

Methane Emissions of Rice Increased by Elevated Carbon Dioxide and Temperature

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ABSTRACT

Methane (CH₄) effluxes by paddy-culture rice (*Oryza sativa* L.) contribute about 16% of the total anthropogenic emissions. Since radiative forcing of CH₄ at current atmospheric concentrations is 21 times greater on a per mole basis than that of carbon dioxide (CO₂), it is imperative that the impact of global change on rice CH₄ emissions be evaluated. Rice (cv. IR72) was planted in sunlit, closed-circulation, controlled-environment chambers in which CH₄ efflux densities were measured daily. The CO₂ concentration was maintained at either 330 or 660 μmol mol⁻¹. Air temperatures were controlled to daily maxima and minima of 32/23, 35/26, and 38/29°C at each CO₂ treatment. Emissions of CH₄ each day were determined during a 4-h period after venting and resealing the chambers at 0800 h. Diurnal CH₄ effluxes on 77, 98, and 119 d after planting (DAP) were obtained similarly at 4-h intervals. Emissions over four-plant hills and over flooded bare soil were measured at 53, 63, and 100 DAP. Emissions were negligible before 40 DAP. Thereafter, emissions were observed first in high-CO₂, high-temperature treatments and reached a sustained maximum efflux density of about 7 mg m⁻² h⁻¹ (0.17 g m⁻² d⁻¹) near the end of the growing season. Total seasonal CH₄ emission was fourfold greater for high-CO₂, high-temperature treatments than for the low-CO₂, low-temperature treatment, probably due to more root sloughing or exudates, since about sixfold more acetate was found in the soil at 71 DAP. Both rising CO₂ and increasing temperatures could lead to a positive feedback on global warming by increasing the emissions of CH₄ from rice.

METHANE is a potent greenhouse gas, and on a per mole basis has a radiative forcing 21 times that of CO₂ (Lashof and Ahuja, 1990; Shine et al., 1995). The concentration of atmospheric CH₄ increased from about 0.75 to 1.73 μmol mol⁻¹ during the past 150 years (Lelieveld et al., 1998). It was increasing at about 1% per year (Khalil and Rasmussen, 1990; Crutzen, 1991) versus 0.4% per year for CO₂ (Hansen et al., 1988; Keeling et al., 1995). However, the rate of increase of CH₄ has declined (Dlugokencky et al., 1998; Etheridge et al., 1998) although year-to-year variations have been

reported (Dlugokencky et al., 2001). The contribution of CH₄ emissions over the last century to the enhanced greenhouse effect is about 20% (Schütz et al., 1991; Shine et al., 1995). Chappellaz et al. (1990) suggested that the natural CH₄ cycle may provide a positive feedback in any future global warming.

Depending on population growth and energy use scenarios, atmospheric CO₂ concentration is expected to rise from about 370 μmol mol⁻¹ currently to about 485 to 1000 μmol mol⁻¹ by 2100 (Prentice et al., 2001). Furthermore, enhanced greenhouse effects of CO₂, CH₄, and other greenhouse gases are predicted to cause an average global warming of 1.4 to 5.8°C by 2100 (Cubasch et al., 2001; Schneider, 2001). Elevated CO₂ typically increases plant photosynthesis and biomass production, whereas increasing temperatures might either decrease or increase photosynthesis and production (Baker and Allen, 1993).

Human activity accounts for about 70% of the total CH₄ emissions (535 Tg yr⁻¹) (Shine et al., 1995). Rice cultivation is the largest anthropogenic source (Hogan et al., 1991). Studies have shown wide differences (about 1 to 60 mg m⁻² h⁻¹) in CH₄ efflux densities from rice cultivation throughout the world (Cicerone and Shetter, 1981; Cicerone et al., 1983; Seiler et al., 1984; Holzapfel-Pschorn and Seiler, 1986; Sass et al., 1990; Yagi and Minami, 1990; Bouwman, 1991; Khalil et al., 1991). Methane emissions from Chinese rice fields have been reported to be 4 to 10 times higher than from European and American fields (Khalil et al., 1991). Factors such as temperature, fertilization, irrigation, readily decomposable soil organic matter, and season can alter CH₄ emission rates from rice cultivation (Lindau et al., 1990, 1991; Yagi and Minami, 1990; Khalil and Rasmussen, 1990).

