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Effects of elevated atmospheric CO_2 concentrations on CH_4 and N_2O emission from rice soil: an experiment in controlled-environment chambers

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Abstract. The effects of elevated concentrations of atmospheric CO_2 on CH_4 and N_2O emissions from rice soil were investigated in controlled-environment chambers using rice plants growing in pots. Elevated CO_2 significantly increased CH_4 emission by 58% compared with ambient CO_2. The CH_4 emitted by plant-mediated transport and ebullition–diffusion accounted for 86.7 and 13.3% of total emissions during the flooding period under ambient level, respectively; and for 88.1 and 11.9% of total emissions during the flooding period under elevated CO_2 level, respectively. No CH_4 was emitted from plant-free pots, suggesting that the main source of emitted CH_4 was root exudates or autolysis products. Most N_2O was emitted during the first 3 weeks after flooding and rice transplanting, probably through denitrification of NO_3^- contained in the experimental soil, and was not affected by the CO_2 concentration. Pre-harvest drainage suppressed CH_4 emission but did not cause much N_2O emission (<10 μg N m^{-2} h^{-1}) from the rice-plant pots at both CO_2 concentrations.

Introduction

Recent anthropogenic emissions of atmospheric gases that absorb infrared radiation may be leading to an increase in global mean surface temperature. Depending on projected population-growth and energy-use scenarios, the atmospheric carbon dioxide (CO_2) concentration is expected to rise from the current level of 370 μmol mol^{-1} to between 485 and 1000 μmol mol^{-1} by 2100 (IPCC 2001). Furthermore, exacerbated effects of CO_2, methane (CH_4), nitrous oxide (N_2O), and other 'greenhouse gases' are predicted to cause an average global warming of 1.4 to 5.8 °C by 2100 (IPCC 2001). CH_4 and N_2O have (respectively) 23 and 296 times the global warming potential (GWP) of CO_2 on a time scale of 100 years (IPCC 2001). Rice paddy soils account for a large fraction of wetland ecosystems and provide a staple food to a large portion of the world's population, especially in Asia. However, rice paddies account for about 17% of the anthropogenic sources of CH_4 (IPCC 1996). On a global scale, 36% of the direct N_2O emissions from agricultural fields results from the application of synthetic N fertilizers (Mosier et al. 1998). Most N_2O emissions are from agricultural uplands; however, rice paddy soils also contribute large amounts of N_2O emissions to the atmosphere when the paddies are flooded to submerge the plants or are drained for harvesting (Cai et al. 1997; Ratering and Conrad 1998; Yan et al. 2000; Xu et al. 2002).

Several studies have been conducted on the CH_4 emissions from rice paddy soils under conditions of elevated atmospheric CO_2 concentration using open-top chambers, free-air CO_2 enrichment, and closed-chamber experiments (Ziska et al. 1998; Allen et al. 2003; Inubushi et al. 2003). Methane emission from flooded rice paddy soils occurs through plant-mediated transport, ebullition, and diffusion. Plant-mediated transport is the dominant pathway (Schutz et al. 1989; Nouchi et al. 1990; Wassmann et al. 1996). However, ebullition may contribute significantly to the overall emission in the case that large amount of fresh organic matter was applied to the soils (Wassmann et al. 2000). Many studies have demonstrated that elevated concentrations of CO_2 have a positive effect on rice biomass production (both aboveground and belowground) and on grain yield (Baker and Allen 1993; Ziska et al. 1997; Sakai et al. 2001; Kim et al. 2001, 2003). Elevated CO_2 increases microbial C in rice paddy soils and accelerates the turnover rate of soil organic C during the middle and later stages of the rice growth season (Cheng et al. 2001; Hoque et al. 2001; Li et al. 2004). The direct effect of elevated CO_2 (600–700 μmol^{-1}) on rice root biomass and tiller number indirectly increases CH_4 emissions from rice fields, because the additional root biomass produces more root exudates and the greater number of tillers results in more surface area for CH_4 emission into the atmosphere (Ziska et al. 1998; Inubushi et al. 2003). Elevated CO_2 also increases dissolved CH_4 concentrations in soil solution and flooding water in rice fields (Li et al. 2004; Cheng et al. 2005a, b), which may result in CH_4 emission to atmosphere by ebullition–diffusion. However, there are no reports on how increased atmospheric CO_2 concentration alters the CH_4 emissions by mediated transport via plant and by ebullition–diffusion through the flooding water/air interface.

In contrast, it has been reported that elevated CO_2 increases plant C/N ratios, nitrogen-use efficiency, and water-use efficiency (Drake et al. 1996) and influences soil–atmosphere exchanges of CH_4 and N_2O (Ineson et al. 1998; Mortin-Olmedo et al. 2002; Mosier et al. 2002). These results were obtained only for grass in upland fields. Recent studies suggest that rice cultivation is an important anthropogenic source of atmospheric N_2O (Akiyama et al. 2005). However, there are no reports on how increased atmospheric CO_2 concentration may influence N_2O emission from rice paddy soils.

The objectives of the present study are (1) to determine how elevated concentrations of atmospheric CO_2 affect CH_4 emission from rice soils by plant-mediated transport and by ebullition and diffusion from the flooding water/air interface; (2) to understand how elevated atmospheric CO_2 influences N_2O emission from rice soil; and (3) to determine whether pre-harvest drainage influences CH_4 and N_2O emission from rice paddies under elevated CO_2.

Materials and methods

Controlled-environment chambers

This research was conducted at the National Institute for Agro-Environmental Sciences, Tsukuba, Japan (NIAES) using a plant growth chamber facility (Climatron, Shimadzu, Kyoto), which consists of six $4\times3\times2$ m ($L\times W\times H$) sunlit chambers with temperature and humidity controlled. The space available for plant growth in each chamber was $4\times2\times2$ m. The frames, rear (north) walls, and floor of each chamber were made of stainless steel. The frames were glazed with 5 mm-thick tempered glass whose transmittance of visible light was more than 80%. Throughout the experiment, the CO_2 concentration was maintained at 383 ± 11 μmol mol^{-1} (day) and 446 ± 40 μmol mol^{-1} (night) in three chambers (ambient CO_2) or at 706 ± 13 μmol mol^{-1} (day) and 780 ± 76 μmol mol^{-1} (night) in three other chambers (elevated CO_2). During the day, the CO_2 concentration was maintained by a computer-controlled system by injecting pure CO_2 to compensate for CO_2 uptake by the rice plants (*Oryza sativa L.* ssp. *japonica*). During the night, CO_2 levels increased due to plant respiration, but were not allowed to increase to >100 μmol mol^{-1} higher than the daytime levels by means of a computer-controlled air ventilation system, which introduced ambient air when necessary to reduce the CO_2 concentration. In this experiment, air temperature inside all controlled-environment chambers was controlled to follow ambient air temperature; the seasonal mean temperature was 24.0 °C. The changes in average soil temperature at a 2 cm depth are shown in Figure 1. A more detailed description of the operation and control of the growth chambers can be found elsewhere (Sakai et al. 2001; Cheng et al. 2005a, b).

Experiment in pots in the controlled-environment chambers

Two stainless-steel containers ($1.5\times l.5\times0.3$ m, $L\times W\times H$) per chamber were filled with soil at 20 cm depth (Sakai et al. 2001; Cheng et al. 2005a, b); in one of container (always the easterly one for consistency) two plastic pots (23×25 cm, $D\times H$) were installed: one pot was not planted, and the other was planted with a hill (three seedlings) of rice plants (Figure 2).

