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ARTICLE

Increased Methane Emissions by an Introduced *Phragmites australis* Lineage under Global Change

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Abstract North American wetlands have been invaded by an introduced lineage of the common reed, *Phragmites australis*. Native lineages occur in North America, but many populations have been extirpated by the introduced conspecific lineage. Little is known about how subtle changes in plant lineage may affect methane (CH_4) emissions. Native and introduced *Phragmites* were grown under current and predicted future levels of atmospheric CO_2 and nitrogen(N) pollution in order to understand how CH_4 emissions may vary between conspecific lineages. We found introduced *Phragmites* emitted more CH_4 than native *Phragmites*, and that CH_4 emissions increased significantly in both with CO_2+N treatment. There was no significant difference in CH_4 production potentials, but CH_4 oxidation potentials were higher in soils from the introduced lineage. Intraspecific plant responses to resource availability changed CH_4 emissions, with plant density, root mass, and leaf area being significantly positively correlated with higher emissions. The absence of CO_2-only or N-only effects highlights a limitation on the generalization that CH_4 emissions are proportional to plant productivity. Our data suggest that intraspecific changes in plant community composition have important implications for greenhouse emissions. Furthermore, global change-enhanced invasion by introduced *Phragmites* may increase CH_4 emissions unless these factors cause a compensatory increase in carbon sequestration.

Keywords Invasive · Conspecific · Congener · *Phragmites* · Methane · Greenhouse Gas · Elevated carbon dioxide · Nitrogen · Wetland

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Introduction

North American tidal and non-tidal wetlands are being rapidly invaded by an introduced genetic lineage of the common reed, *Phragmites australis* subsp. *australis* (hereafter introduced *Phragmites*) (Saltonstall 2002). Introduced *Phragmites* has replaced native plant species in Atlantic Coast tidal wetlands (Marks et al. 1994; Chambers et al. 1999), including a genetic lineage that is native to North America, *Phragmites australis* subsp. *americanus* (hereafter native *Phragmites*) (Saltonstall 2002). The replacement of native plant communities by invasive species like introduced *Phragmites* has the potential to change the radiative forcing of a wetland. Earlier work has shown that differences in plant species (van Hannen et al. 1999) or cultivar (Lou et al. 2008) can have profound effects on methane (CH_4) emissions. Such differences in CH_4 emissions are attributed to differences in plant traits that influence the balance between plant-supported CH_4 production and oxidation (Sutton-Grier and Megonigal 2011) and ecophysiological phenomena that regulate the ventilation of CH_4 through plants to the atmosphere (Sharkey et al. 1991; Garnet et al. 2005).

Plant community composition, productivity and physiology respond to a variety of global change forcing factors such as rising atmospheric CO_2 concentrations and nitrogen (N) pollution. Elevated CO_2 generally stimulates CH_4 emissions in both natural ecosystems and agricultural systems (Xu et al. 2004; Lou et al. 2008; van Groenigen et al. 2011). However, different plant species vary in their growth response to elevated CO_2 (Poorter and Navas 2003), and in their sensitivity to elevated CO_2 stimulation of CH_4 emissions (Vann and Megonigal 2003), making it difficult to predict the effects of elevated CO_2 on radiative forcing when it is accompanied by a change in dominant plant species.

The effects of N availability on wetland CH_4 emissions can also be strongly influenced by the effects of N on plants. For example, Granberg et al. (2001) found both increases and decreases in CH_4 emissions from a poor fen depending on sedge density and the sedge response to N. On similar

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sites, N stimulated CH_4 emissions in the presence of some plant species but not others (Nykanen et al. 2002). However, the biogeochemical mechanisms by which N addition affects CH_4 emissions are fundamentally different from those of elevated CO_2 because N directly affects both plant and microbial communities, while all direct elevated CO_2 effects are mediated by plants only. This is one reason the effects of N on CH_4 emissions can be positive, negative or nil even within relatively simple and managed wetland systems such as rice paddies (Cai et al. 2007).

Tidal wetlands support some of the highest carbon sequestration rates on Earth (Donato et al. 2011; Mcleod et al. 2011), making them attractive ecosystems for carbon management. However, these systems are also capable of emitting enough CH_4 to completely offset the radiative benefits of carbon sequestration, especially in low salinity systems (Poffenbarger et al. 2011). Thus, there is a need to understand how interacting global change factors such as elevated CO_2, anthropogenic N pollution, and plant invasion will alter CH_4 emissions and the radiative balance of tidal wetlands.