Whiting and Chanton (1993) showed that CH₄ efflux densities of wetland systems were linearly related to photosynthetic CO₂ uptake rates, which were generally higher in fertile, warm wetland systems [such as cattail (*Typha* spp.) and rice]. Therefore, we speculated that elevated CO₂ would enhance CH₄ emissions via the consequences of enhanced photosynthetic rates (Baker et al., 1990; Baker and Allen, 1993; Allen et al., 1995). Greater photosynthesis would provide larger amounts of available nonstructural carbohydrates (Rowland-Bamford et al., 1990, 1996). Larger amounts of carbohydrates could increase translocation of photoassimilates to roots and increase root exudation as a substrate for methanogenesis (Minoda and Kimura, 1994; Minoda et al., 1996; Watanabe and Kimura, 1998). In other words, increased CO₂ → increased photosynthesis → increased nonstructural carbohydrates → increased translocation

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Abbreviations: DAP, days after planting; SPAR, Soil-Plant-Atmosphere Research.

to roots → increased root exudates → increased substrate for methanogenesis → increased CH₄ emissions. We measured directly the first response (photosynthetic CO₂ uptake rate) and the last step (CH₄ efflux) in this process in paddy culture rice under precisely controlled CO₂ concentrations and air temperatures. Our hypothesis was that increased photosynthetic CO₂ uptake (due primarily to elevated CO₂ concentration) would cause an increase of CH₄ emissions. Furthermore, elevated temperature might modify the CO₂ uptake and emissions response.

MATERIALS AND METHODS

A tropical lowland indica-type rice (cv. IR72) was grown at Gainesville, Florida, USA in eight outdoor, closed-circulation, controlled-environment plant growth chambers, known as Soil-Plant-Atmosphere Research (SPAR) chambers, that were exposed to sunlight (Baker et al., 1994; Allen et al., 2003). An aluminum frame supported transparent polyester film (Mylar; ALMAC Plastics, Atlanta GA) that formed the chamber walls. Aboveground chamber dimensions were 2.0 × 1.0 m in cross-section by 1.5 m in height. Each chamber was attached to a lysimeter (soil container) that was 2.0 × 1.0 m in cross-section and 0.6 m deep. This lysimeter provided a water-tight rooting environment for growing rice in flooded soil culture. Three pots constructed from cylindrical PVC pipes with end-caps (inside diameter of 0.20 m, inside depth of 0.45 m) were placed into each lysimeter before filling the lysimeters with soil. These pots were used to isolate root systems of individual hills of plants for sampling periodically during the experiment. Each PVC-pipe pot was surrounded by a slightly larger cylinder (inside diameter of 0.25 m) to facilitate removal of the pots and to prevent cave-in of the adjacent soil. The pots were placed along the centerline of the 2.0-m length of each lysimeter to fit into the planting pattern described later. Each lysimeter and the three pots were filled with a 0.5-m depth of topsoil (Monteocha loamy sand; sandy, siliceous, hyperthermic Ultic Alaquods). The soil had been previously screened sequentially through 19- and 6-mm circular-hole screens of a large mechanical shaker to remove most residual plant materials and large soil aggregates. To decrease decomposable soil organic matter, the soil was then stockpiled outdoors for one year with no new plant growth and placed in the lysimeters about six months before beginning the experiment. After this period of treatment, residual soil organic matter content was 43 g kg⁻¹. When the experiment was initiated, flood water was maintained at a height of 0.05 m above the soil surface using a float-actuated valve that supplied deionized water to each lysimeter.