The soil used in the pots was same as in the containers. Bulk soil was collected from the plow layer (top 20 cm) of a rice field in Yawara, Ibaraki Prefecture, Japan. The soil was classified as an alluvial soil (Table 1). Because the soil had been piled up outdoors for 2 years before being used, visible plant residues were absent. Moist soil (water content of 40.0% w/w) was passed through a 2-mm sieve. One day before rice transplanting, 7.0 kg (5.0-kg dry soil equivalent) of soil was mixed with 1.53 g NH_4C1 and 0.869 g KH_2PO_4 and was used to fill each pot. The levels of NPK fertilizers were 0.4:0.20:0.25 g pot^{-1} (equivalent to 100:113:75 kg ha^{-1} of N:P_2O_5:K_2O).

The rice cultivar used was Nipponbare, a variety popular among Japanese farmers. Rice seedlings were transplanted into the pots and the pots were flooded on May 15, 2002. At the panicle-formation stage of rice growth

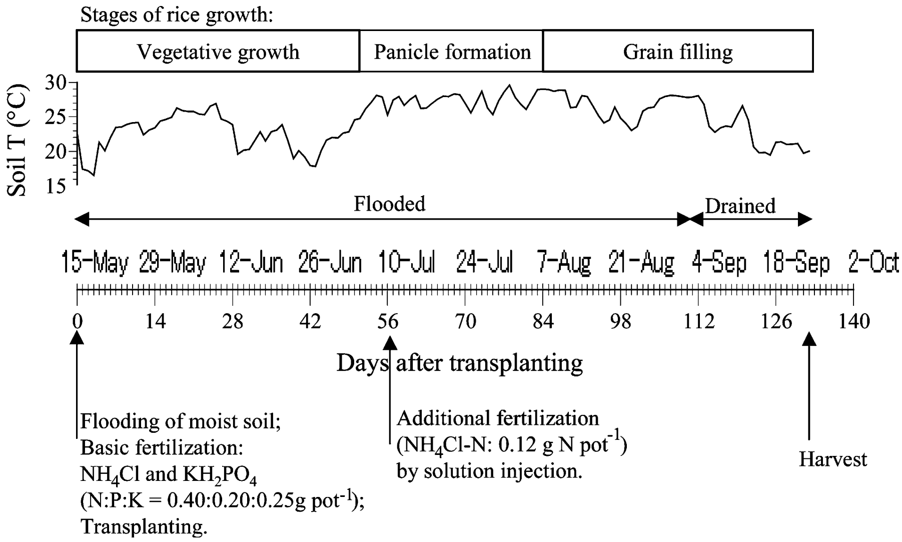

Figure 1. Experimental schedule and changes in daily average soil temperature (2-cm depth) for rice plants grown in pots in controlled-environment chambers under ambient- and elevated-CO_2 conditions.

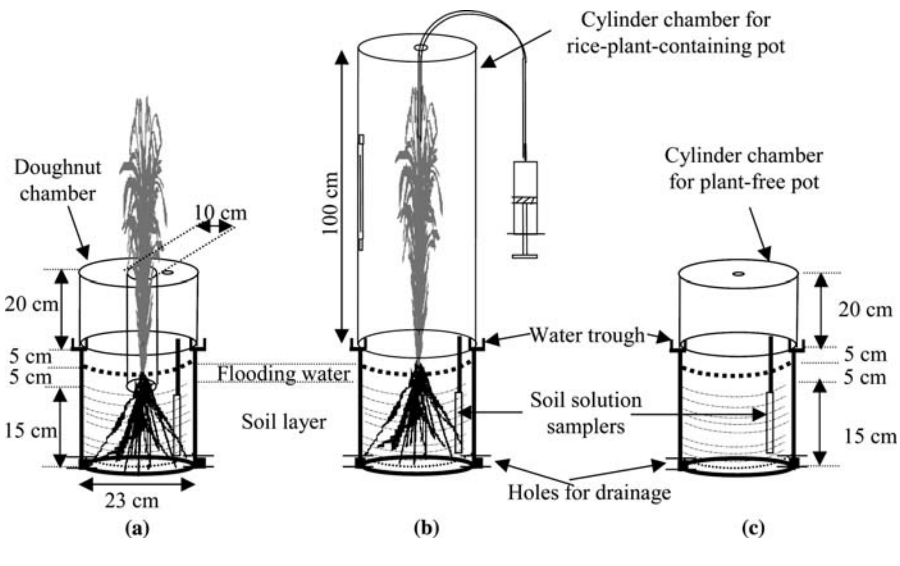

Figure 2. Diagram showing (a) a doughnut-shaped chamber and (b) a large cylindrical chamber used to measure CH_4 and N_2O emitted by ebullition–diffusion from flooding water and by plant-mediated transport plus ebullition–diffusion in the same pot containing a rice plant, and (c) a small cylindrical chamber used to measure CH_4 and N_2O emitted from a plant-free pot.

Table 1. Major properties of the experimental soil.

Soil type	Alluvial
Clay content (%)	35.0
Water content (w/w, %)	40.0
Organic C (mg g^{-1} DW)	30.1
Total N (mg g^{-1} DW)	2.63
C/N ratio	11.5
NO_3^--N (μg g^{-1} DW)	48.0
NH_4^+-N (μg g^{-1} DW)	1.2

(56 days after transplanting), NH_4Cl solution (0.12 g N pot^{-1}) was injected into each plant-containing pot at a depth of 5 cm, near the rice plant, as additional fertilization (Figure 1). The flooding water was maintained at a 5-cm depth until September 2; then, all pots were drained, and the water level was maintained at 5 cm below the soil surface by raising all the pots in the flooding stainless-steel containers and opening the hole at the bottom of the pots (Figure 2). Rice was harvested on September 25, 2002.

CH_4 and N_2O fluxes from the plant-free pots and the pots containing rice plants

Three types of chambers were used to for measuring the CH_4 and N_2O fluxes due to plant-mediated transport and ebullition–diffusion from plant-free pots and from pots containing rice plants (Figure 2). The top of each pot (with or without plants) was surrounded by a water-filled trough, which allowed a chamber to stand. During sampling periods, a chamber was placed on top of each pot so as to capture gas exchanged between the pots and the atmosphere.

To measure how much of the CH_4 and N_2O fluxes occurred by means of ebullition–diffusion from flooding water in the rice-plant pots, a doughnut-shaped chamber (external circular wall: 23×20 cm, internal wall: 10×28 cm, $D \times H$) was used during the flooding period (Figure 2a). With the internal wall being sealed by water and, hence, the emission from plant being not included in doughnut-shaped chamber, emission by ebullition–diffusion was measured and corrected by the ratio of the area covered by the doughnut-shaped chamber to that of the entire pot. To measure the fluxes from the entire rice-plant and plant-free pots, two sizes of cylindrical chamber (23×100 cm and 23×20 cm, $D \times H$) were used (Figure 2b, c). The doughnut-shaped chambers and the small cylindrical chambers were made of 0.3-cm-thick polyvinyl chloride; the large cylindrical chambers were made of 0.3-cm-thick transparent acrylic.

CH_4 and N_2O fluxes were determined once or twice per 2 weeks. Our previous study showed the linearity of the CH_4 concentration increase during the first 30 min after installing the chamber (Inubushi et al. 2003). We therefore took gas samples at 0 and 30 min after the doughnut or cylindrical chamber was placed on a pot. The gas sample was drawn from the chamber with a 12-ml plastic syringe. The collected gas samples were immediately transported from the field to the laboratory and analyzed (as described below) for CH_4 and N_2O.

