of our study site was open water in which *Lemna sp.* became abundant during the growing season. The land-use surrounding the site was irrigated row crop agricultural with some pastureland present as well.

Data from a High Plains Regional Climate Center station located near Cambridge, NE (approximately 20 km west of the study site) shows the climatological total precipitation during the growing season(May-October) to be 454 mm and the average maximum July temperature is 32.7° C (based on the previous 100-years of record). Data from the same station during 2009 recorded precipitation during the growing season at 640 mm and an average maximum July temperature of 28.9° C. A water balance was also being conducted on the study site since 2008 and therefore I had access to continuous data for air temperature, water temperature, and other climatic variables since the summer of 2008 (Table 1).

Four weeks prior to the first sampling period, experimental collars and PVC chambers were installed at the site within three distinct habitat types (*P.australis* dominated area, *Scripus sp.* dominated area, and an open water area). Within each habitat type, 3 collars and 3 PVC chambers were installed and used as replicates (n = 3). The collars were constructed with 3 mm plexi-glass, and three different sizes were created to accommodate different plant heights and water depths (17.5 cm x 17.5 cm x 36 cm for *P.australis*; 17.5 cm x 17.5 cm x 18 cm for *Scirpus sp.*; 19.5 cm x 19.5 cm x 36 cm for open water). All three collars had a 2.5 cm ledge 30 cm from the top of the collar to support the chambers during incubations. Due to extensive root growth, the collars were unable to be buried in the sediment, but were anchored into the top ~5 cm of sediment using cinder blocks. Next to each plexi-glass collar, PVC chambers (10.16 cm diameter) were driven into the soil approximately 25 cm. The PVC chambers did not enclose any plants and chamber caps were equipped with luer lock valves to facilitate headspace sampling.

2.2 Net Ecosystem Exchange (NEE) of carbon

Net Ecosystem Exchange of carbon dioxide (NEE_{CO2}) in an ecosystem is defined as

$$NEE_{CO2} = GPP - R_{TOT} \tag{1}$$

where GPP is gross primary productivity and R_{TOT} is community respiration, each expressed as mass of C produced or consumed per unit area per unit time ($M\ L^{-2}\ T^{-1}$). Community respiration can be subdivided into:

$$R_{TOT} = R_P + R_S \tag{2}$$

Where R_P is plant respiration and R_S is soil respiration due to microbial activity also in units of g C per unit area per unit time. In wetlands, methanogenesis should be incorporated to conduct a full carbon balance and the definition of NEE of carbon is revised accordingly:

$$NEE = NEE_{CO2} - \text{methanogenesis} \tag{3}$$

Where methanogenesis is the production of methane in units of g C per unit area per unit time (Figure 2).

This study used a dynamic closed chamber technique developed by Whiting et al. (1992) and modified by Drosler (2005) to measure NEE_{CO2}. Two chambers were constructed of 3mm plexi-glass with dimensions of 51 x 51 x 76 cm and 46 x 46 x 244 cm, with the shorter chamber used in open water and the taller chamber used for the vegetated areas. Chambers were designed to fit tightly over each collar and when installed created an air-tight seal. Fans were placed within each chamber for air circulation, and ice packs were placed in front of each fan to minimize temperature differences between inside the chamber and ambient air. Doors were cut into each chamber and sealed with closed cell foam to allow ice pack placement. Inside and ambient air temperatures were continuously monitored during incubations using solar shielded sensors (HOBO Pro v2, Onset Computer Corporation, Pocasset, MA, USA). Carbon dioxide and water vapor concentration were continuously measured using an infrared gas analyzer (LI-840, LI-COR Inc., Lincoln, NE, USA) equipped with a miniature rotary vein pump (135 FZ, 0.7 L min^{-1}, Schwarzer Precision, Essen, Germany). Carbon dioxide concentrations (ppm) were converted to masses (mg) using the ideal gas

law and converted to rates using a simple linear regression of mass versus time
(Appendix 2).

A full C balance which included NEE_{CO2} incubations and PVC chamber
incubations was conducted 5 times over the growing season during 2009, beginning in
early June and ending in early October. To determine NEE_{CO2}, the rate of change in CO_2
concentration was measured with the chamber exposed to sunlight during peak PAR
(between 10:00 and 14:00). Incubations typically lasted 5 minutes, unless CO_2 became
limiting, and in those instances the time period was shortened to maintain a linear rate of
change. The same procedure was used to measure R_{TOT}, except the chamber was covered
with reflective insulation to inhibit photosynthesis.

2.3 Soil Respiration and Methanogenesis

Soil respiration (R_S) and methanogenesis rates were measured using 24-hour
incubations in which headspace from the PVC chambers was sampled at the beginning
and end of the diel period. Samples were collected using gas-tight syringes and stored in
10 mL glass, vials sealed with aluminum crimp tops equipped with open top septa and
stored at 4°C until analyzed in the laboratory. Samples were run on a gas chromatograph
(8610C, SRI Instruments, Torrance, CA, USA) equipped with a HayeSep T column
(Valco Instruments Co. Inc., Bandera, TX, USA). Carbon dioxide was measured using a
thermal conductivity detector, and methane (CH_4) was measured using a flame ionization
detector. The production of CO_2-C produced per unit time per unit area was used to
estimate R_S, while methanogenesis rates were based on the production of CH_4-C
produced per unit time per unit area of the PVC chamber (Appendix 3). Plant respiration

is defined as the difference between R_T and R_S (equation 2). NEE was then estimated with NEE_{CO2} and methanogenesis estimates (equation 3).

2.4 Diel Measurements

On 11 August 2009 through 12 August 2009, a 24-hour run was conducted in the *P.australis* habitat and *Scirpus sp.* habitat with a sampling frequency of 4 hours to examine the diurnal changes in C dynamics. The NEE_{CO2} and methanogenesis incubations allowed me to assess the diurnal variability of the carbon flux within the wetland. CO_2 dynamics were conducted on a single collar within the two vegetated habitat types due to time constraints associated with the frequent temporal sampling and large incubation chambers. In conjunction with the CO_2 measurements, methanogenesis incubations were conducted using 4-hour incubations. Methanogenesis rates from each sampling period represent the average rate from the three chambers within each habitat type. Due to insect swarming I was unable to conduct the overnight sampling period (02:00) for CO_2 exchange and likewise the overnight methanogenesis values represented an 8-hour incubation (10:00-06:00).

2.5 Soil and Plant Characteristics

At the end of the 2009 field season, aboveground biomass was harvested from each replicate in both the *P.australis* and *Scirpus sp.* habitat types. The plant biomass was dried for 14 days at 30°C and weighed. Soil cores were also collected from each replicate in all three habitat types at the end of the growing season. Intact PVC cores (3.175 cm x 5 cm) were dried at 105°C for approximately 12 hours to measure bulk density based on a dry mass basis. Approximately 25 g of dry soil was placed in a furnace

at 550°C for 6 hours to measure organic matter content based on the loss on ignition method (American Public Health Association, 1998). Subsamples of the dried soil were analyzed for carbon and nitrogen content using a Costech ECS 4010 (Costech Analytical Technologies Inc., Valencia, CA).