Preplant fertilizer (80 kg ha⁻¹ for both P and K) was applied on 8 July 1992. Rice seeds imbibed water in a shallow tray for 4 d and then they were planted on 20 July in 50 hills spaced 0.2 × 0.2 m. Nitrogen was applied as urea on 27 July (7 DAP) at 112.5 kg ha⁻¹ of N, on 20 August (31 DAP) at 56.25 kg ha⁻¹ of N, and on 21 September (63 DAP) at 56.25 kg ha⁻¹ of N. On 28 July (8 DAP), seedlings were thinned to four plants per hill (100 plants m⁻²) and a 0.05-m height of flooded water above the soil was established. Each of the three PVC pots, spaced to contain a four-plant hill of rice, received the same fertilizer rates and water levels as the rest of the lysimeter.

Air flowed continuously from top to bottom within each chamber, driven by fans located in external recirculating air-handling ductwork. The air-handling system contained cold- and hot-water heat exchangers and an electrical resistive-heat

coil used to control dewpoint and dry bulb air temperatures. In the air-handling ductwork, air first passed over the cold-water (4–8°C) heat exchanger using a proportional controller to regulate a valve that controlled the water flow rate, thereby controlling chamber dewpoint temperature. Dewpoint temperature was measured in the air stream before it reentered the chambers with a dewpoint hygrometer (Model Dew-10; General Eastern Instruments, Watertown, MA). Condensate from the drip-pan of the cold water heat exchanger flowed through a tipping-bucket rain gauge for measuring transpiration rates. Next, circulated air passed over the hot-water (45–50°C) heat exchanger, with water flow regulated to raise air temperature to slightly below the setpoint dry bulb air temperature. Air temperature was next fully restored to setpoint with electrical resistive heat using a proportional controller. Chamber dry bulb air temperature was measured with an aspirated, radiation-shielded thermocouple suspended 0.3 m above the plant canopy. The CO₂ concentration of each chamber was measured with a dedicated infrared gas monitor (Valtronics, Concord, CA). The output from each monitor was checked periodically, and corrected if necessary, by an infrared gas analyzer (Model 865; Beckman Instruments, Fullerton, CA). Calibration of this infrared gas analyzer was checked periodically using gases traceable to National Institute of Standards and Technology (NIST) standards. The setpoint CO₂ concentrations were maintained by supplying pure CO₂ from a compressed gas cylinder for injection by mass flow controllers. Dewpoint temperature, dry bulb air temperature, and CO₂ concentration were measured every 2 s for environmental control by a controller-datalogger microprocessor at each chamber (Model CR-10T; Campbell Scientific, Logan, UT) and averaged and recorded every 5 min. Specific methods for controlling environmental set points (hardware, control algorithms) as well as the quality of those controls are given by Pickering et al. (1994).

Daytime CO₂ concentration was maintained at 330 (four chambers) or 660 (four chambers) μmol mol⁻¹. Dry bulb air temperature was controlled to follow a sinusoidal-type pattern between daily maxima and minima of 32/23, 35/26, and 38/29°C in each CO₂ treatment (Baker et al., 1994). The CO₂ treatments were duplicated at 38/29°C. Dewpoints were controlled to 18, 21, and 24°C for the respective air temperatures. The microprocessors also computed and recorded plant photosynthetic carbon dioxide exchange rate (CER) and evaporation rate responses at 5-min intervals (Pickering et al., 1994; Allen et al., 1995). All microprocessor data were downloaded daily to files in a PC host processor.

Daytime photosynthetic CER data were later summed for each chamber for each day to obtain daytime total CO₂ uptake. Periods of time when the SPAR chambers were open for other measurements were identified and these values were not included in the daytime CER summations. These daily daytime CER data were then summed across the growing season for each treatment. The seasonal summation covered the period from 32 through 129 DAP. The data before 32 DAP were not used because extensive data were missing from one of the chambers; furthermore, leaf area index was low during this period of seedling establishment and initial growth. Leakage corrections were applied to the whole-season data based on CER measurements after all the aboveground biomass was removed. This leakage correction was essentially nil for the 330 μmol mol⁻¹ treatments, and typically decreased the 660 μmol mol⁻¹ treatment raw data values less than 3%.