Sampling of the flooding water and soil solution

The flooding water and soil solutions were sampled 1 day before or after gas sampling. At each sampling, about 12 ml of flooding water in each pot was collected with a 20-ml plastic syringe (without a needle); a needle was attached and, with the syringe held vertically, part of the water was transferred to a 19-ml semi-vacuum bottle (filled with pure N_2 gas at 0.5 atm) fitted with a rubber stopper and screw cap. About 9.5 ml of flooding water was sucked into the bottle by the time the pressure in the bottle reached 1 atm. The amount of flooding water collected and the headspace volume were determined by weighing the bottle before and after sampling. Irrigation water was added at least 4 days before sampling to minimize disturbances to ebullition and diffusion processes.

The soil solution in each pot was sampled with a Rhizon soil-solution sampler (10 Rhizon SMS-MOM; Eijkelkamp Agrisearch Equipment, Giesbeek, the Netherlands). This consists of a 10-cm-long microporous polymer tube (2.5-mm outside $D \times 1.5$ mm inside D) and a 50-cm-long PVC tube, (2.7-mm outside $D \times 1.0$-mm inside D). The microporous polymer tube was inserted vertically into the soil in each pot before transplanting the rice plants (Figure 2). Prior to sampling, about 5 ml of solution was sucked out of the polymer tube with a 10 ml vacutainer (Terumo Ltd., Tokyo) to remove impurities from the tube. Then a 19-ml semi-vacuum bottle (filled with pure N_2 gas at 0.5 atm) fitted with a rubber stopper and screw cap was connected to the polymer tube. About 9.5-ml of soil solution was sucked into the bottle by the time the pressure in the bottle reached 1 atm. The amount of soil solution collected and the headspace volume were determined by weighing the bottle before and after sampling.

Concentrations of CH_4, N_2O, water-soluble organic carbon (WSOC), $NH_4^{\ +}$, and NO_3^- in the gas and water samples

After sampling, all samples were taken to the laboratory, where the concentrations of CH_4 and N_2O in the air samples and in the headspace of the flooding water and soil solution samples were immediately analyzed within 48 h. CH_4 concentrations were determined with a gas chromatograph (GC-7A; Shimadzu, Kyoto) fitted with a flame-ionization detector (Inubushi et al. 2003). N_2O concentrations were determined with a gas chromatograph (GC-8A; Shimadzu, Kyoto) equipped with an electron-capture detector (Cheng et al. 2002).

After analyzing the CH_4 and N_2O levels, all flooding water and soil solution samples were stored in a freezer at −18 °C prior to analysis of the total WSOC with a total organic carbon (TOC) analyzer (TOC −5000; Shimadzu, Kyoto), and of $NH_4^{\ +}$-N and NO_3^{-}-N concentrations with a TRAACS 2000 Continuous-Flow Analyzer (Bran + Luebbe, Nordersterdt, Germany).

Other data measurements

Rice growth parameters, including shoot height and tiller number, were determined once or twice per 2 weeks. At harvest, the rice plant from each pot was separated into ear, stem, leaf, and root compartments, then each sample was oven-dried for 48 h at 80 °C and the dry weight biomass was determined.

We setup three additional pots for rice plants and three additional pots for plant-free soil outside the controlled-environment chambers to permit measurements of soil oxidation/reduction potential (Eh) changes during the entire rice growth period. Management of these pots was the same as for the pots in the controlled-environment chambers. Platinum-tipped electrodes were inserted into the soil of each pot at depths of 7 and 12 cm and remained in place throughout the experimental period. An ORP meter (RM-10P, TOA Electronics Ltd., Tokyo) was used to measure Eh changes once or twice per week.

Calculations and statistical analyses

The fluxes of CH_4 and N_2O were calculated from the increases in the gas concentrations inside the measurement chambers per m^2 and per hour as follow (Yagi et al. 1996).

$$F = p(V/A)(\mathrm{d}C/\mathrm{d}t),$$

where p is the density of CH_4 or N_2O at the temperature recorded inside the chambers, V is the aerial volume of the chamber, A is the corss sectional area of the chambers, and dC is the increase in CH_4 or N_2O concentration inside the chamber in unit of time (dt; 30 min). The total emissions from both plant-free and plant-containing pots (including emission by ebullition–diffusion) under ambient and elevated CO_2 treatments were accumulated throughout the growing season (133 days) to estimate cumulative emissions. On the other hand, the cumulative emissions via by ebullition–diffusion only were estimated by accumulating the fluxes during the flooding period (110 days).

Concentrations of CH_4 and N_2O dissolved in the flooding water and in the soil solution were calculated by Bunsen's coefficients according to the concentration of CH_4 and N_2O in the headspace volume (Cheng et al. 2005b).

Student's t test was used to determine significant differences between the two treatments (ambient and elevated CO_2) for plant parameters and total emissions of CH_4 and N_2O.

Results

Shoot height, tiller number, and rice plant dry weight

The shoot height of the rice plants increased until the grain-filling stage under both CO_2 treatments; there were significant ($p < 0.05$) differences between ambient- and elevated-CO_2 treatments after the grain-filling stage began (Figure 3a). The number of tillers on the rice plants increased until the panicle-initiation stage, and the average number of tillers was smaller in the plants under ambient CO_2 than under elevated CO_2 during the vegetative stage of rice growth. However, the tiller numbers subsequently decreased until harvest in both CO_2 treatments, and there were no differences between the ambient and elevated CO_2 treatments (Figure 3b).

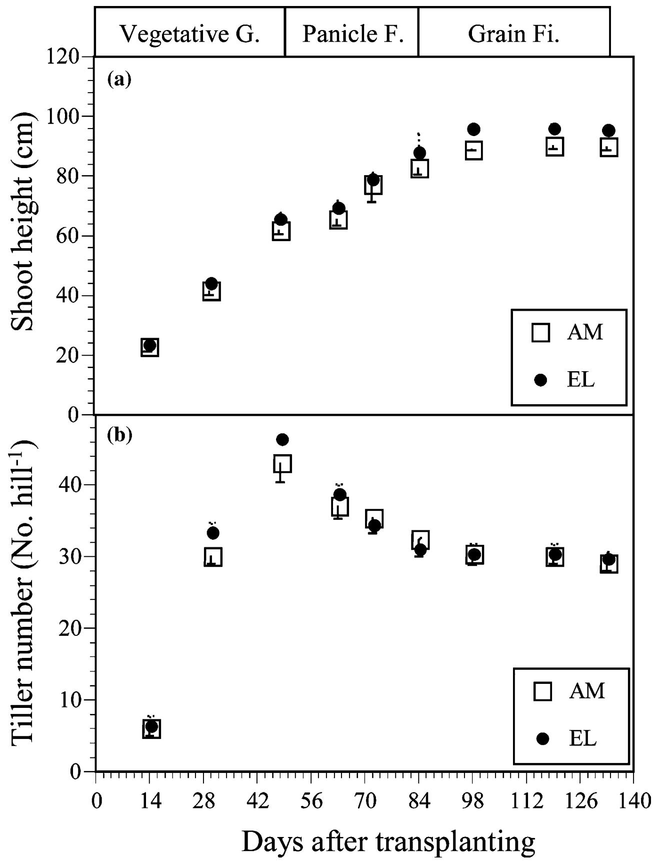

Figure 3. Changes in (a) shoot heights and (b) tiller numbers of rice plants that were grown under ambient-CO_2 (AM) and elevated-CO_2 (EL) conditions. Bars indicate standard deviation. Shown the top of figures are the rice plant growth stages. Vegetative G. means vegetative growth stage; Panicle F. means panicle formation stage; and Grain Fi. means grain-filling stage.