2.6 Statistical Analysis

Two-way repeated measure ANOVA was used to determine statistical differences between the habitat types in this study. The significance level for the test was set as $\alpha =$ 0.05 and pair-wise comparisons were made using the Holm-Sidak test. All the components of the C balance were square-root transformed to satisfy normality and heterogeneity of variances for statistical analyses. SigmaStat 3.1 was used to generate descriptive statistics and perform statistical tests.

3. Results

3.1 Net Ecosystem Exchange of Carbon

Net Ecosystem Exchange of carbon reached peak values in late-June in both the *Scirpus sp.* and *P.australis* habitats, while the open water area did not significantly deviate from zero over the growing season (Figure 3). *P. australis* and *Scirpus sp.* habitats reached peak production during late June, with rates of fixation equal to 2174 ± 846 and 550 ± 42 mg C m^{-2} hr^{-1} (all values in this paper are mean $\pm$ 1 standard deviation) respectively. Overall, significant differences were observed in NEE ($F_{8,44} = 11.96$; p <0.001). Specifically, the results revealed that *P.australis* had higher NEE values than *Scirpus sp.* (p = 0.002) and open water (p < 0.001) and that *Scirpus sp.* had higher NEE values than open water (p = 0.02). *P.australis* showed significantly higher NEE rates

than open water throughout the entire sampling season within each sampling date. Early in the growing season *P. australis* had significantly higher NEE than *Scirpus sp.*, but as the season progressed rates became similar. Also, early in the growing season the *Scirpus sp.* habitat had significantly higher NEE rates than the open water habitat, but as the season progressed no significance was observed between the two habitats. The vegetated habitats' seasonal change in NEE correlates well with the amount of PAR received during the sampling period and air temperature on each specific date (Table 1). The seasonal averages for NEE were 52.7 ± 92.6, 258 ± 186, and 920 ± 752 mg C m^{-2} hr^{-1} for open water, *Scirpus sp.*, and *P. australis* habitats respectively.

3.2 Methanogenesis/Soil Respiration

Methanogenesis rates were highly variable within each habitat type through the first three sampling dates, with peak production in mid-July reaching 39.7 ± 15.3, 14.5 ± 8.6, and 34.2 ± 20.2 mg C m^{-2} hr^{-1} in *P. australis*, *Scirpus sp.*, and open water habitats respectively (Figure 4). Methanogenesis showed strong seasonality with low rates early in the growing season, peaking in July, and dropping off as the growing season progressed. The seasonal distribution of methanogenesis rates correlates with the seasonal change in water temperature. There was no significant difference observed among the habitat types due to the high variability. The average seasonal CH$_4$ emissions rates were 16.3 ± 13.7, 9.96 ± 3.2, and 19.9 ± 8.4 mg C m^{-2} hr^{-1} for *P.australis*, *Scirpus sp.*, and open water, respectively. The seasonal distribution of methanogenesis rates correlates with the seasonal change in water temperature.

R_s (Figure 5) displayed the same seasonality and had magnitudes similar to those of methanogenesis in all three habitats types, although the *P. australis* habitat did not show the seasonal "ramp up" in soil respiration that was observed in methanogenesis. Peak R_s rates in mid-July were 38.7 ± 8.00, 35.6 ± 13.1, and 35.7 ± 13.1 mg C m^{-2} hr^{-1} for *P.australis*, *Scirpus, sp.*, and open water, respectively. In terms of overall, growing-season average, there were significantly different R_s rates observed among the three habitat types ($F_{8,44} = 2.501$; $p = 0.039$). The peak R_s rates were 26.8 ± 12.1, 15.9 ± 13.3, and 21.4 ± 13.7 mg C m^{-2} hr^{-1} for *P.australis*, *Scirpus sp.*, and open water, respectively. *P.australis* had significantly higher R_s than open water and *Scirpus sp* on 04 June 09 (p=0.006; p=0.011). On the 22 Jun 09 sampling date *P.australis* had significantly higher R_s than *Scirpus sp.* (p=0.009). Throughout the remainder of the growing season all three habitat types had statistically similar R_s. The seasonal average R_s rates were 25.4 ± 14.2, 14.3 ± 14.2, and 18.5 ± 15.4 mg C m^{-2} hr^{-1} for *P.australis*, *Scirpus sp.*, and open water, respectively

3.3 Diel Measurements

The 24 hour sampling of NEE illustrates a typical daily curve of NEE with peak rates being reached in both the *Scirpus sp* and *P.australis* in early afternoon between 14:00:00 and 15:00:00 hrs (Figure 6). Peak daytime (nighttime) NEE was approximately 3 times higher in *P.australis* than *Scirpus sp.* habitats. The diel changes in NEE within each habitat type was positively correlated with PAR over the 24-hour sampling. The diel changes in methanogenesis rates (Figure 7) showed relatively consistent rates among habitats from early evening to early morning (19:00 to 08:00). However, the *P.australis*

habitat had a distinct peak in early afternoon (13:00 to 14:00) while the *Scirpus sp.*

habitat remained relatively constant throughout the 24 hours.

3.4 Soil Characteristics and Plant Biomass

Growing-season biomass production of *P. australis* was roughly 10 times higher

than the biomass produced by the native plants (Table 2). The open water habitat had the

lowest soil bulk density, and the highest %C, %N, and soil organic matter. The native

habitat had the highest bulk density, and the lowest %C, %N, and soil organic matter

(Table 2). Statistics were not performed on the data due to the small sample size, but

there does seem to be a tendency for higher percent organic matter, carbon, and nitrogen

andlower bulk density in the sediments below *P. australis* compared to the native

habitats.

4. Discussion

4.1 NEE

This study documents the impact that *P. australis* has on carbon dynamics in a

riverine wetland in the Great Plains region. The prolific growth of *P. australis* was

characterized by high NEE relative to native vegetation over daily and seasonal time

scales, with peak values reaching 2.2 g C m^{-2} hr^{-1}. Few studies have directly measured

NEE for *P. australis*. Zhou et al. (2009) examined *P. australis* in a freshwater tidal

wetland in China and documented peak NEE$_{CO2}$ values of 1.2 g C m^{-2} hr^{-1}; however, their

measurements did not include methanogenesis. The freshwater tidal wetland examined

by Zhou et al. (2009) had average water depths between 1.9 and 2.7 m, and it's possible

thatthe deep water relative to this study may have suppressed aboveground biomass and

primary production. Zhou et al. (2009) report aboveground biomass of approximately

1450 g m^{-2} compared to this study, in which water depths were less than 1 m and *P.*

australis aboveground standing stocks exceeded 5000 g m^{-2}. Several studies have

documented NEE$_{CO2}$ for other wetland species. *Typha angustifolia* employs a growth

strategy similar to *P. australis* and is considered a nuisance species in wetlands in certain

geographic regions. This species has been shown to reach similar peak NEE$_{CO2}$ (~2.5 g C

m^{-2} hr^{-1}) as *P. australis* in a northern wetland (Ontario, Canada), but the shorter growing

season in this location limited aboveground net biomass production to 1600 g m^{-2}

(Bonneville et al. 2008). A study of tidal wetlands in New York, USA examined

Spartina sp. and measured higher values of NEE$_{CO2,}$ with rates reaching 3.5 g C m^{-2} hr^{-1}.

