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Enhanced CH_4 emissions from a wetland soil exposed to Elevated CO_2

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Abstract. Methane emissions from wetland soils are generally a positive function of plant size and primary productivity, and may be expected to increase due to enhanced rates of plant growth in a future atmosphere of elevated CO_2. We performed two experiments with *Orontium aquaticum*, a common emergent aquatic macrophyte in temperate and sub-tropical wetlands, to determine if enhanced rates of photosynthesis in elevated CO_2 atmospheres would increase CH_4 emissions from wetland soils. *O. aquaticum* was grown from seed in soil cores under ambient and elevated (ca. 2-times ambient) concentrations of CO_2 in an initial glasshouse study lasting 3 months and then a growth chamber study lasting 6 months. Photosynthetic rates were 54 to 71% higher under elevated CO_2 than ambient CO_2, but plant biomass was not significantly different at the end of the experiment. In each case, CH_4 emissions were higher under elevated than ambient CO_2 levels after 2 to 4 months of treatment, suggesting a close coupling between photosynthesis and methanogenesis in our plant-soil system. Methane emissions in the growth chamber study increased by 136%. We observed a significant decrease in transpiration rates under elevated CO_2 in the growth chamber study, and speculate that elevated CO_2 may also stimulate CH_4 emissions by increasing the extent and duration of flooding in some wetland ecosystems. Elevated CO_2 may dramatically increase CH_4 emissions from wetlands, a source that currently accounts for 40% of global emissions.

Introduction

Vascular plants enhance CH_4 emissions from wetlands. Carbon assimilation by plants is the ultimate source of organic substrates for methanogenic bacteria (Oremland 1988) and plant vascular tissue is a conduit for CH_4 diffusion from sediments to the atmosphere (Chanton & Dacey 1991). The positive correlation that exists between CH_4 emission rates and net ecosystem production in North American wetlands (Whiting & Chanton 1993) is evidence that plant productivity is a key process regulating CH_4 emission from wetlands at a regional scale. The central role of plant production is also supported by observations that amendments of rice straw stimulate methane production in paddy soils (Sass et al. 1991; Cicerone et al. 1992; Watanabe et al. 1995), and additions of H_2 or labile carbon compounds often increase CH_4 produc-

tion in laboratory soil incubations (Yavitt et al. 1987; Valentine et al. 1994). Environmental factors that influence photosynthesis or plant production in wetlands may indirectly regulate methane emissions.

Carbon dioxide concentrations have increased dramatically during this century, and are expected to double again by the end of the next century (IPCC 1995). Although it is well established that most plants respond to elevated CO_2 with increased rates of photosynthesis (Curtis 1996; Sage 1994; Gunderson & Wullschleger 1994), there are few studies of the impact of increased photosynthesis on other ecosystem processes (Field et al. 1992). Plant detritus provides organic carbon compounds that fuel most biogeochemical transformations in soils and sediments, and an increase in their supply may be expected to impact all heterotrophic soil processes, including methanogenesis.

There are other mechanisms by which elevated CO_2 could stimulate methane emissions. An increase in plant biomass may promote methane diffusion from soils by increasing the volume of porous vascular tissue. Lower transpiration rates – a common response of plants to elevated CO_2 – may raise water tables or lengthen periods of inundation. Each of these effects would stimulate CH_4 emissions from wetland ecosystems, which presently account for 40% of all global sources of CH_4 (Cicerone & Oremland 1988), and constitute important biological feedbacks on climate change.

Dacey et al. (1994) reported that elevated CO_2 increased CH_4 emissions from a brackish tidal marsh by 80% after 4 years of treatment. They suggested that this effect was due, in part, to an increase in leaf and root detritus in the high CO_2 treatment, although it was unclear how rapidly such an effect could occur. Hutchin et al. (1995) observed an increase in CH_4 emissions of 145% after exposing intact cores from an ombrotrophic mire to elevated CO_2 for just 6 weeks. Based on evidence that methanogenesis is limited by the availability of labile organic carbon compounds, we also proposed that elevated CO_2 would increase CH_4 emission rates over relatively short periods of time. A rapid response would indicate a tight temporal coupling between photosynthesis and methanogenesis in wetland ecosystems, although other mechanisms that could explain such an observation must be considered. The objective of our study was to determine if short-term exposures to elevated CO_2 would increase CH_4 emissions from a freshwater wetland plant-soil system.