We evaluated how CH_4 emissions may change with elevated CO_2 and N pollution by comparing native and introduced genetic lineages of the common reed, *Phragmites australis*. We previously demonstrated greater growth and productivity in the introduced lineage under ambient field conditions (Mozdzer and Zieman 2010) and under predicted global change conditions (Mozdzer and Megonigal 2012). As a consequence of greater growth in an elevated CO_2 environment, we hypothesized an increase in CH_4 emissions proportional to plant growth.

Methods

The experimental design is summarized below and described in detail by Mozdzer and Megonigal (2012) who investigated phenotypic plasticity in response to global change factors. Individual rhizome fragments of native or introduced *Phragmites* were planted (11–12 June, 2009) into 15-liter pots (24 cm×24 cm×33 cm deep) (n=48 native and n=48 introduced) containing reed-sedge peat (Baccto, Houston, TX) and kept in a greenhouse at the Smithsonian Environmental Research Center until shoot emergence. The native and introduced *Phragmites* plants used in this study were previously genetically identified and grown in a common environment at the University of Rhode Island since 2006 (Meyerson et al. 2010). Each pot was considered an independent experimental unit because there was no hydrologic connectivity between pots. Four macropores (holes) were bored vertically into the soil (1.25 cm diameter×25 cm deep) to allow water movement throughout the pot. Upon emergence of the first shoots (19 June), individual pots were randomly assigned a CO_2 and N treatment, and transferred to one of six CO_2 controlled outdoor chambers as described in Wolf et al. (2007). Three replicate chambers had ambient atmospheric CO_2, and the other three replicate chambers were elevated to 330±23 ppmv above ambient concentration. Within each chamber, half the plants were assigned to either a control N treatment (no added N) or an added N treatment, where N was added every two weeks as NH_4Cl (0.058 mol N in 14 ml DI water) to yield a N loading rate of 25 g N m^{-2} y^{-1}, representative of current levels of anthropogenic N pollution in Atlantic coast wetlands (Hopkinson and Giblin 2008) where native an introduced lineages coexist. The soil surface was ~8 cm below the top of the pot, and soils were continuously inundated by at least 3 cm of water with daily additions of tap water. Fifty-two (n=27 native, n=25 introduced) rhizome fragments emerged resulting in two to four internal replicates per treatment per chamber. On 21 July, 0.29 g Potash (Espoma Quick Solutions) and 0.24 g Triple Phosphate (Espoma Quick Solutions) were added to alleviate an apparent macronutrient deficiency, yielding an N-P-K of 10:1:1 in the N-fertilized treatment and 0:1:1 in the control treatment.

Methane emissions were measured over the course of one week, beginning 11 August, by enclosing the aboveground leaves and stems within an opaque PVC chamber (150 cm height×25 cm diameter) 2 months after planting. Because the chambers blocked light, emissions represent the diffusive pathway through plants, not the light-driven pressurized pathway that can be up to five times higher. However, the lack of light during these short-term (2 h) measurements did not interfere with the effects of elevated CO_2 on methane emissions, which operate through the cumulative influence of higher photosynthetic rates on plant biomass, not instantaneous coupling between photosynthesis and methanogensis (Megonigal et al. 1999; Vann and Megonigal 2003). The chambers were supported by an adjustable frame and placed so that the chamber bottom was below the flood water to form a seal against CH_4 exchange. Although care was taken not to disturb the sediments, the tops of the PVC chambers were initially left open (uncapped) in order for soil and floodwater CH_4 concentrations to return to equilibrium. After approximately thirty minutes, the top of the chambers were sealed with closed-cell neoprene foam. Gas samples (20 ml) were collected every 20 min with polyurethane syringes through a rubber septa sampling port and analyzed for [CH_4] on a Shimadzu GC-14A gas chromatograph equipped with a flame ionization detector (Kyoto, Japan). These two hour flux measurements were performed daily between 10:30 to 14:00 to control for diurnal variation. Emissions were measured on six pots at a time, one from each chamber. Methane emission rate was calculated from the linear increase of CH_4 concentration over time; fluxes with r^2 values <0.90 were not used in our analysis. Redox potentials were determined at 5, 15, and 30 cm below the surface of the soil with a platinum electrode referenced to a calomel electrode.