Unfortunately, no biomass measurements are available for this study (Houghton and

Woodwell 1980). Combined, these results indicate that *P. australis* in our study system

achieves instantaneous NEE$_{CO2}$ rates that are near the high end of recorded values for

other freshwater wetland systems. Coupled with a longer growing season and different

environmental conditions, these rates achieve aboveground standing stocks that exceed

amounts found in similar studies.

Comparison of the aboveground biomass of *P. australis* and native species at our

site further illustrates the ability of invasive species to shift wetland carbon balance. At

the site, I found aboveground biomass to be ten times higher in habitats dominated by *P.*

australis compared to the native. *P. australis* can also have substantial, yet varying

belowground biomass. One study found a wide range of belowground biomass (34-

170%) relative to aboveground biomass (Brix et al. 2001). If belowground production

tracks the high aboveground production rates of *P. australis* found in this study, then the impact of this invasive plant on wetland C budgets could be much greater than suggested above. In addition, *P. australis* biomass has been documented to decompose slower than native species (Windham 2001) adding to its potential to alter carbon dynamics. I did not see the impacts of the increased biomass production in our soil cores, but creation of soil organic matter (OM) is a long term process, and it's possible that the recent *P. australis* invasion (<10 years) has not had enough time to impact soil OM pools in our site. Alternatively, *P. australis* litter may disperse evenly through the wetland system, obscuring differences between soil OM developing under native vegetation and *P. australis*. Comparing soil organic matter in restored and reference wetlands, Ballentine and Schneider (2009) found that soil OM in the restored site was ~30% that of the reference site after 55 years, suggesting that the fingerprint of *P. australis* in wetland soil organic matter may require decades to centuries to develop.

4.2 Methanogenesis

Values of methanogenesis documented in this study were high compared to previously reported values of methanogensis in freshwater wetlands. A recent review by Bridgham et al. (2006) found that average hourly methane fluxes from North American freshwater wetlands averaged 3.3 mg C m^{-2} hr^{-1} (range: 0 – 468 mg C m^{-2} hr^{-1}), with values rarely exceeding 14.6 mg C m^{-2} hr^{-1}. Our average hourly value was 13.5 mg C m^{-2} hr^{-1}, and ranged from 2.6 to 40 mg C m^{-2} hr^{-1} over the growing season. Although high, our values are not outside the range of reported values for freshwater wetlands. A study

of methane fluxes in a Nebraska wetland dominated by *P. australis* using eddy covariance found methanogenesis rates ranging from 1.7 to 23 mg C m^{-2} hr^{-1} (Kim et al. 1998). Crill et al. (1988) reported methane fluxes ranging from 0.4 to 31 mg C m^{-2} hr^{-1} in Minnesota peat lands and bogs. Within an Amazon River floodplain, methane fluxes averaged ~31 mg C m^{-2} hr^{-1}, with a range of 0 to 163 mg C m^{-2} hr^{-1} (Devol et al. 1988).

In this study, plants were excluded from the chambers when measuring methanogensis. CH_4 flux via plant-mediated transport has been shown to be a flow path through which CH_4 reaches the atmosphere (Shannon and White 1994, Sorrell and Boon 1994, Shannon et al. 1996). Therefore, our rates of methanogenesis may be an underestimate. Existing studies suggest that *P. australis* may have significant plant-mediated transport of CH_4, representing as much as 34 – 75% of total CH_4 flux (Brix et al. 1992, Armstrong and Armstrong 1991; Kim et al. 1998). Given the radiative forcing potential of methane, incorporating plant mediated transport is strongly encouraged in future studies of methane fluxes from wetland with significant *P. australis biomass.* However, the relative contribution of methane flux in this C balance was low (~2%) and even if I multiply measured methanogenesis rates by four (roughly correlating to 75% of total methane flux being due to plant mediation), seasonally averaged NEE in the *P. australis* habitat only changes from 920 to 875 mg C m^{-2} hr^{-1} (~5% reduction). Therefore, even if the CH_4 flux values are adjusted because the values may have significantly underestimated CH_4 flux, the change in the total carbon balance was minimal.

Data from this study illustrate that methanogenesis was similar between the open water, native, and *P. australis* habitats over the course of the entire growing season (i.e., prior to plant emergence, during plant growth, and after senescence). Some studies have correlated a peak in methanogenesis during midday due to plant-mediated transport or net primary production (Kim et al 1998). In this study, I observed the same pattern for methanogenesis in the absence of plants (Figure 7). The wetland examined in this study was completely inundated throughout the growing season (water levels 0.5-1.25 m). During the previous summer (2008) water quality monitoring was unable to detect dissolved oxygen and average redox potentials in the surface water averaged -442 mV. Assuming the 2009 growing season maintained similar conditions, methanogenesis may have been occurring at shallow soil depths. Plant-mediated transport of methane is likely to be most important when methane production is occurring deeper in the soil profile and a strong gradient from oxidized, shallow sediments to reduced, deep sediments exists. The strongly reduced conditions documented at the site indicate that plant-mediated transport is not likely to be a major pathway for methane flux in this wetland.

4.3 Carbon Sequestration/Global Warming

Based on both diel and seasonal sampling (Figure 3, 6) I have estimated an annual carbon budget for 2009 at this wetland site. Assuming diel patterns are representative of the daily change in NEE throughout the growing season, I calculated rates of NEE (Figure 8) based on our peak daily NEE values, measured at various times throughout the season. By integrating under the curve a daily mean estimate for carbon exchange was made.

This daily value was applied to a period of days before and after the actual sampling date

(Table 3). Estimates for the remaining time periods were made using the nearest

measured rates of soil carbon fluxes (i.e. daily April values were based on the measured

04 June 2009 soil carbon fluxes). Monthly carbon fluxes (g C m^{-2}) were calculated based

on daily estimates within the associated time periods (Figure 9). Annual NEE estimates

were made assuming negligible soil carbon fluxes during winter months (December to

February). Based on these estimates, a series of invasion scenarios were applied to

investigate the potential impacts of *P. australis* invasion on the annual carbon flux at this

study site (Table 4). As the invasion of *P. australis* progressed from pre-invasion

conditions to 90% cover, carbon sequestration in this wetland increases significantly,

suggesting that while *P. australis* invasion may have other unfavorable consequences,

decreasing carbon sequestration in wetlands is not likely to be one of those effects.

However, a strict carbon balance does not take into account the radiative forcing factors

of other greenhouse gases such as methane. Methane gas has a longer half life in the

atmosphere than carbon dioxide and a radiative forcing factor 21 times higher than

carbon dioxide (IPCC 1995). Taking into account the associated C-CO_2 equivalents of

our methane emissions, the annual greenhouse gas emissions would be significantly

different. *P. australis* has a high enough NEE_{CO2} to overcome the contribution of

methane to greenhouse gas emissions within its habitat (5.2 g C-CO_2 m^{-2} y^{-1}). However,

under current vegetation conditions at our study site *P.* australis NEE_{CO2} does not balance

the methane emissions and NEE_{CO2} from native species and open water habitats (-403 g

C-CO_2 m^{-2} y^{-1}and -1566 C-CO_2 m^{-2} y^{-1}). The combination of low biomass production in

native vegetation stands and the high methane production rates from open water and native habitats result in this site being a net contributor of greenhouse gases to the atmosphere (Table 4). Even under a scenario in which *P. australis* invades all of the vegetated region of this wetland, methane fluxes from the open water areas maintain positive net rates of greenhouse gas emissions. However, as the *P. australis* invasion continues, the magnitude of this contribution will fall as NEE_{CO2} rates increase, yielding a system that has less global warming potential than the present condition.