Flood-water pH and soil redox potentials at 0.05-, 0.20-, and 0.40-m depths in the soil were measured manually two to three times a week using platinum wire electrodes in the soil and a saturated calomel reference electrode in the flood

water. Potentials were measured with a millivolt meter (Model 407; Thermo Orion, Beverly, MA). On 29 September (71 DAP), water samples from a high- and low-CO₂ treatment chamber were extracted at 0.10-m depths for determination of the concentration of dissolved acetate, a precursor in one of the main pathways of methanogenesis (Reddy et al., 1986). Shoot growth stages, number of tillers, leaf area index, and shoot biomass samples were taken at 29, 46, 70, 86, and 120 to 126 DAP as described by Baker et al. (1994) and Allen et al. (1995). All remaining plants (120 per chamber) were removed on 134 DAP. Water was sampled for CH₄ content at the flooded soil–water interface and soil water was extracted at a soil depth of 0.17 m at four to six locations in each chamber on 11 December (143 DAP), stored in airtight bottles, and analyzed by a headspace technique adapted from Campbell et al. (1989).

Methane emissions were measured two ways: on a whole-chamber basis and on an individual-hill basis using cuvettes described later. The first method used an automated sampling system that pumped air sequentially from each of the eight SPAR chambers, and then from the outdoor atmosphere, in a 27-min cycle to a gas chromatograph (GC; Varian [Palo Alto, CA] Aerograph Model 2400) with a flame ionization detector (FID). A multipoint automatic sampling valve (Valco, Houston, TX) was used to control the air selection and injection process. The chromatographic output was calibrated periodically using known mixtures of methane-in-air traceable to NIST standards. The GC output was sampled at 0.1-s intervals by a Campbell CR-10T microprocessor and CH₄ concentration associated with each peak computed by algorithm. Data were saved daily to the PC host processor files. Methane emission from each chamber was determined each day from 14 DAP onward using the slope of linear regressions of CH₄ concentrations of air samples taken every 27 min across a 4-h period after the chambers were automatically flushed with outside air, and then resealed at 0800 h. Since the chambers remained sealed for the daylight period to obtain photosynthetic CO₂ uptake rate data, only one measurement of emission rate was obtained each day. On 77, 98, and 119 DAP, diurnal CH₄ emissions were obtained by venting and resealing each chamber every 4 h, starting at 0800 h. At 136 DAP, diurnal CH₄ efflux densities were measured from the stubble that remained after all the plant shoots had been removed by clipping at 0.05 m above the floodwater level.

At 53, 63, and 100 DAP, the second method of measuring CH₄ efflux densities within each chamber was used. Cuvettes (PVC cylinders with sealed top-caps, inside diameter of 0.15 m, inside length of 0.95 m) were placed both over individual hills of plants and over flooded bare soil between hills of plants. Also, these same cuvettes were used on 134 DAP to measure emissions from both intact individual hills of plants and from rice stubble immediately after cutting. The SPAR chambers were opened temporarily for installing the cuvettes and for sampling gas from the cuvettes. Syringe gas samples were drawn through a serum stopper installed in the wall of each PVC cuvette. Syringe gas samples were then manually injected into the GC and output from the FID detector recorded on a strip chart. Methane emissions were determined from the slopes of linear regressions of CH₄ concentrations vs. time of four or five sequential samples taken every 10 min. All the cuvette measurements were made during 1000 to 1600 h.