Methods

We collected seeds of *Orontium aquaticum* from a tidal freshwater swamp on the North Carolina coast in spring of 1993 and 1994. *Orontium aquaticum* is

an emergent aquatic macrophyte that occurs throughout the southeastern US coastal plain (Odum et al. 1984). *O. aquaticum* is similar in morphology and appearance to emergent aquatic macrophytes that have been used in previous studies of CH_4 emissions [i.e., *Peltandra virginica* (Chanton et al. 1992) and *Sagittaria lancifolia* (Schipper & Reddy 1996)]. We chose this species because it is common at our field site and bears fruit in the spring when our studies began. Soils collected from the study site had a silty clay loam texture with 22% organic carbon content. Plants were raised from seed under ambient and elevated concentrations of CO_2 in trays of field soil (4 cm deep) that were continuously flooded with one-half strength Hoagland's solution.

We performed experiments in the summers of 1993 and 1994 to determine if elevated CO_2 would influence CH_4 emissions from a wetland plant-soil system over a relatively short period of time. The 1993 experiment was performed in a glasshouse using relatively small volume containers filled with a mixture of 75% sand and 25% field soil. The design of the study was intended to minimize the contribution of the native soil organic carbon to CH_4 production, so that we could more easily observe changes in the contribution of recent photosynthates. Based on the results of the 1993 study, we undertook a similar experiment in 1994 using controlled environmental chambers and unamended soil (without sand addition) from our field site.

Glasshouse experiment

Seedlings were transferred after 8 weeks (30 July 1993) into polyvinyl chloride (PVC) pots (7.5 cm-i.d. by 25 cm deep) filled 20 cm deep with a sand-soil mixture. Glasshouses at the Duke University Phytotron Facility were automatically controlled (Hellmers & Giles 1979) to maintain CO_2 partial pressures of 35 or 70 Pa. Plants were exposed to natural light intensity and photoperiod; photon flux densities in August were about 1500 μmol m^{-2} s^{-1} at mid-day. Glasshouse temperatures were maintained on a day/night schedule of 27/22 C, with the thermoperiod adjusted to follow the photoperiod. Soils were continuously flooded with one-half strength Hoagland's solution and occasionally flushed with fresh nutrient solution to prevent salt accumulation. Evaporation of flood-water and algal growth were minimized by placing a 2 cm-thick styrofoam disk on the surface of each pot in both experiments.

Methane emissions were determined after 9 and 14 weeks of treatment using a static chamber technique. Both plants and soils were enclosed with a 7.6 cm-i.d. PVC chamber capped with a plastic end-cap that was sealed with silicon. The flux chambers were joined to the pots with a PVC coupling modified with a single internal O-ring at each end to ensure an air-tight seal. A rubber septum (Vacutainer stopper) in the end-cap was used to sample the

headspace 4 times over a period of 3 hours. Methane concentrations were immediately determined on a Varian 3700 gas chromatograph with a flame ionization detector, using a Porapak Q 80/100 mesh column at 50 C and He at 30 ml min^{-1} as the carrier gas.

Photosynthesis, conductance, relative humidity and photon flux density were measured with a model 6200 Licor Infrared Gas Analyzer (IRGA)(Licor Inc., Lincoln, NE) inside the glasshouses at treatment CO_2 concentrations. We used the second youngest shoot on each plant to control for leaf age effects. The plants were harvested at the end of the experiment and roots were recovered on a 2 mm-mesh sieve by a combination of floating and washing. Mass was determined after drying at 70 C to constant weight.