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Table 1. Climatic conditions during the six sampling events in this study, as measured at the weather station at the site. Means and ranges in parenthesis are based on the typical period of time (10:00-14:00) it took to sample net ecosystem exchange of CO_2 at all 3 habitat types in the wetland. Photosynthetic active radiation (PAR) is the total amount received during the sample period

Date	Air Temperature °C	Water Temp °C	PAR mol m^{-2}	Solar Radiation W m^{-2}	Wind Speed m s^{-1}
4-Jun-09	20.2 (15.6-22.6)	13.6	2.45	695 (339-1218)	1.15 (0.22-2.36)
22-Jun-09	30.6 (28.2-32.8)	14.4	3.52	992 (843-1042)	0.81 (0.17-1.54)
15-Jul-09	28.3 (26.1-29.9)	18.8	3.19	888 (383-1163)	0.88 (0.32-1.34)
6-Aug-09	26.5 (23.4-29.9)	18.3	1.72	479 (160-1204)	1.30 (0.85-2.07)
7-Oct-09	18.9 (13.5-24.0)	12.6	2.34	733 (584-792)	0.68 (0.32-1.07)

Table 2. Plant biomass and soil characteristics sampled within individual collars at the end of the growing season on 07 October 2009. The soil characteristics represent the top 5 centimeters of the soil profile. All values are mean ± 1 standard deviation.

Habitat	Aboveground Biomass Dry g m^{-2}	Bulk Density g cm^{-3}	Organic Matter %	Soil Carbon %	Soil Nitrogen %
P.australis	5394±1815	0.58±0.2	6.2±1.9	3.13±1.6	0.19±0.10
Scirpus sp.	564.2±139.2	0.76±0.4	5.3±2.2	2.24±1.6	0.13±0.10
Open water	N/A	0.27±0.01	10.6±1.0	5.31±2.1	0.32±0.14

Table 3. NEE sampling dates that were applied to the associated time periods for estimating yearly carbon flux.

NEE Sampling datet	Time period
4-Jun-09	27-May – 12-June
22-Jun-09	13-June – 3-July
15-Jul-09	4-July – 27-July
6-Aug-09	28-July – 23-August
7-Oct-09	24-August – 7-0ct

Table 4. Annual carbon sequestration (Mg C yr^{-1}) and C-CO$_2$ equivalents at the study site based on species distribution scenarios. Carbon sequestration values in parenthesis represent low and high estimates based on low and high measured peak NEE rates.

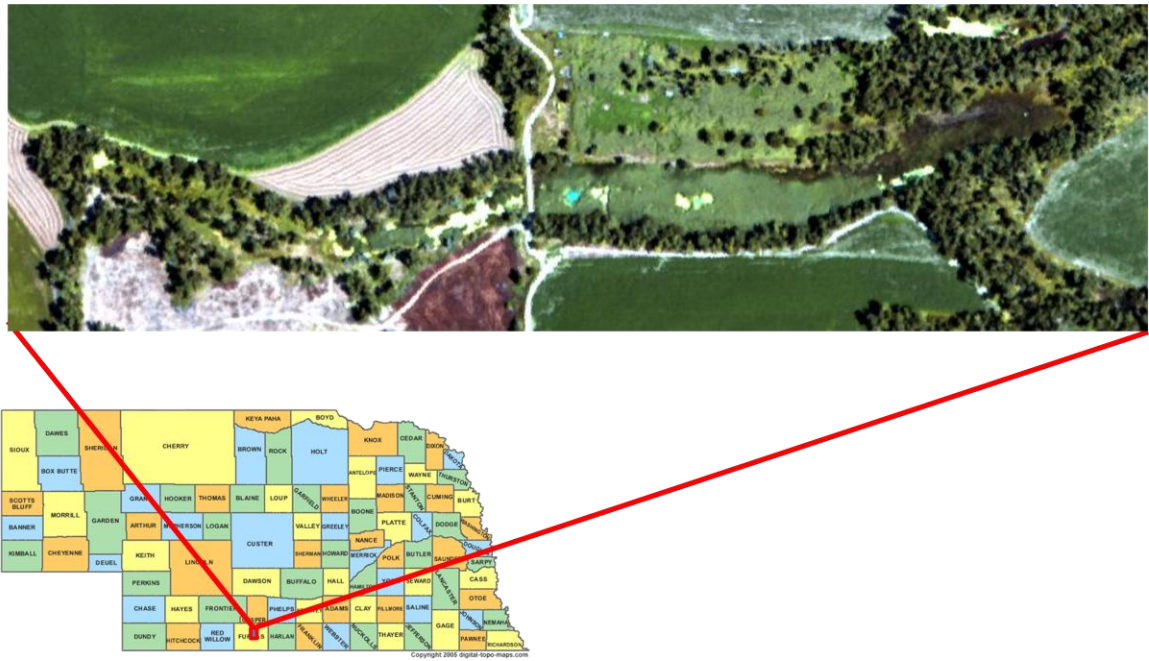| Wetland Condition	Species Distribution %Native %Open Water % *P. australis*	Carbon Sequestration Mg C yr^{-1}	C-CO$_2$ equivalents Mg C-CO$_2$ yr^{-1}
Pre-invasion	90% 10% 0%	3.8 (1.9-5.2)	-18.9
Low	60% 10% 30%	7.8 (4.5-11.3)	-14.5
Present day	10% 38% 52%	10.7 (6.4-15.7)	-11.2
Heavy	0% 10% 90%	15.8 (9.6-23.4)	-5.5

Fig. 1. Aerial photograph of wetland in Furnas County, Nebraska. The site is

approximately 36,000 m^2 (~700 x 60 m).