Root samples were obtained by removing one pot from each chamber at 29, 70, and 120 to 126 DAP, the latter dates being at the final sampling. Shoots were cut for sampling and the pots containing the soil and roots were frozen immediately. Later, the PVC pots containing the frozen soil and roots were cut into 5-cm depth segments. Roots were then washed out

and frozen again until later when root length density was determined. Lengths of subsampled roots were measured by the methods of Newman (1966) and Tennant (1975). Root length density was calculated by dividing root length by the soil volume that contained the roots. After measuring root length, roots were dried and weighed for biomass.

An analysis of variance (ANOVA) was conducted on the daily CH₄ efflux density measurements, which included effects of temperature, [CO₂], DAP, temperature × [CO₂], DAP × temperature, DAP × [CO₂], and DAP × temperature × [CO₂]. Also, an ANOVA was conducted on CH₄ contents of the soil water sampled after final harvest and on root biomass and root length densities.

RESULTS

The seasonal daytime CO₂ uptake of rice increased with both increasing temperature treatments and increasing CO₂ concentrations. The values were 51.8, 62.7, and 72.5 mol CO₂ m⁻² for the 32/23, 35/26, and 38/29°C maximum and minimum temperature treatments at 330 μmol mol⁻¹ CO₂, and 78.6, 85.6, and 95.7 mol CO₂ m⁻² for the 32/23, 35/26, and 38/29°C maximum and minimum temperature treatments at 660 μmol mol⁻¹ CO₂. These values compare closely with seasonal daytime CO₂ uptake data reported for soybean [*Glycine max* (L.) Merr.] (Jones et al., 1985), namely 53.0 and 84.7 mol CO₂ m⁻² for 330 and 660 μmol mol⁻¹ CO₂ treatments grown at 31°C daytime and 23°C nighttime.

After soil flooding was established at 8 DAP, redox potentials at the 0.20-m depth of each lysimeter dropped rapidly from about +500 mV to below 0 mV during the next two days (Fig. 1). Redox potentials for the 0.05-m depth decreased less rapidly but came to similar values eventually (data not shown). Likewise, redox potentials at the 0.40-m depth were similar to those at 0.20 m (data not shown). Apparently, there was little nitrate in the soil that could be reduced and thus slow the rapid decrease of redox potential. Redox potentials generally continued to decrease until about 40 DAP presumably due to reduction of Mn⁴⁺, Fe³⁺, and SO₄²⁻. These data indicate that redox potentials decreased to the point that this factor would not be limiting for methanogenesis (Reddy et al., 1986; Yu et al., 2001). The pH of the

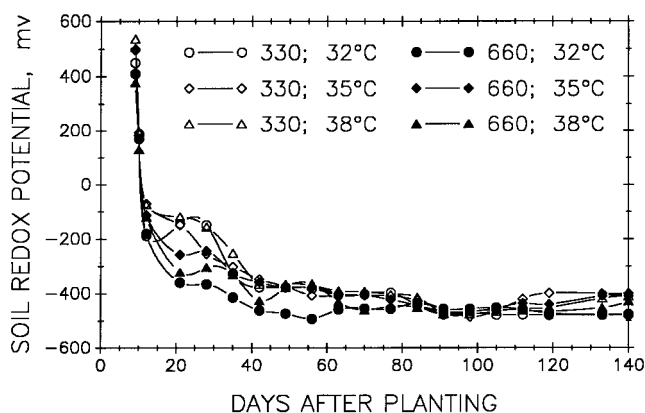


Fig. 1. Redox potentials at a depth of 0.20 m in the soil of each of the lysimeters (relative to a saturated calomel reference electrode placed in the flood water).

surface flood water was close to 7 in all chambers throughout the experiment.

Acetate concentrations at 71 DAP in the 0.10-m depth soil water were 15.1 ± 1.2 mg L⁻¹ in the high-CO₂ treatment with high temperature (38/29°C) but only 2.5 ± 0.5 mg L⁻¹ in the low-CO₂ treatment at intermediate temperature (35/26°C). The weekly average CH₄ efflux density for these two treatments was 3.89 and 0.87 mg m⁻² h⁻¹ at the time of the soil solution samplings (Fig. 2), which is directly proportional to the acetate concentrations.