At harvest, elevated CO_2 significantly ($p < 0.05$) increased ear and root dry weights by about 20% and stem dry weights by 10%; leaf dry weights decreased by 6%, although the difference was not significant. The total aboveground dry weights and total dry weights were also significantly ($p < 0.05$) increased by elevated CO_2, by about 11–12% in both cases (Table 2).

Soil Eh

Soil Eh was measured in other pots, outside the controlled-environment chambers. The treatments and management were otherwise the same as for the pots in the controlled-environment chambers. According to previous experiments in our Rice FACE (free-air CO_2 enrichment) study, Eh changes were not influenced by treatment with elevated CO_2 (unpublished data). Therefore, the Eh changes should be the same in this experiment as in the controlled-environment chambers. The patterns of Eh change between rice-plant-containing and plant-free pots were clearly different (Figure 4). The Eh values at 7- and 12-cm depths decreased after moist soil was flooded (the same day that rice plants were transplanted). There were no obvious differences between rice-plant and plant-free pots in the first 4 weeks after flooding and rice transplanting. However, between ca. 40 and 80 days after flooding and rice transplanting, Eh decreased quickly in the rice-plant pots and reached about −100 mV on average. Conversely, the Eh decreased slowly in the plant-free pots and stayed above 0 mV on average until harvest. These results clearly indicate that rice plant growth accelerates reductive reactions in the soil relative to the same soil lacking plants.

Concentrations of WSOC and CH_4 dissolved in the flooding water and soil solution

The concentrations of WSOC dissolved in the flooding water in the plant-free pots ranged from 10 to 20 μg C ml^{-1} during the whole flooding period (Figure 5a). The concentrations of WSOC dissolved in the soil solution in the plant-free pots was 15–20 μg C ml^{-1} during the early period, increased to about 40 μg C ml^{-1} during the middle period, then remained constant (Figure 5c). There were no significant differences between the ambient- and elevated-CO_2 treatments with respect to concentrations of WSOC dissolved in the flooding water and soil solution in the plant-free pots.

For rice-plant-containing pots, the concentrations of WSOC dissolved in the flooding water and soil solution were similar to those in plant-free pots during the vegetative growth stage of rice, i.e., during the first 7 weeks (Figure 5b and d). The concentrations of WSOC dissolved in the flooding water and soil solution in the rice-plant pots increased after 7 weeks of flooding. The WSOC concentration in the soil solution decreased when the pots were drained before

Table 2. Comparison of plant dry weights, and of CH_4 and N_2O emissions from pots under ambient- and elevated-CO_2 conditions (The data are mean ± SD, * and ns indicate $p < 0.05$ and no significance, respectively, by Student's *t* test).

Parameter	Ambient CO_2	Elevated CO_2	Elevated/ambient	Significance
Total dry weights (g pot^{-1})	91.6 ± 2.7	103.0 ± 3.8	1.12	*
Aboveground DW	81.1 ± 1.8	90.2 ± 32	1.11	*
Ear	32.3 ± 2.2	38.9 ± 1.3	1.20	*
Stem	33.6 ± 1.3	37.0 ± 2.0	1.10	*
Leaf	15.2 ± 0.3	14.3 ± 0.3	0.94	ns
Root DW	10.6 ± 10.8	12.8 ± 0.8	1.21	*
Cumulative CH_4 emission from plant-free pots (mg C pot^{-1})	−1.1 ± 0.3	−1.6 ± 0.4	1.45	ns
Cumulative CH_4 emission from rice-plant pots (mg C pot^{-1})	917.0 ± 156.9	1446.7 ± 206.2	1.58	*
By ebullition–diffusion from flooding water	69.2 ± 22.5	96.4 ± 29.3	1.39	ns
Ratio of plant-mediated transport by plant to total CH_4 emission during flooding period (%)	86.7	88.1	1.02	
Ratio of ebullition–diffusion from flooding water to total CH_4 emission during flooding period (%)	13.3	11.9	0.90	
Cumulative N_2O emission from plant-free pots (mg N pot^{-1})	18.0 ± 1.7	16.1 ± 1.7	0.90	ns
Cumulative N_2Oemission from rice-plant pots (mg N pot^{-1})	11.7 ± 1.9	11.6 ± 2.0	1.00	ns
By ebullition–diffusion from flooding water	10.5 ± 1.8	10.3 ± 1.8	0.98	ns
Ratio of plant-mediated transport by plant to total N_2O emission during flooding period (%)	8.7	10.4	1.20	
Ratio of ebullition–diffusion from flooding water to total emission during flooding period (%)N_2O	91.3	89.6	0.98	

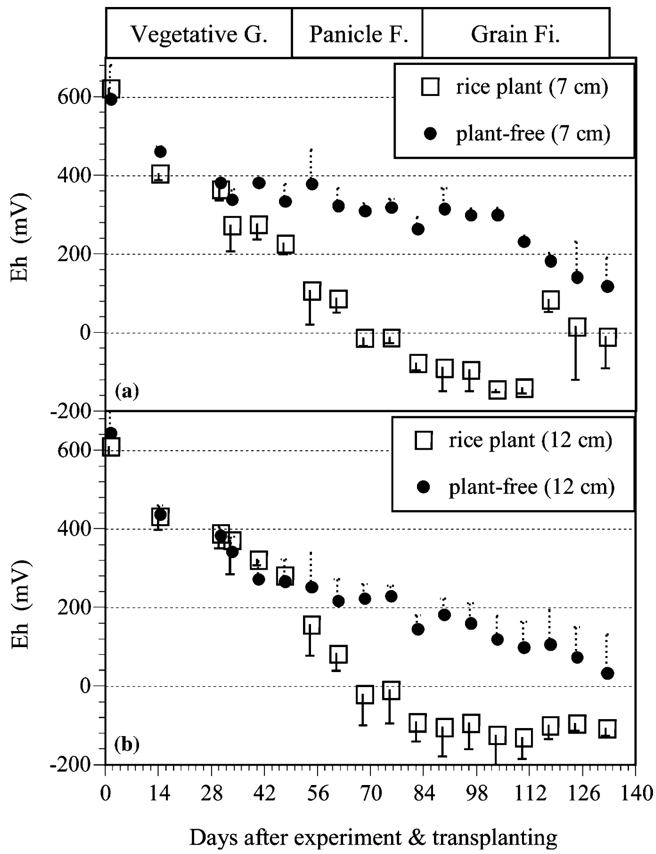

Figure 4. Changes in the Eh values at (a) 7-cm and (b) 12-cm depths in pots with and without rice plants. Shown the top of figures are the rice plant growth stages. See Figure 3 for abbreviations.

harvest (Figure 5d). The average concentrations of WSOC dissolved in the flooding water and soil solution in rice-plant pots under elevated CO_2 were higher than those under ambient CO_2 conditions during the grain-filling stage of rice growth, from 12 weeks until harvest (Figure 5b, d).