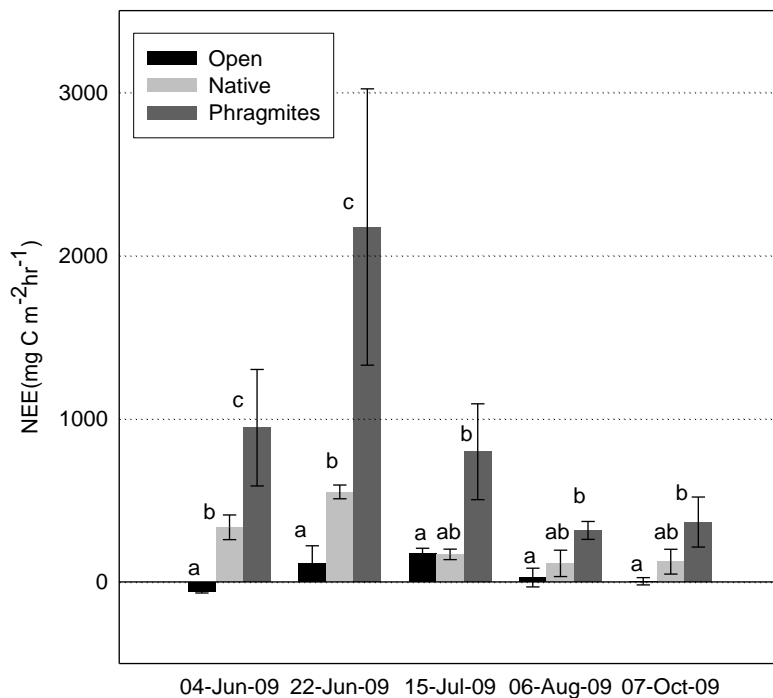**Fig. 2. Theoretical Carbon Balance for the studied wetland**

$$NEE_{CO2}=GPP\text{-}R_p\text{-}R_s$$
$$NEE=NEE_{CO2}\text{-}Methanogenesis$$

R_p

CH_4 R_s

GPP
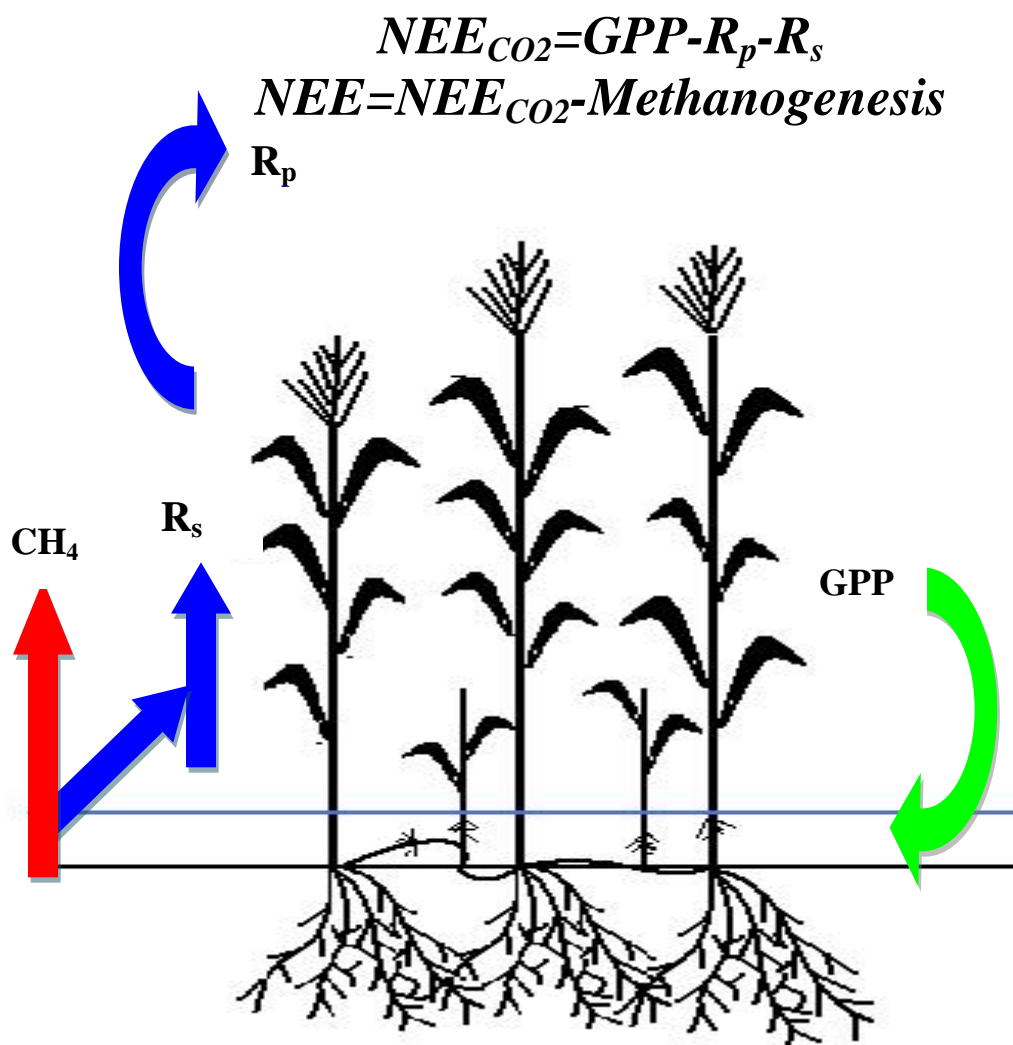
Fig. 3 Net ecosystem exchange of carbon (NEE; mg C m^{-2} hr^{-1}), in which positive values represent C fixation and negative values represent a release of C to the atmosphere. Error bars represent ± 1 standard deviation. Within each sampling date, values with different letters indicate a significant difference using the Holm's Sidak pairwise comparison test (alpha =0.05). Data was square-root transformed to satisfy normality and heterogeneity of variances for statistical analyses.
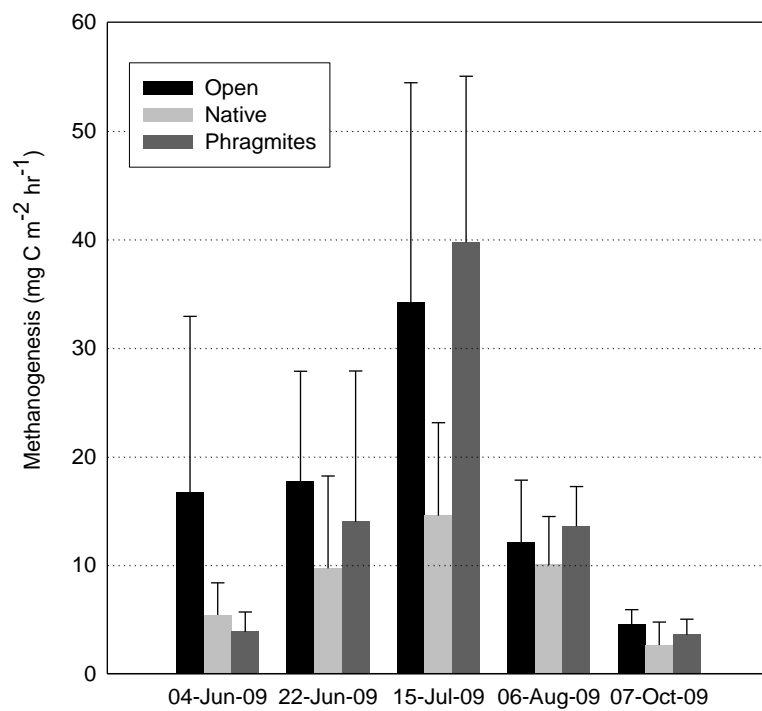
Fig. 4. Methanogenesis rates (mg C m^{-2} hr^{-1}) from PVC cores that exclude vegetation in the study wetland. Error bars represent ± 1 standard deviation.