Methane emissions were negligible from 14 to 40 DAP (Fig. 2). A small mid-season peak was observed at about 70 to 77 DAP in all CO₂ and temperature treatments. All the treatments showed a gradual rise in CH₄ emissions over the 80- to 100-DAP period. By 100 DAP, the 660 μmol mol⁻¹ treatments had reached CH₄ emission rates of about 2.5, 4, and 5 mg m⁻² h⁻¹ for the low-, intermediate-, and high-temperature treatments, respectively. These emission rates were maintained until after final harvest. Likewise, low- and intermediate-temperature treatments of rice grown at 330 μmol mol⁻¹

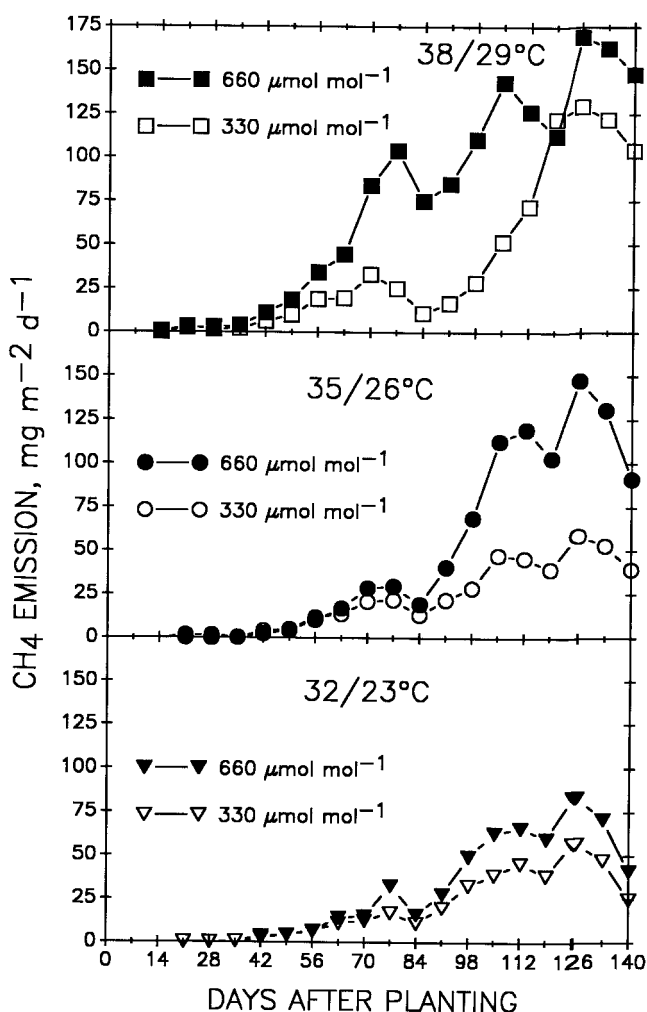


Fig. 2. Season-long CH₄ emission from flooded-soil rice culture at 330 and 660 μmol mol⁻¹ CO₂ concentrations and 32/23, 35/26, and 38/29°C day-night maximum and minimum air temperatures. Data are daily emission rates averaged over weekly periods.

CO₂ reached CH₄ efflux densities of about 1.5 mg m⁻² h⁻¹ at about 100 DAP, and maintained these emission rates until after final harvest. The CH₄ efflux densities of rice grown at 330 μmol mol⁻¹ were similar at all three temperatures until 100 DAP, but then emissions by the high-temperature treatment at 330 μmol mol⁻¹ increased until near the end of the season and attained maximal values of about 4 mg m⁻² h⁻¹ near the end of the season. Results from the analysis of variance showed a significant temperature, CO₂, and DAP effect on season-long CH₄ efflux density (Table 1). A significant interaction also occurred between temperature × [CO₂], DAP × temperature, and DAP × [CO₂]. The total seasonal emissions were calculated to be 2.50, 2.97, and 5.22 g m⁻² for rice grown at the 32/23, 35/26, and 38/29°C in 330 μmol mol⁻¹ CO₂ and 3.83, 6.46, and 10.06 g m⁻² for rice grown at these respective temperatures in 660 μmol mol⁻¹ CO₂ concentrations.