The changes in the concentrations of CH_4 dissolved in the flooding water and soil solution in both the plant-free and rice-plant-containing pots under ambient- and elevated-CO_2 conditions were similar to those for WSOC throughout the experimental period (Figure 6). Similarly, the average concentrations of CH_4 dissolved in the flooding water and soil solution in rice-plant pots under elevated CO_2 were obviously higher than those under ambient CO_2 conditions during the grain-filling stage of rice growth, except after drainage (Figure 6b, d). For the period from 4 to 9 weeks after flooding, however, the concentration of CH_4 dissolved in soil solution was lower in the rice-plant pots than in the plant-free pots (Figure 6c, d).

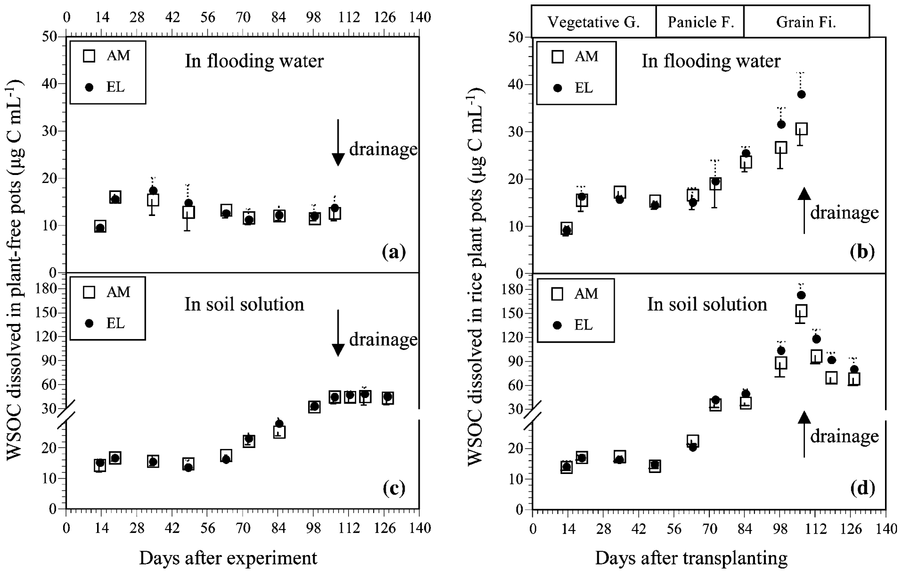

Figure 5. Changes in the concentrations of WSOC dissolved in (a, b) flooding water and (c, d) soil solution in (a, c) plant-free pots and (b, d) pots containing rice plants in controlled-environment chambers at ambient (AM) and elevated (EL) CO_2 concentrations. Bars indicate standard deviation, Shown the top of figures are the rice plant growth stages. See Figure 3 for abbreviations.

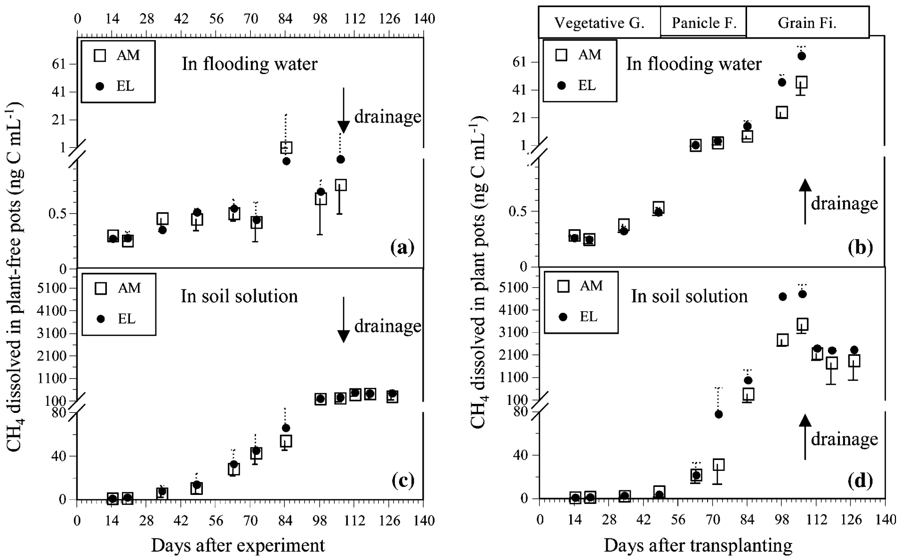

Figure 6. Changes in the concentration of CH_4 dissolved in the (a, b) flooding water and the (c, d) soil solution in (a, c) plant-free pots and (b, d) pots containing rice plants in controlled-environment chambers at ambient (AM) and elevated (EL) CO_2 concentrations. Bars indicate standard deviation. Shown the top of figures are the rice plant growth stages. See Figure 3 for abbreviations.

CH_4 fluxes from plant-free pots and rice-plant-containing pots by plant-mediated transport and ebullition–diffusion

Seasonal changes in the CH_4 fluxes from the plant-free pots and the rice-plant pots by ebullition–diffusion through the flooding water and by ebullition–diffusion plus plant-mediated transport are shown in Figure 7. CH_4 fluxes from the plant-free pots were between -0.05 and 0.05 mg C m^{-2} h^{-1} on average. The negative values indicated a net CH_4 absorption. The cumulative CH_4 fluxes for the plant-free pots under ambient- and elevated-CO_2 conditions were -1.1 and -1.6 mg C pot^{-1}, respectively, during the whole 133 days (the entire experimental period) (Table 2).

For rice-plant pots, the CH_4 fluxes by ebullition–diffusion through the flooding water were usually very low during the vegetative growth period, i.e., until 10 weeks after flooding (and rice transplanting). However, the CH_4 fluxes from the flooding water by ebullition–diffusion increased after the middle of the panicle-formation stage (10 weeks after flooding, Figure 7b). The cumulative CH_4 emissions from the flooding water by ebullition–diffusion from the rice-plant pots under ambient- and elevated-CO_2 conditions were 69.2 and 96.4 mg C pot^{-1}, respectively, throughout the 110 days of flooding, but these values were not significantly different (Table 2).

The total CH_4 fluxes from the rice-plant pots by ebullition–diffusion plus plant-mediated transport were also relatively low during the early period of rice

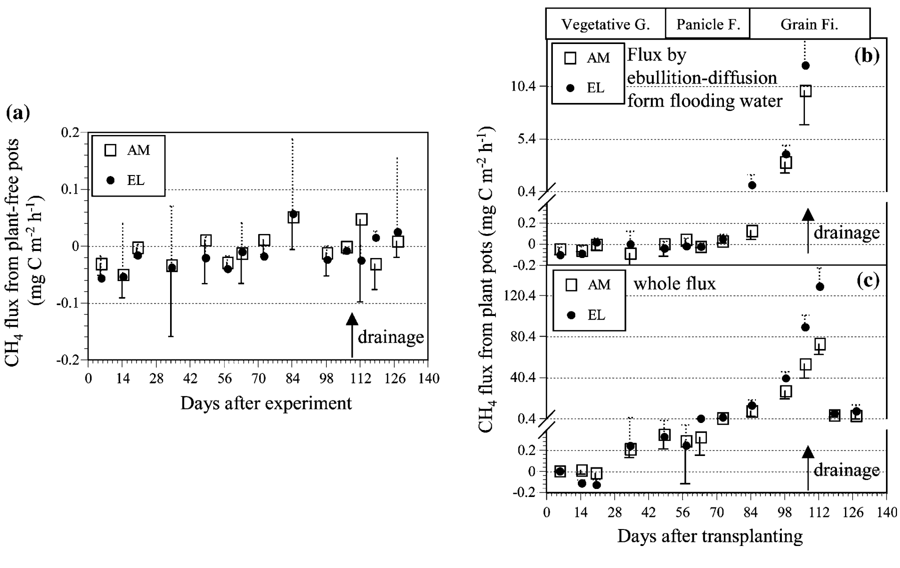

Figure 7. Changes in the CH_4 flux from (a) plant-free pots and (b, c) pots containing rice plants, for (b) flux by ebullition–diffusion from flooding water and (c) total flux (ebullition–diffusion plus plant-mediated transport), in pots in controlled-environment chambers at ambient (AM) and elevated (EL) CO_2 concentrations. Bars indicate standard deviation. Shown the top of figures are the rice plant growth stages. See Figure 3 for abbreviations.