Fig. 5. Soil respiration rates (mg C $m^{-2}hr^{-1}$) from PVC cores that exclude vegetation in the study wetland. Error bars represent ± 1 standard deviation. Within each sampling date, values with different letters indicate a significant difference using the Holm's Sidak pairwise comparison test (alpha =0.05). Data was square-root transformed to satisfy normality and heterogeneity of variances for statistical analyses.
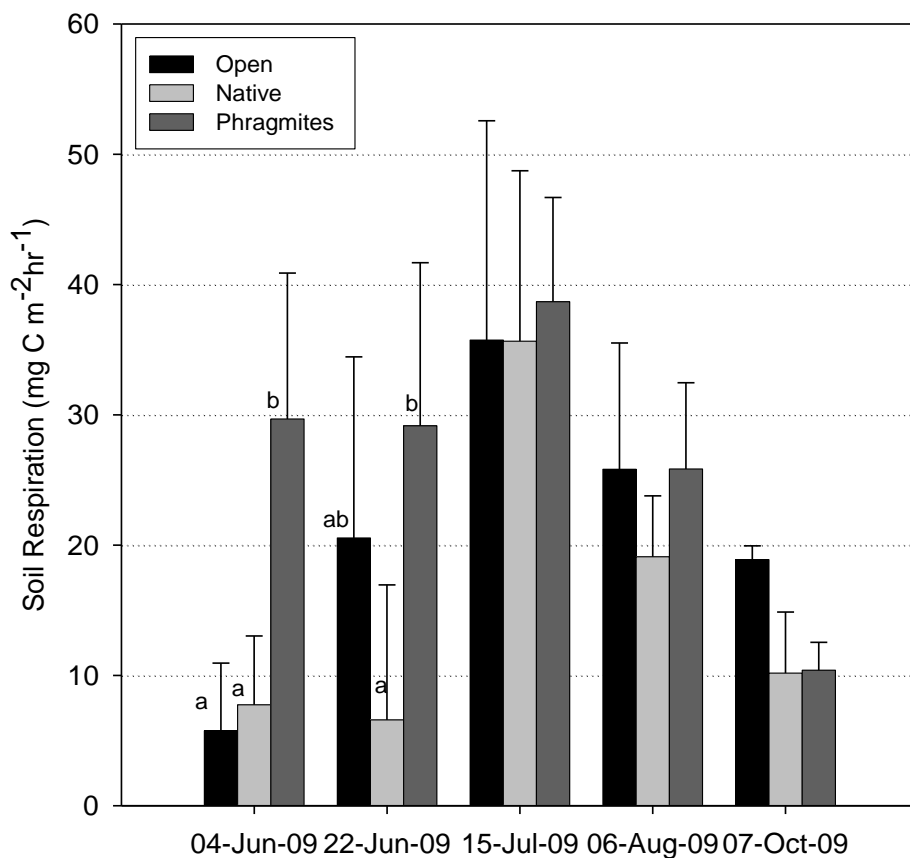
Fig. 6. Net ecosystem exchange of carbon rates (NEE; mg C m^{-2}hr^{-1}) in which positive values represent C fixation and negative values represent a flux of C to the atmosphere. Measurements were taken on individual plots within the native species and *Phragmites australis* habitat types every four hours from 11 August 2009 to 12 August 2009. The secondary axis shows the daily change in photosynthetic active radiation (PAR) (μmol m^{-2} s^{-1}).
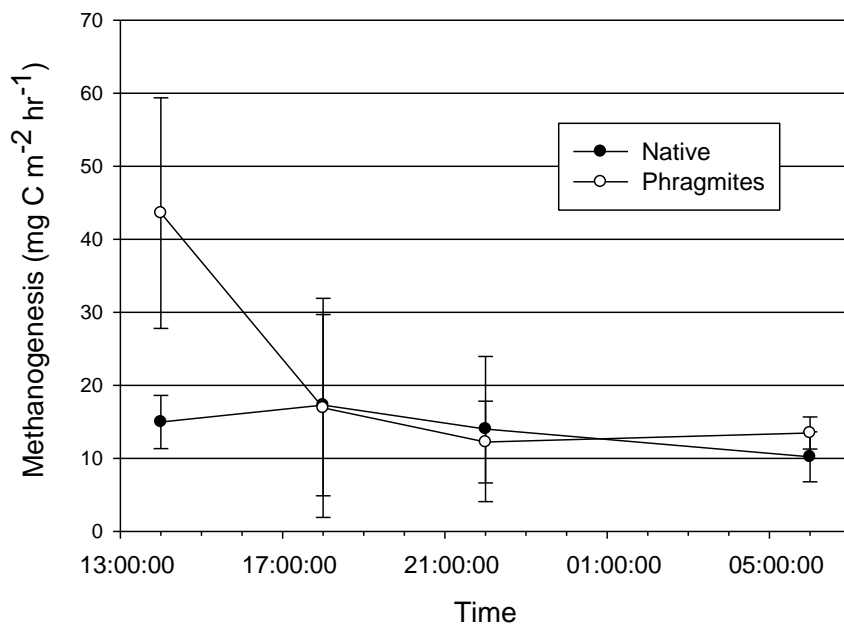
Fig. 7. Methanogenesis rates (mg C m^{-2} hr^{-1}) collected from the headspaces of the PVC

cores using 4-hour incubation periods (except for the 22:00:00 incubation which was an 8

hour) on 11 August 2009 to 12 August 2009. Error bars represent ± 1 standard deviation.
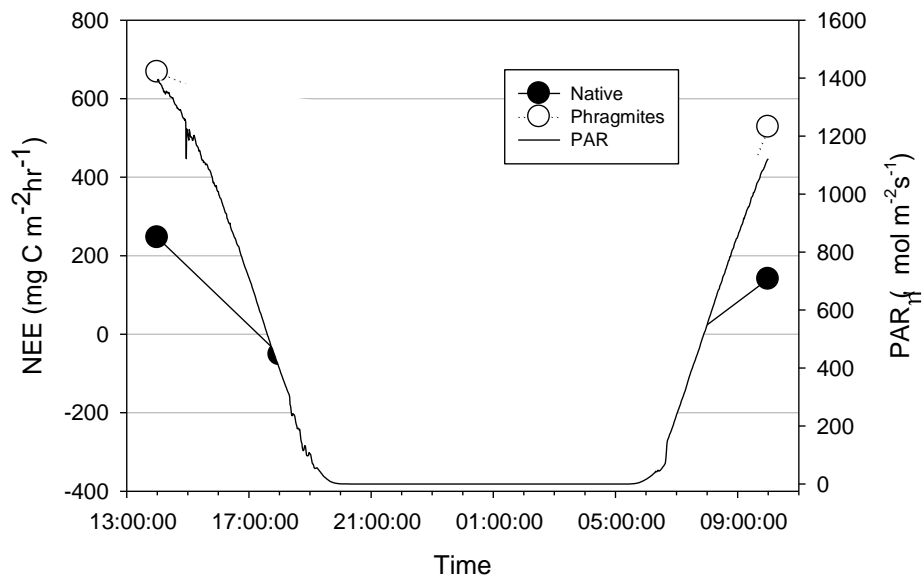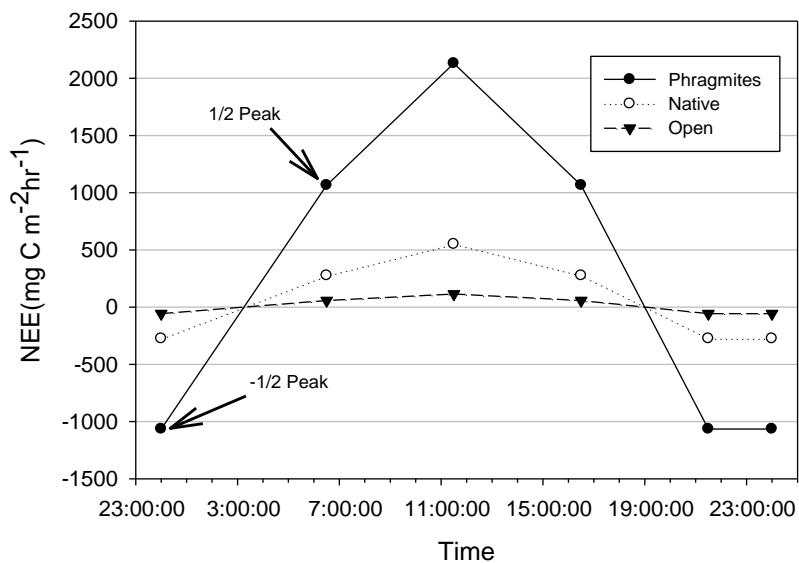
Fig. 8. Modeled daily change in net ecosystem exchange of carbon rates (NEE; mg C m$^-$^{2}hr$^-$^{1}) in which positive values represent C fixation and negative values represent a flux of C to the atmosphere. The shape of these curves was based on the diel experiment conducted on 11-Aug-09 and 12-Aug-09 while the values are on peak NEE rates measured on 22-Jun-09.