During all diurnal measurements, greatest CH₄ emissions were generally obtained around midday followed by a gradual decline in emissions to a minimum around midnight (Fig. 3–6). After the midnight depression, CH₄ efflux density increased and eventually regained the level of the higher morning emission rates. At 78 DAP, diurnal CH₄ efflux density was greatest at the highest CO₂ (660 μmol mol⁻¹) and temperature (38/29°C) treatment, about 3 to 5 mg m⁻² h⁻¹ (Fig. 3). Differences of emissions among all the other treatments on this date were small (less than 1 mg m⁻² h⁻¹). However, at 99 DAP, diurnal CH₄ efflux densities were greater in the high-CO₂ treatments independent of the temperature regime (Fig. 3, 4).

Results from the PVC-cylinder cuvette method are presented in Table 2. Bare soil contributed little or no CH₄ efflux compared with emissions through plants during each sampling. However, at 53 DAP a gas bubble from the soil was apparently detected in one of the chambers (Table 2). Methane emissions from the individual hills of plants increased considerably at 100 DAP, with the highest efflux densities observed from the 660 μmol mol⁻¹ CO₂ treatment.

Figures 5 and 6 show the results of diurnal flux densities of CH₄ at 121 DAP from the intact rice plant canopy and at 139 DAP from the stubble. The CH₄ efflux densities were similar for both the intact canopy and the stubble. Only at the lowest temperature treatment (32/23°C) were the intact plant canopy emission rates higher than the stubble emission rates.

Table 1. The *F* values from analysis of variance (ANOVA) of mixed three-factor (temperature [TEMP], CO₂ concentration, and days after planting [DAP]) experiment on methane efflux densities throughout the growing season. The model *R*² = 0.097***.

Source	df	<i>F</i> value
TEMP	2	124.52***
[CO ₂]	1	331.70***
TEMP × [CO ₂]	2	40.27***
DAP	65	38.28***
DAP × TEMP	124	2.17***
DAP × [CO ₂]	65	5.01***
DAP × TEMP × [CO ₂]	121	1.03NS