At the conclusion of the experiment (20–27 August), a 30 cm^3 core was removed from each pot and stored at 4 °C under high-purity N_2 gas to be used for assays of CH_4 production and oxidation potential. Plant biomass was sorted into stems, leaves, roots, and rhizomes to determine biomass. Plant leaf area was determined for each pot by measuring the total leaf area with a LI-3000 leaf area meter (LiCor Biosciences, Lincoln, NE). Plant parts were washed, oven dried at 60 °C to constant mass, and weighed.

One month later, soil samples were transferred from cold storage to an anaerobic chamber (95 % N_2 and 5 % H_2) and processed. Approximately 3 g wet weight root free soil was slurried in 10 ml of degassed DI water and sealed in 70 ml serum bottles with butyl stoppers. Bottles were subsequently flushed with high-purity N_2 to remove H_2 from the headspace. Methane production potentials were determined over a period of 4 days at room temperature by analyzing headspace samples (200 μl) for [CH_4]. Methane accumulation rates were linear (r^2>0.90), and are expressed as per day per gram dry soil.

Methane oxidation potentials were determined by a similar design with the following exceptions. Soils were processed in a wet condition outside the anaerobic chamber in an aerobic environment, upon sealing the headspace of the serum bottle was amended to increase [CH_4] to ~15,000 μl l^{-1}, and bottles were continuously agitated on a shaker table. CH_4 oxidation potentials were estimated as the linear (r^2>0.90) consumption of CH_4 measured four times over 18 h, and are expressed as consumption per day per gram dry soil.

Statistical Analysis

The experimental design was factorial with two levels of CO_2 (ambient & elevated), two levels of N (control & enriched), and two genetic lineages (native and introduced). Data were analyzed using SAS version 9.2 (SAS Institute Inc., Cary, NC). To prevent pseudoreplication, within chamber replicates were averaged to create a single chamber mean per treatment resulting in a sample size (n) of 3 per treatment for the subsequent ANOVA. We determined the effects of CO_2, N, and lineage on CH_4 emissions, CH_4 potentials, CH_4 oxidation potentials, and redox using ANOVA (Proc GLM). The data were log transformed when necessary to meet the assumption of normality. CO_2 and N were treated as fixed effects, and plant genotype was a random effect. Pearson correlation coefficients were determined using Proc Corr in SAS to determine relationships between plant parameters and CH_4 emissions. To reduce the risk of type II error from the limited replication of our experimental design (n=3), we interpreted differences at α=0.10 to be significant.