Fig. 9. Monthly NEE (g C m^{-2}) within each habitat type based on model data.

Appendix 1. Calculation of CO_2 Flux

Ideal Gas Law

$$PV = nRT \qquad n = \frac{PV}{RT}$$

Where

P = partial pressure of CO_2 (atm)
V = volume of the chamber (L)
R = Gas constant (atm K^{-1} mol^{-1})
T = Temperature (K)
n = number of moles of CO_2

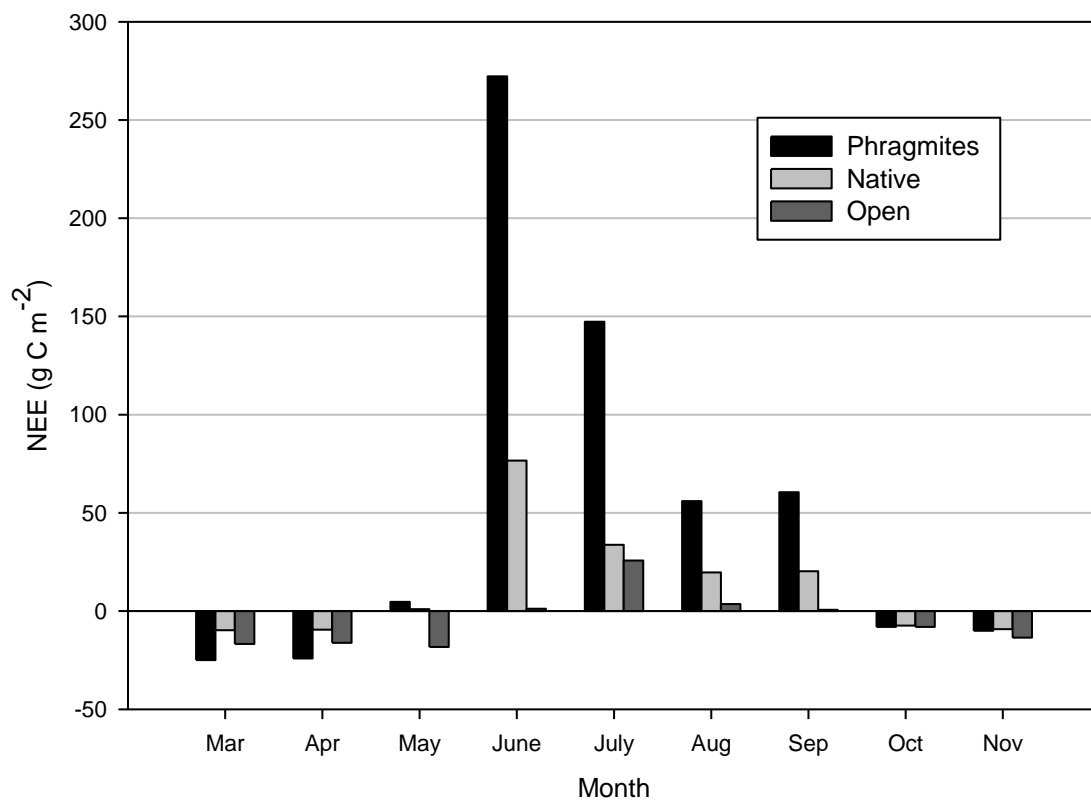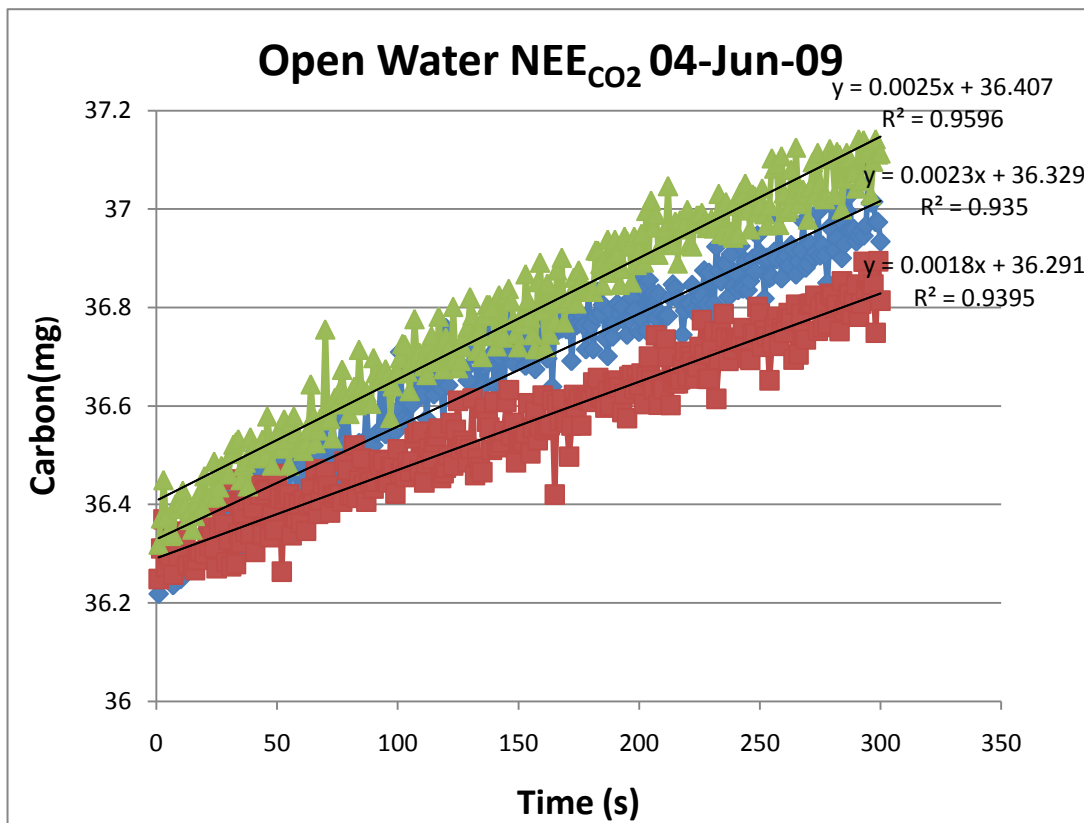| Time	CO2	CO2	Temperature	Temperature	CO2	CO2	C
s	ppm	atm	°C	K	mol	mg	mg
1	369.57	0.00037	20.126	293.276	0.00302	132.8986	36.21822
2	369.91	0.00037	20.126	293.276	0.003023	133.0209	36.25154
3	370	0.00037	20.126	293.276	0.003023	133.0532	36.26036
4	369.89	0.00037	20.126	293.276	0.003022	133.0137	36.24958
5	369.98	0.00037	20.079	293.229	0.003024	133.0674	36.26421
6	370.27	0.00037	20.079	293.229	0.003026	133.1717	36.29264
7	369.69	0.00037	20.079	293.229	0.003021	132.9631	36.23579
8	370.22	0.00037	20.079	293.229	0.003026	133.1537	36.28774
9	369.89	0.00037	20.079	293.229	0.003023	133.035	36.25539
10	369.75	0.00037	20.031	293.181	0.003022	133.0064	36.2476
11	369.81	0.00037	20.031	293.181	0.003023	133.028	36.25349
12	369.96	0.00037	20.031	293.181	0.003024	133.082	36.26819
13	370.22	0.00037	20.031	293.181	0.003026	133.1755	36.29368
14	369.98	0.00037	20.031	293.181	0.003024	133.0892	36.27015
15	370.25	0.00037	19.984	293.134	0.003027	133.2076	36.30244
16	369.95	0.00037	19.984	293.134	0.003024	133.0997	36.27303
17	370.01	0.00037	19.984	293.134	0.003025	133.1213	36.27891
18	370.3	0.00037	19.984	293.134	0.003027	133.2256	36.30734
19	371.17	0.000371	19.984	293.134	0.003034	133.5386	36.39264
20	370.21	0.00037	19.936	293.086	0.003027	133.2151	36.30446
21	370.65	0.000371	19.936	293.086	0.003031	133.3734	36.34761
22	370.21	0.00037	19.936	293.086	0.003027	133.2151	36.30446