Controlled chamber experiment

Soils were collected, sieved free of woody detritus and roots, and used to fill PVC pots (7.6 cm-i.d. by 40 cm deep) to a depth of 30 cm. After 4 weeks (14 July 1994), 32 similar-size seedlings were transferred into randomly assigned pots in each treatment. Six additional pots per treatment remained unplanted for a no-plant control. The plants were raised in growth chambers controlled at CO_2 partial pressures of either 35 or 72 Pa for a period of 6 months. Plants and CO_2 treatments were rotated at monthly intervals to mitigate possible chamber effects. Photon flux density was 1000 μmol m^{-2} s^{-1} and temperature was 30C day/25 C night on a 12-hour cycle. Photosynthesis was measured under growth CO_2 concentrations at a photon flux density of 1300 μmol m^{-2} s^{-1}. Gas exchange measurements were made as described for the glasshouse experiment. The plants were continuously flooded with one-half strength Hoagland's solution. Conductivity measurements in mid-September showed lower salt concentrations in the soil solution (mean = 0.787 m℧) than in the pure Hoagland's solution (1.264 m℧), with no significant difference between treatments (P = 0.61). Platinum redox electrodes were inserted horizontally into 4 pots per treatment at depths of 5 cm and 28 cm below the soil surface and allowed to equilibrate for 1 d before reading with a pH meter.

Eight plants from each treatment were harvested for biomass at the end of the experiment. The soils from 8 additional pots were sectioned at 4-cm intervals and dried at 110 C to constant weight to determine gravimetric water content. Fresh subsamples from these pots were centrifuged at 3500 rpm for 5 min and the supernatant was analyzed for SO_4 on a Dionex 2101i ion chromatograph.

Statistics

Methane fluxes were based on a linear-regression between CH_4 concentration inside static chambers and time (SAS Institute 1987). Because fluxes in the growth chamber experiment were high and easily measured (Figure 1), slopes with regression coefficients (r^2) < 0.90 were discarded (1 observation) and the chambers were compared with a t-test on untransformed data. Methane emissions in this experiment were normally distributed as determined by the Shapiro-Wilk Statistic using the SAS univariate procedure. In the glasshouse experiment, low regression coefficients ($r^2 < 0.90$) were not discarded because these data were assumed to indicate below-detection-limit emission rates, and this information was relevant to our hypothesis. Low emission rates were probably caused by a combination of sandy, low organic C soils and small pots. For the two-month sample, we used a parametric t-test on transformed data because the distributions were log-normal despite having 3 values (2 ambient, 1 elevated) below the detection limit. For the 3-month sample, the non-parametric Kuskal-Wallis test was used to compare treatments (SAS procedure nlin) because 10 values were below the detection limit (7 ambient, 3 elevated).

We considered tests of the median to be appropriate in this study because our pots were self-contained units that were wholly sampled for CH_4 emissions (Parkin & Robinson 1992). Statistical analyses were used to judge differences between experimental groups, but because glasshouses and chambers were not replicated, the presence or absence of a difference cannot be interpreted as unequivocal support for treatment effects.

Results and discussion

Methane emission rates were higher in elevated CO_2 than in ambient CO_2 atmospheres after two to four months of treatment. In the initial glasshouse experiment, the two groups were nearly significantly different after two months ($P = 0.06$), and after three months this difference was particularly dramatic ($P = 0.04$, Figure 1). We obtained a similar result when the study was repeated in growth chambers. Although there were no differences between the chambers during the first two months of the study, CH_4 emissions were higher in the elevated CO_2 chamber than in the ambient CO_2 chamber after four months ($P \leq 0.01$ in months 5 and 6). The magnitude of this increase (136%) suggests that future CH_4 emissions from wetlands may increase dramatically from a source that presently accounts for 40% of the CH_4 emissions globally. The response of our pots to elevated CO_2 was similar to the 145% increase reported by Hutchin et al. (1995) for cores from an ombrotrophic

Table 1. Gas exchange characteristics of *Orontium aquaticum* grown under ambient and elevated CO_2. Values are means ± 1 standard error, with significant differences indicated by asterisks on the larger mean. Relative humidity inside the glasshouses was similar to cuvette values; however, the relative humidity of the growth chambers (ca. 70%) was higher than cuvette levels.