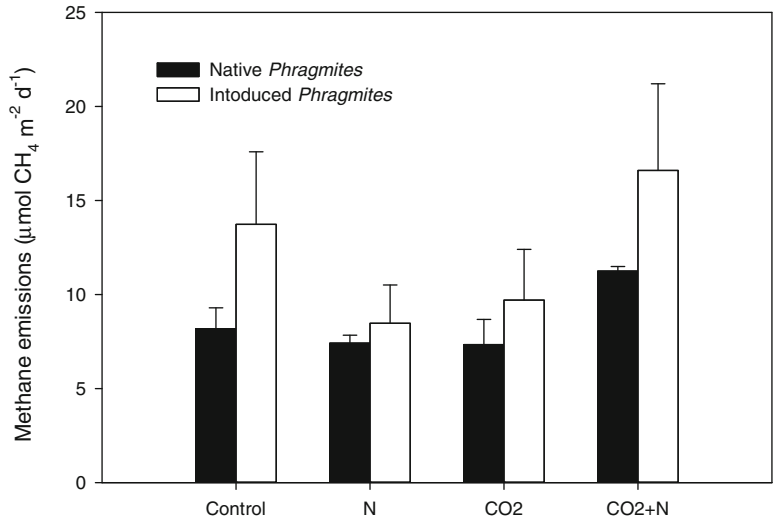
Results

Introduced *Phragmites* emitted more CH_4 than the native type (p=0.061), and CH_4 emissions in both lineages were stimulated by the combination of elevated CO_2 and N (p=0.031, Fig. 1a). Methane emissions pooled across all treatments were positively correlated with plant growth parameters, including root mass (p=0.032), ramet density (p<0.001), and leaf area (p=0.008) (Fig. 2). Root mass, ramet density, and leaf area were significantly greater in the introduced than the native genotype (data in Mozdzer and Megonigal 2012). No significant differences were observed in potential CH_4 production between lineages or among treatments (Fig. 1b). Potential CH_4 production was negatively correlated with redox potential (p=0.019, R^2=0.23, Fig. 3a). Potential CH_4 oxidation was greater in the introduced lineage (p=0.004), and there was a non-significant trend that suggested a reduction in oxidation potentials in the native lineage treated with added N (GxN, p=0.103, Fig. 1c). There was a positive relationship between CH_4 oxidation potentials and root mass (p=0.023, R^2=0.13, Fig. 3b). Redox potentials measured in the pots at soil depths of 5, 15, and 30 cm were not affected by genotype, elevated CO_2, and N; however, the combination of CO_2 and N lowered redox potentials in the introduced lineage at 15 and 30 cm depths (genotype×CO_2×N, p=0.074 and p=0.094, respectively, Table 1).

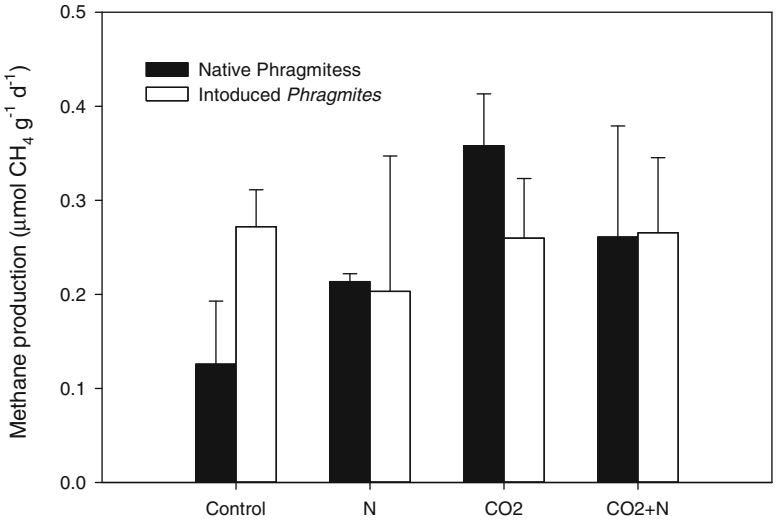
Discussion

Methane emissions varied significantly between two genotypes of *Phragmites australis*, with the introduced lineage generally associated with higher CH_4 emissions. Our data show that genetic variation within a single species has the potential to change the radiative forcing of a wetland. Previous studies have reported that invasive plant species can stimulate wetland CH_4 emissions through species replacement (Cheng et al. 2007; Ding et al. 2010) or the response of invasive species to elevated CO_2 (Kao-Kniffin et al. 2011), and that genetic variation among rice cultivars produced by selective breeding causes variation in CH_4 emissions (Watanable et al. 1995). Our study contributes to the observation that even the relatively subtle genetic differences among con-specific genotypes produced through natural breeding can alter CH_4 emissions.

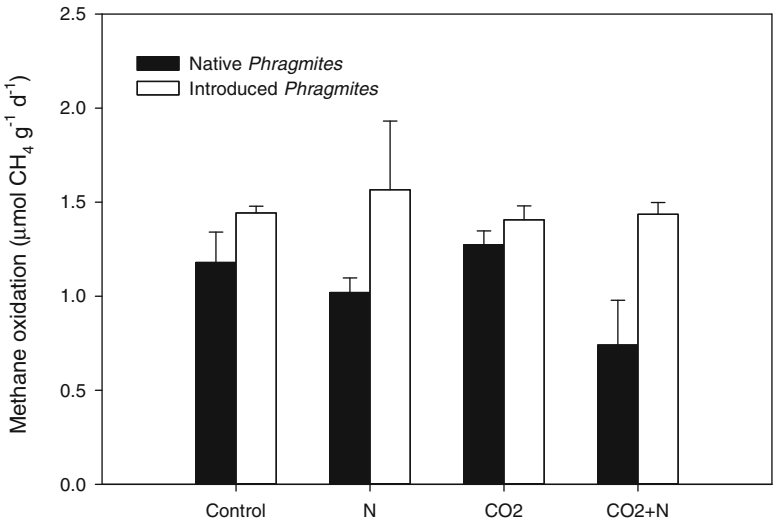
Caution should be exercised in the application of these results to wetland management. The CH_4 emission rates measured in this experiment do not reflect field conditions because: (i) emissions measured in darkness represent diffusive plant emissions only, and not light-driven pressurized CH_4 transport that is two to five times greater (Kim et al. 1998); (ii) although our experimental system was designed to accommodate large plants, the rooting depth of *Phragmites*