growth (until 10 weeks after flooding), but increased quickly thereafter, then decreased sharply after the flooding water was drained. This occurred in both the ambient- and elevated-CO_2 treatments (Figure 7c). The cumulative CH_4 emissions from the rice-plant pots under ambient- and elevated-CO_2 conditions were 917.0 and 1446.7 mg C pot $^{-1}$, respectively, throughout the 133 days of the experiment. The elevated-CO_2 treatment significantly increased the cumulative CH_4 emissions, by 58% relative to the ambient-CO_2 treatment (Table 2).

Concentrations of N_2O, NO_3^-, and NH_4^+ dissolved in the flooding water and soil solution

The experimental soil contained a relatively large amount of NO_3^--N (48.0 μg g^{-1} DW) before being flooded (Table 1). Relatively large amounts of NO_3^--N and N_2O were detected in the flooding water and soil solution during the first 4 weeks in the pots with and without rice plants under both ambient- and elevated-CO_2 conditions (Figure 8). The concentrations of NO_3^- -N and N_2O decreased more slowly in the plant-free pots than in the rice-plant pots.

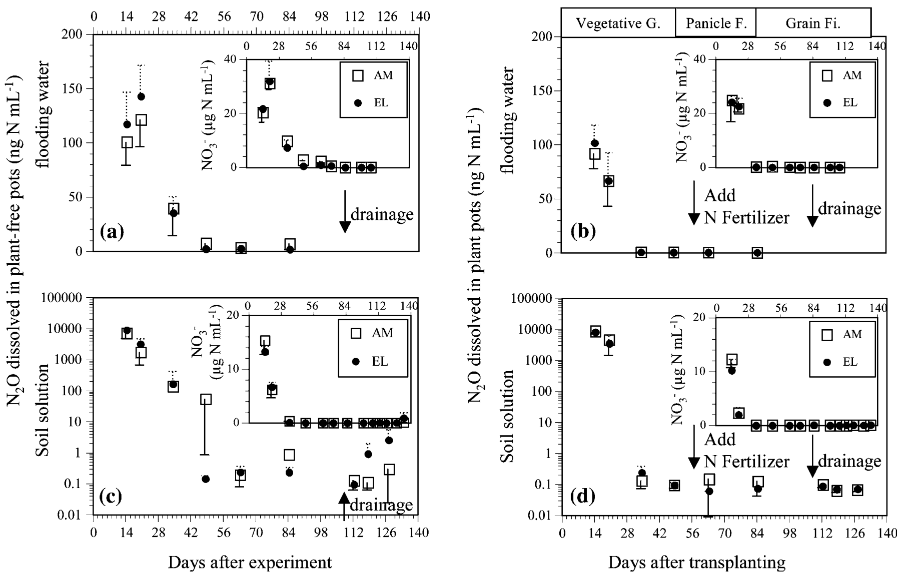

Figure 8. Changes in the concentration of N_2O dissolved in the (a, b) flooding water and the (c, d) soil solution in (a, c) plant-free pots and (b, d) pots containing rice plants in controlled-environment chambers at ambient (AM) and elevated (EL) CO_2 concentrations. Bars indicate standard deviation. Shown the top of figures are the rice plant growth stages. See Figure 3 for abbreviations. Insets show changes in the concentration of NO_3^--N dissolved in the flooding water and soil solution.

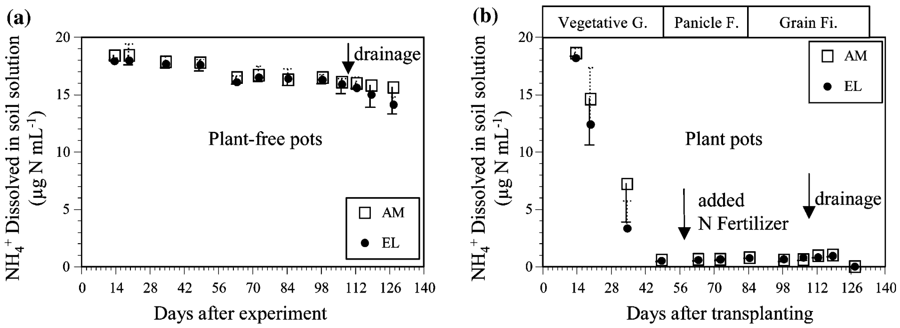

Figure 9. Changes in the concentration of NH_4^+ -N dissolved in the soil solution in (a) plant-free pots and (b) pots containing rice plants in controlled-environment chambers at ambient (AM) and elevated (EL) CO_2 concentrations. Bars indicate standard deviation. Shown the top of figures are the rice plant growth stages. See Figure 3 for abbreviations.

The concentrations of NH_4^+-N detected in the flooding water were very low (< 0.2 μg N ml^{-1}), except for the first sampling, 13 days after flooding and rice transplanting, when the average concentrations were 1.9 and 3.1 μg N ml^{-1} for the plant-free and rice-plant pots, respectively. Concentrations of NH_4^+-N in the soil solution decreased to 1μg N ml^{-1} by 7 weeks after transplanting in the rice-plant pots, and decreased more quickly in the pots under elevated-CO_2 than ambient-CO_2 conditions, on average (Figure 9b). However, the average concentrations of NH_4^+-N dissolved in the soil solution in the plant-free pots changed very slowly, from 18.4 to 15.8 μg N ml^{-1} and from 17.9 to 14.1 μg N ml^{-1}, respectively, under ambient- and elevated-CO_2 conditions (Figure 9a).

N_2O fluxes from plant-free pots and rice-plant pots by plant-mediated transport and ebullition–diffusion

Seasonal changes in the N_2O fluxes from the plant-free and the rice-plant pots by ebullition–diffusion through the flooding water or by ebullition–diffusion plus plant-mediated transport are shown in Figure 10. Average N_2O fluxes from the plant-free pots increased to about 600 μg N m^{-2} h^{-1} by 3 weeks after flooding, then decreased and remained at a low level (about 10 μg N m^{-2} h^{-1}) until after the flooding water was drained, at which point they increased again (Figure 10a). The cumulative N_2O emissions for the entire 133 days of the experiment from the plant-free pots under ambient- and elevated-CO_2 conditions were 18.0 and 16.1 mg N pot^{-1}, respectively, and these values were not significantly different (Table 2).