Date	MPa [CO_2]	Sample Sizee	Photosynthesis (μmol m^{-2} s^{-1})	Transpiration (mol m^{-2} s^{-1})	Cuvette Rel. Humidity (%)
Glasshouse					
2 months	35	8	13.6±0.42	7.57±0.36	54±4
	70	9	21.4±0.99**	8.16±0.28	65±1
3 months	35	8	19.2±0.80	7.43±0.29*	59±4
	70	9	32.9±3.16*	5.66±0.42	68±2
Growth Chamber					
6 months	35	9	18.1±0.66	14.11±0.99	31±1
	72	10	27.8±1.62**	9.30±0.95**	31±1

* $P \leq 0.01$.
** $P \leq 0.001$.

mire, and higher than the 80% increase reported by Dacey et al. (1994) for soils in a brackish tidal marsh studied in situ. It appears that large increases in methane emissions in response to elevated CO_2 can occur in a wide variety of wetland ecosystems.

Net photosynthetic rates were 54–71% higher under elevated CO_2 (Table 1), a result consistent with studies of *Scirpus olneyi* (Arp & Drake 1991), *Eriophorum vaginatum* (Hutchin et al. 1995), and a large number of upland plant species (Curtis 1996; Sage 1994; Gunderson & Wullschleger 1994). In a previous study of *Eriophorum vaginatum*, higher photosynthetic rates under elevated CO2 conditions were short-lived due to down-regulation (Tissue & Oechel 1987). Our photosynthesis measurements were made on relatively young leaves only, and the actual increase in CO_2 assimilation on a whole-plant basis is likely to have been smaller than measured due to leaf aging effects (Field & Mooney 1983). Nonetheless, the data suggest that methane emissions increased because of higher photosynthetic activity and release of additional organic carbon to soils.

Plant biomass tended to be higher in elevated CO_2 than in ambient CO_2 atmospheres (Table 2), but there were no significant differences between the two groups in either experiment ($P > 0.10$). Coarse and fine root biomass comparisons in the growth chamber study had P-values of 0.11. Hutchin et al. (1995) also reported that high photosynthetic rates in elevated CO_2 environments did not increase biomass accumulation in an ombrotrophic mire community, and suggested that the excess organic carbon may have been