Effect	F	p
Genotype (G)	4.1	**0.061**
N	0.5	0.511
CO_2	1.0	0.334
CO_2× N	5.6	**0.031**
G × N	0.1	0.833
G × CO_2	0.0	0.879
G × CO_2 × N	1.1	0.308



Effect	F	p
Genotype (G)	0.03	0.861
N	0.10	0.760
CO_2	2.00	0.176
CO_2 × N	0.22	0.642
G × N	0.05	0.821
G × CO_2	0.97	0.339
G × CO_2 × N	1.23	0.283



Effect	F	p
Genotype (G)	11.3	**0.004**
N	1.2	0.286
CO_2	0.5	0.483
CO_2 × N	0.9	0.352
G × N	3.0	0.103
G × CO_2	0.0	0.971
G × CO_2 × N	0.3	0.576

Fig. 1 Effects of elevated CO_2 and N pollution on mean (**a**) net CH_4 emissions from static chambers, (**b**) CH_4 production potentials from soil incubations, and (**c**) CH_4 oxidation potentials from soil incubations on both native and introduced *Phragmites australis*. Effect tables summarizing three way genotype×CO_2×N ANOVA tests are shown beside each panel

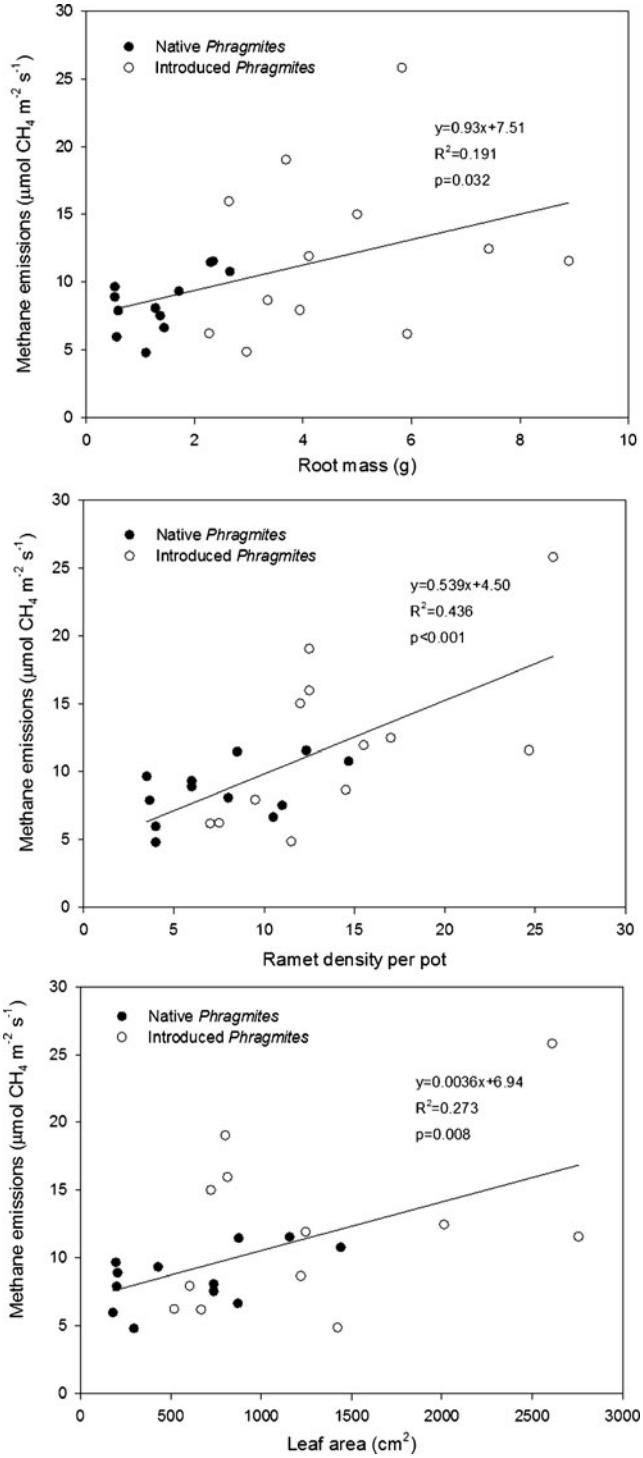


Fig. 2 Relationship between CH_4 emissions and (**a**) root mass, (**b**) ramet density, and (**c**) leaf area in native and introduced *Phragmites australis*