Open Water NEE$_{CO_2}$ 04-Jun-09

$y = 0.0025x + 36.407$
$R^2 = 0.9596$

$y = 0.0023x + 36.329$
$R^2 = 0.935$

$y = 0.0018x + 36.291$
$R^2 = 0.9395$

	NEE$_{CO_2}$	NEE$_{CO_2}$
Collar	mg s^{-1} chamber area	mg m^{-2} hr^{-1}
O1	0.0023	42.93
O2	0.0018	33.73
O3	0.0025	45.99

Appendix 2. Calculation of R_{soil} and Methanogenesis rates

$$C\ produced(mg) = \Delta ppm * density(mg\ L^{-1}) \times volume\ of\ chamber(L)$$

Density of CO$_2$ at STP							
1799 mg L^{-1}							
Sample	Pre conc	Post conc	Δ	Δ	Headspace Height	Volume	C $_{Produced}$
	ppm	ppm	ppm	mg L^{-1}	cm	L	mg
O1	397.27	1478.18	1080.91	1.94	8.26	0.67	0.36
O2	474.55	1450.91	976.36	1.76	22.86	1.85	0.89
O3	634.55	4510.91	3876.36	6.97	16.51	1.34	2.55
N1	627.27	7694.55	7067.27	12.71	9.53	0.77	2.68
N2	500.91	1111.82	610.91	1.10	17.15	1.39	0.42
N3	605.45	3056.36	2450.91	4.41	20.76	1.68	2.03
P1	1218.18	9829.09	8610.91	15.49	27.31	2.21	9.36
P2	410.91	4692.73	4281.82	7.70	27.94	2.27	4.76
P3	410.91	7908.18	7497.27	13.49	18.42	1.49	5.50

$$R_{Soil}\ (mg\ C\ m^{-2}hr^{-1}) = \frac{C_{produced}(mg)}{Time_{incubation}(hr) \times\ Area_{Chamber}(m^2)}$$

Sample	C Produced	Time	Area	R$_{soil}$
	mg	hr	m^{-2}	mg C hr^{-1} m^{-2}
O1	0.36	27.00	0.0081	1.62
O2	0.89	27.12	0.0081	4.04
O3	2.55	27.13	0.0081	11.58
N1	2.68	27.18	0.0081	12.16
N2	0.42	27.20	0.0081	1.89
N3	2.03	27.22	0.0081	9.18
P1	9.36	27.18	0.0081	42.46
P2	4.76	27.17	0.0081	21.62

$$C\ produced(mg) = \Delta ppm * density(mg\ L^{-1}) \times volume\ of\ chamber(L)$$

Density of CH$_4$ at STP							
717 mg L^{-1}							
Sample	Pre conc	Post conc	Δ	Δ	Headspace Height	Volume	C $_{Produced}$
	ppm	ppm	ppm	mg L^{-1}	cm	L	mg
O1	1147.74	14527.48	13379.73	9.59	8.26	669.26	4.81
O2	9558.46	55022.74	45464.27	32.60	22.86	1853.33	45.23
O3	4106.96	24955.16	20848.19	14.95	16.51	1338.52	14.98
N1	9923.19	18147.86	8224.67	5.90	9.53	772.22	3.41
N2	1211.41	9970.43	8759.02	6.28	17.15	1390.00	6.54
N3	1464.54	13838.39	12373.85	8.87	20.64	1673.15	11.11
P1	7221.30	10319.03	3097.73	2.22	27.04	2191.81	3.64
P2	581.28	6950.25	6368.97	4.57	27.94	2265.19	7.74
P3	496.81	4966.11	4469.29	3.20	18.42	1492.96	3.58

$$Methanogenesis\ (mg\ C\ m^{-2}hr^{-1}) = \frac{C_{produced}(mg)}{Time_{incubation}(hr) \times\ Area_{Chamber}(m^2)}$$

C Produced	Time	Area	Methanogenesis	
mg	hr	m^{-2}	mg C hr^{-1} m^{-2}	
4.81	27.00	0.0081	21.95	
45.23	27.12	0.0081	205.74	
14.98	27.13	0.0081	68.10	
3.41	27.18	0.0081	15.47	
6.54	27.20	0.0081	29.64	
11.11	27.22	0.0081	50.37	
3.64	27.18	0.0081	16.54	
7.74	27.17	0.0081	35.16	
3.58	27.18	0.0081	16.25	