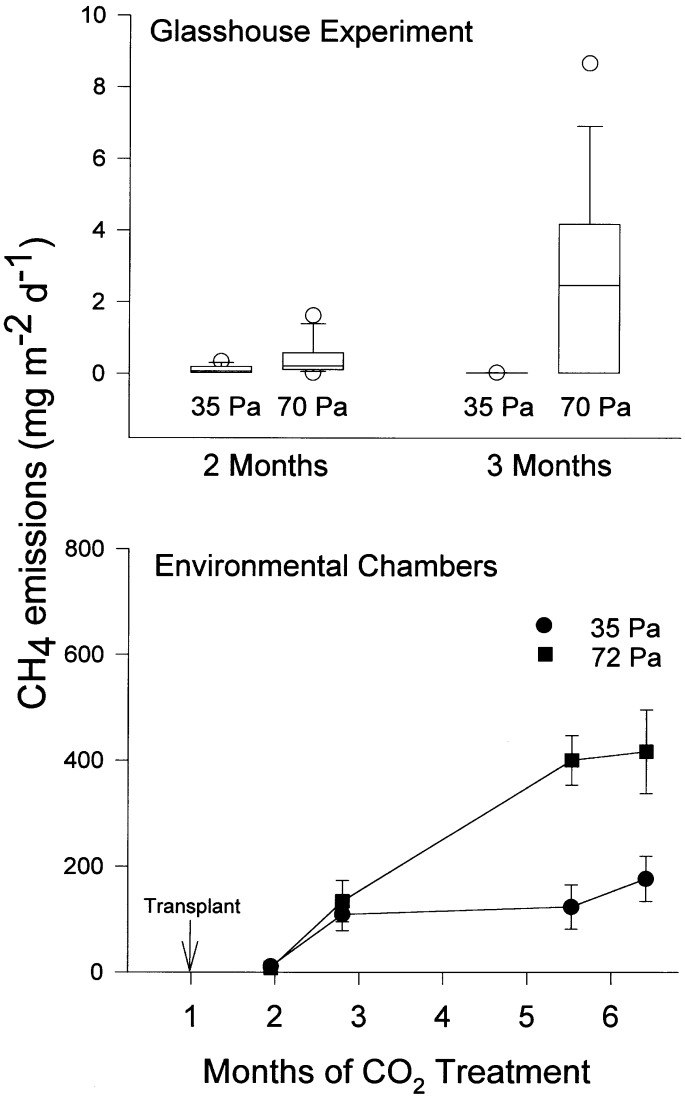

Figure 1. Methane emissions under ambient and elevated levels of atmospheric CO_2 in two independent experiments. Box plots for the glasshouse experiment encompass the 25th to 75th percentiles in emissions; horizontal caps represent the 10th and 90th percentiles; circles are the 5th and 95th percentiles. The median is indicated with a horizontal line inside the box. Values in the environmental chamber experiment are means ± 1 standard error.

released by root exudates. More rapid rates of leaf and root turnover under elevated than under ambient CO_2 conditions is another possible explanation for this result.

Table 2. Dry mass (g) of *Orontium aquaticum* plants at the end of two elevated CO_2 experiments. Values are means ± 1 standard error based on 9 samples in the glasshouse study and 8 samples in the growth chamber study. Change in biomass due to elevated CO_2 (Δ) was calculated as (elevated-ambient) ÷ ambient. There were no significant differences in between-treatment comparisons ($P \geq 0.10$).

	Glasshouse			Growth Chamber		
	35 Pa	70 Pa	%Δ	38 pa	72 Pa	%Δ
Shoot	1.48±0.14	1.91±0.26	29	5.37±0.40	5.95±0.77	11
Fine Root[a]	nd	nd	nd	2.36±0.18	2.81±0.22	19
Course Root	nd	nd	nd	12.96±0.79	15.20±1.07	17
Total Root	2.51±0.36	2.77±0.32	10	15.32±0.93	18.01±1.27	18
Total Plant	3.99±0.43	4.68±0.56	17	20.69±1.22	23.96±1.97	16

[a] nd = not determined

Water table depth and redox potential exert strong control over methane emissions from wetlands (Moore & Dalva 1993; Wang et al. 1993; Funk et al. 1994). We maintained anaerobic conditions in the soil profile by continuously flooding the surface (5 cm deep) and sealing the bottom of our pots with a rubber cap. Redox potentials indicated that the soils were anaerobic with no significant differences between treatments in depth-wise comparisons ($P > 0.27$, Table 3). Nonetheless, we found evidence that differences in transpiration rates (Table 1) affected the water balance in our pots. The gravimetric water content declined with depth in both treatments, indicating that transpiration rates were greater than water percolation rates in this fine-textured soil (Figure 2). The water content of soils with plants grown at ambient and elevated CO_2 were significantly different at 28 cm ($P = 0.05$). A higher gravimetric water content in elevated CO_2 pots, compared to ambient CO_2 pots, indicates a long-term shift toward a more positive water balance under elevated CO_2. Drake (1992) reported lower rates of whole-stand transpiration from elevated CO_2 than ambient CO_2 chambers in a brackish tidal marsh despite an increase in leaf biomass. Leaf biomass was similar between treatments in our study (Table 2).

Most wetlands experience periods when evapotranspiration and runoff exceed precipitation, causing the water table to fall and O_2 infusion into the soil (Megonigal et al. 1993; Faulkner & Patrick 1992). On sites where transpiration is an important component of the water budget, elevated CO_2 may extend the portion of the growing season when soils are saturated and anaerobic. Transpiration accounted for up to 74% of evapotranspiration losses from a tidal freshwater marsh in Virgina (Hussey & Odum 1992), and was shown to be a driving force for O_2 infusion into salt-marsh sediments (Dacey & Howes 1984). More studies that quantify the importance of transpiration in wetland