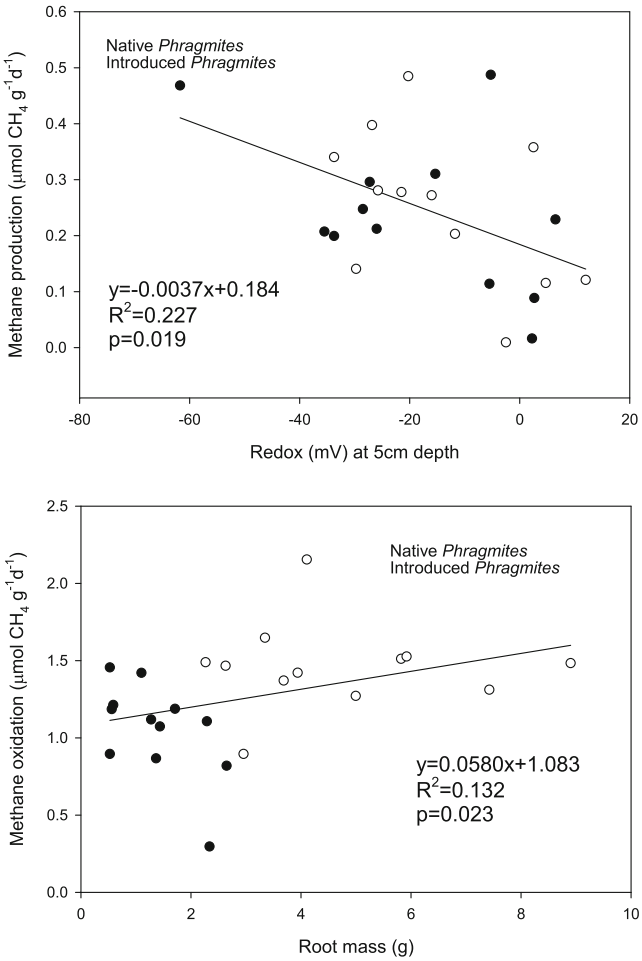


Fig. 3 Relationship between (**a**) CH_4 production potentials at and redox at 5 cm depth and (**b**) CH_4 oxidation potentials and root mass in native and introduced *Phragmites australis*

growing in situ exceeds those in this study; (iii) our study does not compare introduced *Phragmites* to other wetland plant species; (iv) the absence of tidal hydrology in this study may have influenced CH_4 oxidation rates (Megonigal and Schlesinger 2002); and (v) a complete accounting of treatment effects on radiative forcing requires data on changes in the soil carbon pool. Rather, these data emphasize that change in CH_4 emissions can occur even with genotype-level substitution of plant species, which in this case increased emissions by 68 % under ambient

Table 1 Mean redox (mV) and SE for each *Phragmites* lineage. Neither genotype, CO_2, or N independently affected soil redox conditions, however, there is a significant genotype×CO_2×N interaction at both the 15 cm (p=0.074) and 30 cm (p=0.094) depths

Depth	Control	SE	N	SE	CO_2	SE	CO_2+N	SE
Native *Phragmites*								
−5	−10.6	9.2	−17.8	12.3	−34.8	13.9	−12.7	11.6
−15	−221.9	7.3	−224.3	8.8	−238.5	11.6	**−200.4**	**15.0**
−30	−173.6	25.1	−187.5	12.1	−200.3	15.0	**−154.8**	**15.0**
Introduced *Phragmites*								
−5	−20.5	6.7	−6.0	7.4	−17.7	10.1	−12.1	12.2
−15	−215.1	4.9	−200.3	8.5	−221.6	21.6	**−227.3**	**11.8**
−30	−192.8	7.8	−173.1	6.4	−153.2	35.6	**−173.6**	**9.2**

conditions (Fig. 1). Because introduced *Phragmites australis* exhibits tremendous genotypic variation (McCormick et al. 2010; Kettenring and Mock 2012), and given the broad geographic extent of introduced *Phragmites* invasion (Chambers et al. 1999; Kettenring et al. 2012), our data argue for field studies that consider the consequences of genotypic variation for important ecosystem services such as carbon sequestration (Brix et al. 2001).