For the rice-plant pots, the N_2O fluxes by ebullition–diffusion through the flooding water and the total fluxes by ebullition–diffusion plus plant-mediated transport were also large during the early stages of rice growth, until 2 or

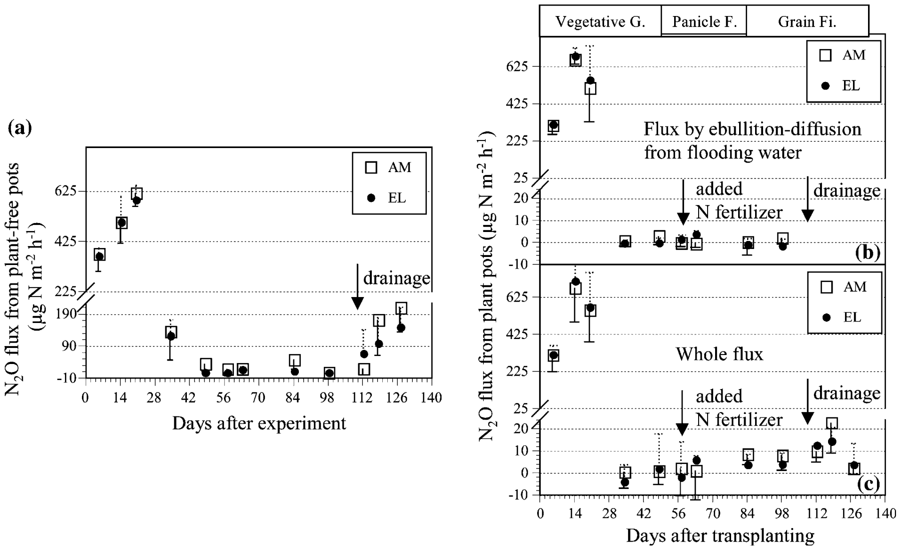

Figure 10. Changes in (a) the N_2O flux from plant-free pots and (b, c) pots containing rice plants, for (b) flux by ebullition–diffusion from flooding water and (c) total flux (ebullition–diffusion plus plant-mediated transport), in pots in controlled-environment chambers at ambient (AM) and elevated (EL) CO_2 concentrations. Bars indicate standard deviation. Shown the top of figures are the rice plant growth stages. See Figure 3 for abbreviations.

4 weeks after flooding, then decreased to zero. The whole flux finally increased to about 10 μg N m^{-1} h^{-1} after the flooding water was drained (Figure 10b, c). Cumulative N_2O emissions by ebullition–diffusion from the flooding water were 91.3 and 89.6% of the total emissions during the 110-day flooding period in the ambient- and elevated-CO_2 treatments, respectively (Table 2). The cumulative N_2O emissions during the entire experimental period from the rice-plant pots under ambient- and elevated-CO_2 conditions were 11.7 and 11.6 mg N pot^{-1}, respectively, which were not significantly different (Table 2).

Discussion

Effect of elevated CO_2 on rice growth in pots

An elevated atmospheric CO_2 concentration (about 700 ppm) directly influenced rice plant growth and biomass production, increasing the aboveground and belowground biomass by 11 and 21%, respectively (Table 2). The effects of elevated CO_2 on rice growth in this pot experiment were consistent with results obtained with rice plants in soil culture in larger containers in the same controlled-environment chambers (Sakai et al. 2001) and in a FACE experiment in the field (Kim et al. 2001; Inubushi et al. 2003). This indicates that the use of small pots (23×25 cm, $D \times H$) in the present experiment did not suppress rice plant growth, and suggests that the effects of elevated atmospheric CO_2 concentration on rice growth in the pots were similar to those in the field.

Effect of elevated CO_2 on CH_4 production and emission from rice soil

It is well known that CH_4 emission from flooded rice paddy soils occurs through plant-mediated transport, ebullition, and diffusion, and that the plant-mediated transport is the dominant pathway (Schutz et al. 1989; Nouchi et al. 1990; Wassmann et al. 1996). Net CH_4 emission is determined by the balance between CH_4 production and CH_4 oxidation in rice plant-paddy soil ecosystems. The amount of CH_4 produced in flooded rice soils is primarily determined by the availability of methanogenic substrates, which originate from both soil organic matter (including incorporated organic materials, such as rice straw) and root exudates or root autolysis products (Yagi and Minami 1990; Minoda et al. 1996; Chidthaisong and Watanabe 1997). Theoretically, CH_4 production in flooded rice soils begins when a soil oxidizer, such as NO_3^-, Fe^{3+}, Mn^{4+}, or SO_4^{2-}, is completely reduced as a result of organic matter decomposition and when the soil Eh has decreased to -150 mV (Inubushi et al. 1984; Wang et al. 1993). In this experiment, the Eh was maintained above 200 mV during the first 4 weeks after flooding (Figure 4), while NO_3^- was completely reduced simultaneously (Figure 8). It is hence suggested that the high $NO3^-$ concentration delayed the Eh decrease, and suppressed CH_4 production.

Average CH_4 fluxes from plant-free pots under both ambient- and elevated-CO_2 conditions ranged between -0.05 and 0.05 mg C m^{-2} h^{-1} (Figure 7a), which is similar to the results from upland fields and forests (Ishizuka et al. 2002). The lack of obvious CH_4 emission from plant-free pots can be explained in two ways. One reason is that there is no direct pathway such as a rice plant to transport CH_4 form the subsurface soil layer, even though a certain amount of CH_4 was dissolved in the soil solution (Figure 6c). Another reason is that substrates for CH_4 production were only present at low levels in the experimental soil because the soil had been piled up outdoors for 2 years before being used, thus most of the easily decomposable organic matter had already been depleted. As a confirmation that the content of easily decomposable organic matter was low in the experimental soil, we found that the average soil Eh values at 7- and 12-cm depths decreased slowly in plant-free pots and stayed above 0 mV throughout the experiment (Figure 4), and that the concentrations of WSOC were also low (10–20μg C ml^{-1}, close to levels in the irrigation water, which were 10–13μg C ml^{-1}) for all pots during the early period after flooding (Figure 5). The concentration of CH_4 dissolved in soil solution was lower in the rice-plant pots than in the plant-free pots for the period from 4 to 9 weeks after flooding (Figure 6c, d), which implies that CH_4 originated from soil C was emitted by plant-mediated transport Figure 7b, c) and was more oxidized in rice-plant pots than that in plant-free pots. The cumulative CH_4

fluxes for the plant-free pots were −1.1 and −1.6 mg C pot^{-1} under ambient- and elevated-CO_2 conditions, respectively, across the whole 133 days of the experiment. This implies that the flooding water may have acted as a CH_4 sink (Table 2).

The CH_4 fluxes from the rice-plant pots as a result of ebullition–diffusion through the flooding water or plant-mediated transport (whole flux minus ebullition–diffusion flux) increased during and after the panicle-formation stage of rice growth (Figure 7b, c). The concentrations of WSOC and CH_4 dissolved in the flooding water and soil solution increased in parallel, and these concentrations in the pots under elevated-CO_2 conditions were larger than under ambient-CO_2 conditions Figure 5b, d, Figure 6b, d). Given the lack of CH_4 flux from the plant-free pots, we confirmed that root exudates, root autolysis products, or both are important sources of CH_4 in the rice-plant pots because root biomass slowly decreases after panicle formation and the carbon in the root is exchanged from new photosynthates carbohydrates (Inubushi et al. 2003; Cheng et al. 2005a). The rapid decrease in soil Eh after the panicle-formation stage of rice growth in the rice-plant pots (Figure 4) may also have been influenced by root exudates or root autolysis products, which accelerate soil reduction processes.