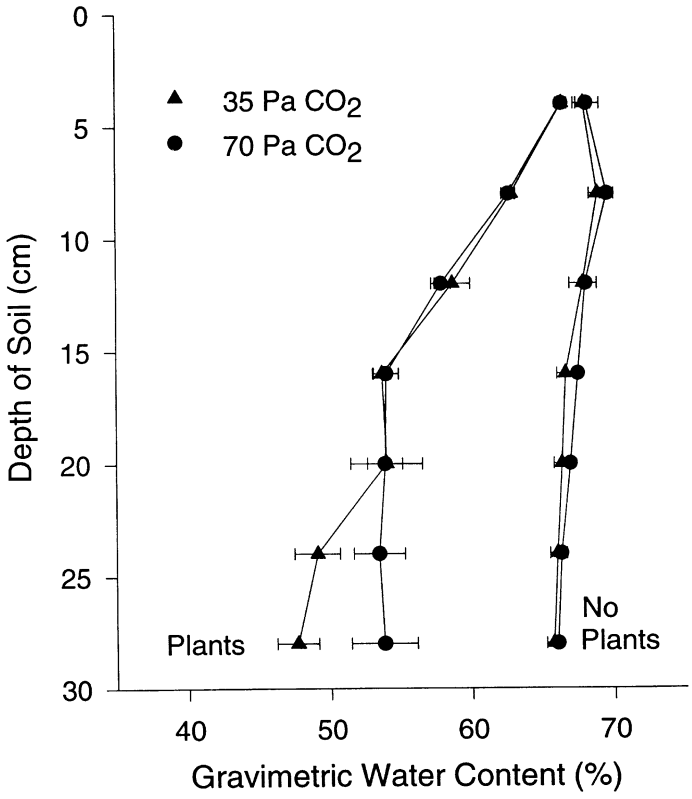

Figure 2. Gravimetric water content (%) at 4-cm intervals for soils in the environmental growth chamber experiment. Values are means±1 standard error.

Table 3. Redox potentials at two depths for pots with *Orontium aquaticum* plants exposed to ambient (38 Pa) or elevated (72 Pa) levels of CO_2, and for pots without plants. Values are means ± 1 standard error (n = 4 for planted pots, n = 2 for unplanted pots).

	5 cm Depth	28 cm Depth
Treatment	Redox Potential (mV)	
No plants	11±41	58±11
Ambient CO_2	45±17	−14±61
Elevated CO_2	71±12	37±16

water budgets are needed. Pulliam & Meyer (1992) developed an empirically-based simulation model of CH_4 emissions from a temperate wetland forest and concluded that emissions are likely to be more sensitive to future perturbations of the water budget than to changes in temperature. A transpiration feedback on CH_4 emissions would augment increased methanogenesis due to increased primary production.

Freeman et al. (1994) proposed that an experimental lowering of the groundwater table in a peatland increased pore-water SO_4 concentrations, through hydrogen sulfide oxidation, and caused competitive inhibition of methanogenesis by sulfate-reducing bacteria. We investigated the possibility that relatively high rates of transpiration had caused SO_4 levels to increase in the ambient CO_2 pots of the growth chamber study, but found that SO_4 levels were not significantly different in the two groups of pots (ambient mean$\pm$se = 1.34$\pm$0.12 mM, elevated = 0.97$\pm$0.24 mM). Thus, the observed differences in CH_4 emissions apparently were not due to a transpiration-induced increase in SO_4-reduction in the ambient pots.

The porous aerenchyma tissue of vascular wetland plants provides a diffusion pathway for gas exchange between sediments and the atmosphere and greatly enhances CH_4 emissions (Chanton & Dacey 1991). This process may contribute to the positive correlation between CH_4 emissions and net ecosystem production observed for North American wetlands (Whiting & Chanton 1993). Although there was a tendency for greater plant biomass in the elevated CO_2 than in the ambient CO_2 treatments in our study (Table 2), the differences were not significant, and roots reached to the bottom of the pots in all treatments. It is unlikely that improved transport of CH_4 through plant tissues can explain the large differences in emissions that we observed.

In conclusion, we have shown that elevated CO_2 can dramatically increase CH_4 emissions from wetland soils and sediments. We believe the effect was due to increased rates of carbon input through root exudation or root turnover. We also speculate that elevated CO_2 may increase CH_4 emissions in some wetland ecosystems by decreasing rates of water loss by transpiration. The significance of this process will depend greatly on the importance of transpiration in the water budgets of particular wetland sites, and the extent to which decreases in transpiration on a leaf-area basis are negated by increases in leaf area.

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