The most parsimonious explanation for the differences in CH_4 emissions we observed is that variation in resource availability regulated plant productivity, which in turn was the primary source of labile carbon supporting methanogenesis. When pooled across treatments, CH_4 emissions were positively related to several measures of plant productivity including root mass, plant density and leaf area (Fig. 2). These data indicate that the net effect of faster growth by the introduced *Phragmites* genotype compared to the native genotype was to stimulate net CH_4 emissions. Plant growth increased significantly with increased resource (i.e. CO_2, N, and $CO_2 \times N$) in the presence of both genotypes (Mozdzer and Megonigal 2012), as did CH_4 emissions (Fig. 2). Similar relationships between plant production and CH_4 emissions have been reported in the past based on field observations (Whiting and Chanton 1993) and experimental manipulations similar to ours (Vann and Megonigal 2003).

Previous studies have reported that elevated CO_2 alone can increase wetland CH_4 emissions (reviewed in van Groenigen et al. 2011). In the present experiment, elevated CO_2 stimulated CH_4 emissions only in combination with added N, providing an example of an interaction among global change factors that must be considered in order to forecast changes in emissions of this greenhouse gas. The absence of CO_2-only or N-only effects highlights a limitation on the generalization that CH_4 emissions are proportional to plant productivity because there were CO_2-only and N-only effects on plant growth (Mozdzer and Megonigal 2012). One reason that CH_4 emissions do not always increase linearly with plant growth is that plants also inhibit CH_4 emissions by regenerating alternative electron accepting compounds in the rhizosphere (Neubauer et al. 2005; Sutton-Grier and Megonigal 2011) and by supporting CH_4 oxidizing bacteria (Fig. 3b) (Megonigal and Schlesinger 2002). Thus, while the net effect of increased plant growth may often be to increase CH_4 emissions as in the present study, there are instances where the net effect is to decrease CH_4 emissions (Sutton-Grier and Megonigal 2011). This insight is useful to consider when managing wetlands for certain species or genotypes.

Differences in CH_4 emissions were likely influenced by treatment effects on CH_4 oxidation. Methane oxidation potentials reflect the size of the methanotroph community at the end of the experiment, which in turn reflects CH_4 and O_2 levels in soils. Higher potential CH_4 oxidation rates in soils planted with the introduced lineage versus the native lineage is consistent with the observation that the introduced lineage produced two to three times more roots in any given treatment (Fig. 3, Mozdzer and Megonigal 2012). Although redox did not differ significantly among the treatments, we suspect that increased root growth caused higher root oxygen loss and stimulated methanotrophic activity.

There are additional caveats to consider in interpreting our data. We did not explicitly measure CH_4 ebullition and therefore cannot unequivocally interpret differences in diffusive CH_4 emissions as differences in total CH_4 emissions. However, our best professional judgment is that significant ebullition from our experimental system was unlikely because of high plant densities. Also, we suspect that differences in plant productivity stimulated CH_4 production (as well as CH_4 emissions), despite the lack of significant differences in CH_4 production potentials across treatments; soils for this assay were collected only from the top 10 cm of the soil profile and did not reflect methanogenic activity in deeper soils that were more anaerobic (Table 1).

In conclusion, our data support the hypothesis that increased plant productivity will increase CH_4 emissions from wetlands (van Groenigen et al. 2011). Productivity increased as the result of genotypic variability within a single species, and as the result of increased resource availability (i.e. elevated CO_2 and N) regardless of genotype. Based on this experiment and previous work showing that introduced *Phragmites* has traits that support relatively high productivity in field settings (Mozdzer and Zieman 2010; Mozdzer and Megonigal 2012; Tulbure et al. 2012), we suggest that the spread of introduced *Phragmites* will increase CH_4 emissions from North American wetlands, and that methane emissions will increase as atmospheric CO_2 concentration continues to rise. These changes in CH_4 emissions will cause radiative forcing unless there is an equivalent increase in carbon sequestration (Poffenbarger et al. 2011).

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