Cumulative CH_4 emissions from the rice-plant pots were increased by 58% in the elevated-CO_2 treatment compared with the ambient-CO_2 treatment (Table 2). This value is consistent with the reported increases in CH_4 emissions (49–60% under conditions of elevated CO_2 concentration to 650 μmol mol^{-1}) in an open-top-chamber experiment (Ziska et al. 1998), and increases (38–51% under conditions of elevated CO_2 to 550 μmol mol^{-1}) in a rice field experiment with free-air CO_2 enrichment (Inubushi et al. 2003). Natural wetlands may behave like flooded rice paddies in terms of their responses of CH_4 emission to elevated CO_2 (Dacey et al. 1994; Hutchin et al. 1995; Megonigal and Schlesinger 1997). CH_4 from rice paddies and natural wetlands accounts for 32.7% of the total global sources to atmosphere (IPCC 1996). If we consider that CH_4 emissions from natural wetlands and rice paddies may be enhanced by elevated CO_2, the GWP of CH_4 could become more important as atmospheric CO_2 increases, rather than less, as was recently predicted (Lelieveld et al. 1998).

In this study, we determined the proportion of CH_4 emissions by ebullition–diffusion relative to the total emission under both ambient- and elevated-CO_2 conditions. During a 110-day flooding period, CH_4 emissions by ebullition–diffusion was 69.2 and 96.4 mg C pot^{-1} under ambient- and elevated-CO_2 conditions, respectively. They accounted for 13.3% (ambient-CO_2) and 11.9% (elevated-CO_2) of the total emissions during the same period (Table 2), which implies the proportion of CH_4 emitted through ebullition–diffusion was not influenced by elevated atmospheric CO_2 concentration. About 90% CH_4 is emitted by plant-mediated transport shown in this study (86.7 and 88.1% for ambient- and elevated-CO_2 conditions) and reported by early research also (Schutz et al. 1989; Wassmann et al. 1996). The CH_4 flux decreased when the flooding water was drained under both ambient- and elevated-CO_2 treatments

(Figure 7b, c), implying that drainage management will have an important role in mitigating future CH_4 emissions from paddy fields, because more CH_4 will likely be emitted from flooded rice paddy soils in the future under increasing atmospheric CO_2 concentration.

Effect of elevated CO_2 on N_2O emissions

Soils are major sources of atmospheric N_2O, which is a byproduct or an intermediate product of microbial nitrification and denitrification (Bouwman 1990; Mosier and Kroeze 2000). Denitrification appears to be the main process by which nitrogen is lost from rice paddy soils. Anaerobic soils have high capacity for reducing N_2O to N_2O, and in fact, the major product of denitrification in anaerobic soils is N_2 rather than N_2O (Mosier 1994).

In this experiment, large N_2O fluxes (300–700 μg N m^{-2} h^{-1}) from all pots with and without rice plants occurred in both ambient- and elevated-CO_2 treatments during the first 3 weeks after flooding and rice transplanting Figure 10). The changes in the concentrations of NO_3^- and N_2O dissolved in the flooding water and soil solution were consistent with the N_2O fluxes (Figure 8). The large N_2O fluxes during the first 3 weeks after flooding can be explained as follows. First, our experimental soil had been piled up outdoors for 2 years before being used, and a substantial portion of the easily decomposable organic C and N had already been converted into CO_2 and NO_3^--N, respectively. We calculated that 240 mg NO_3^--N (in 5.0 kg of dry soil) was present in each pot before flooding (Table 1), which would have constituted a large source for anaerobic denitrification of NO_3^- to N_2O and N_2. Second, the presence of less-easily decomposable organic C in this soil would have delayed the denitrification progress and increased the ratio of N_2O to N_2, because limiting the availability of organic C impedes denitrification (Granli and Bockman 1994). The high value of soil Eh at 7- and 12-cm depths ($>$300 mV) and the low WSOC concentrations (10–20 μg C ml^{-1}) until 4 weeks after flooding (Figures 4 and 5, discussed in the previous section) are consistent with the explanation that the presence of less-easily decomposable organic C delayed the denitrification progress and increased the ratio of N_2O to N_2. Third, N uptake by small rice plants was limited to the early stage of rice growth (Figure 9), meaning that the basic fertilizer NH_4^+ could have been nitrified into NO_3^- in the flooding water and would have contributed to N_2O emission by nitrification–denitrification.

The cumulative N_2O emissions were 11.7 and 11.6 mg N pot $^{-1}$ from rice-plant pots under ambient- and elevated-CO_2 conditions, respectively, during the entire experimental period (Table 2). There was no difference between ambient- and elevated-CO_2 conditions, because most N_2O was emitted during the first 3 weeks after flooding by denitrification of NO_3^- in original soil, while elevated atmospheric CO_2 concentration could not affect denitrification process in flooding water and submerged soils. Since rice plant prefers $NH_4{}^+$ -N to NO_3^--N for N nutrition (Murayama et al. 1984), the high concentration of NO_3^--N could not been absorbed by rice plants, though rice plant absorbed more N for growth under elevated CO_2 from fertilized NH_4^+ -N (Kim et al. 2001, 2003). This may explain the result that the elevated CO_2 did not change N_2O emission in our experiment. N_2O emitted by ebullition–diffusion through the flooding water accounted for 91.3 and 89.6% of the total emissions during the same flooding period for ambient- and elevated-CO_2 conditions, respectively. That indicated plant-mediated transport is not main pathway for N_2O emission in flooding rice paddy.

The N_2O emitted from the rice-plant pots was low (< 10 μg N m^{-2} h^{-1}) after 3 or 4 weeks after flooding, the pots received N fertilizer at 56 days (for panicle formation) and even though the flooding water was drained at 110 days (for the grain-filling stage of rice growth) (Figure 10b, c). The finding that <1 μg N ml^{-1} of N_2O dissolved in the soil solution was present in the rice-plant-containing pots under either ambient- or elevated-CO_2 conditions during the panicle-formation and grain-filling stages Figure 8d) may indicate that the amount of N existed in these pots was insufficient to contribute to N_2O emission into the atmosphere (Figure 10b, c). Similar results were reported by Nishimura et al. (2004), who found that no N_2O is emitted from rice fields under conventional Japanese water management practices, in which a mid-season drainage and subsequent intermittent flood irrigation were carried out during middle to later growth stages (Suzuki 1997).

More N_2O was clearly emitted from the plant-free pots than from the rice-plant pots during the middle stages of rice growth and after draining the flooding water, which we attribute to the absence of N uptake by plants in the plant-free pots (Figure 10a). The large amount of NH_4^+ that remained in the soil and decreased very slowly in the plant-free pots until the end of the experiment (Figure 9a) suggests that the N_2O emitted from the plant-free pots originated in the surplus NH_4^+ -N. NH_4^+ -N appears to be used as a source for N_2O production when excess N fertilizer (> 300 kg N ha^{-1}) is applied, as has been suggested by several researchers in China and the Philippines (summary given by Nishimura et al. 2004). It should be noted that the N_2O emission from this study was contributed by a large NO_3^- concentration and a less easily decomposable C in the original soil before flooding.

In conclusion, elevated concentration of atmospheric CO_2 significantly increased CH_4 emission by 58%, but there was no difference between the CO_2 concentrations in the proportion of CH_4 emitted via the plant-mediated transport to the total emission. N_2O emission from rice soil was not influenced by elevated CO_2. Of total N_2O emission, about 90% was due to ebullition–diffusion from flooding water during the first 3–4 weeks after flooding for the both CO_2 concentrations. This result could be attributed to the high NO_3^- concentration and a less easily decomposable C present in the soil used for the experiment. Pre-harvest drainage suppressed CH_4 emission but did not cause much N_2O emission (<10 μg N m^{-2} h^{-1}) from the rice-plant pots at both CO_2 concentrations.

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