*** Significant at the 0.001 probability level.

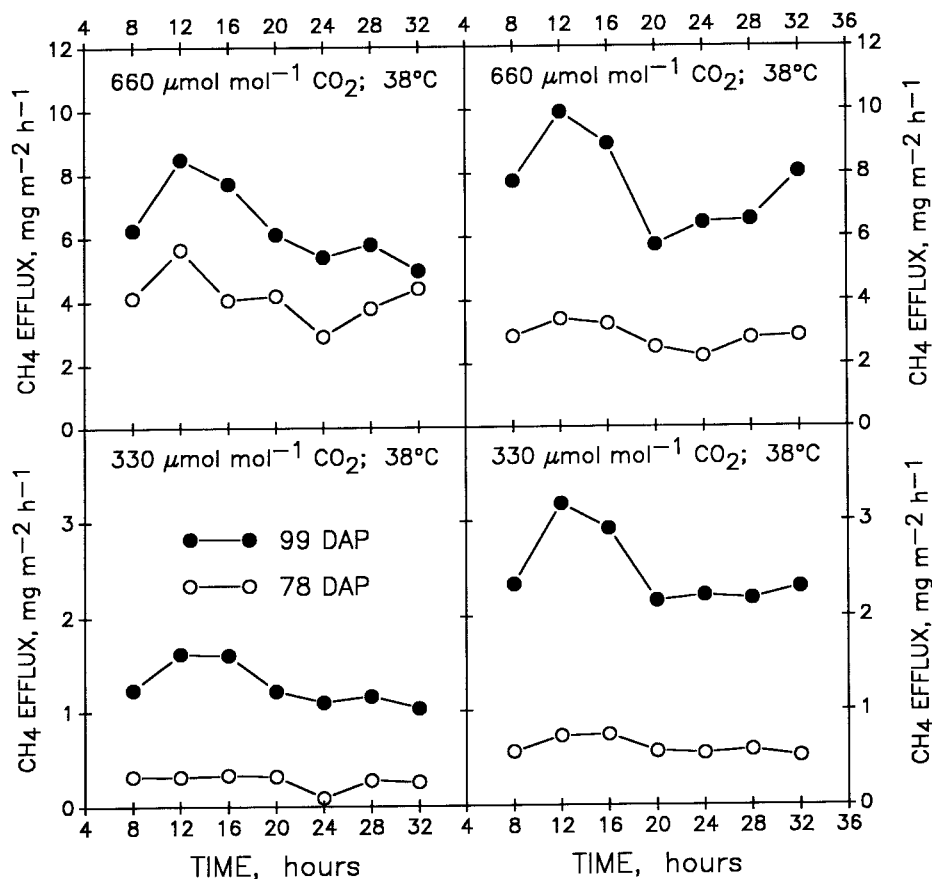


Fig. 3. Diurnal CH_4 emission at 78 and 99 d after planting (DAP) from flooded-soil rice culture at 330 and 660 $\mu\text{mol mol}^{-1}$ CO_2 concentrations and 38/29°C day-night maximum and minimum air temperatures (labeled 38°C). Data are shown from duplicate chambers.

Table 3 shows CH_4 emissions obtained by placing PVC cuvettes over individual hills of intact plants and over rice stubble after clipping. Emissions from the stubble plants were measured about one hour after clipping the plant canopy with about 0.05 m of stem protruding above the floodwater level. In most cases, CH_4 emissions from the stubble were very similar to emissions from the intact plant canopy. The results from Table 3 also show the highest CO_2 treatment to have the highest CH_4 efflux density. The CH_4 efflux density was also higher in the elevated temperature treatments.

The CH_4 contents of the soil water near the end of the season (data not tabulated) were not significantly different among CO_2 treatments, but were significantly different among temperature treatments ($P < 0.10$) and between depths ($P < 0.0001$). The CH_4 contents were low for the soil-water interface samples [less than 0.07 mg (CH_4) L^{-1} (water)]. Average CH_4 contents were much higher at the 0.17-m soil depth, and decreased as air temperature increased. The means and standard errors were 1.26 ± 0.14 , 1.14 ± 0.06 , and 0.86 ± 0.08 mg (CH_4) L^{-1} (water) for the 32/23, 35/26, and 38/29°C range.

Elevated CO_2 increased root biomass at 70 DAP ($P < 0.05$) and at final harvest ($P < 0.10$), but not at 31 DAP (Table 4). The midseason and final harvest data are consistent with other experiments which show that higher CO_2 concentration stimulates total dry matter

production (Baker and Allen, 1993). The effects of CO_2 on root length density was significant only at 70 DAP ($P < 0.05$). The effect of temperature was not significant on root biomass or on root length density, except root length density decreased with increasing temperature at 70 DAP ($P < 0.10$). More than 50% of the root biomass was concentrated within 5 cm of the soil surface (Fig. 7, 70 DAP). Root length density (Y) was linearly related to root biomass (X) across the whole sampling period. In the 0.00- to 0.5-m depth, $Y = 0.26 + 4.32X$, $r^2 = 0.99$, $n = 23$, and in the 0.05- to 0.10-m depth, $Y = 0.07 + 39.6X$, $r^2 = 0.98$, $n = 23$.

Finally, the combination of elevated CO_2 and increasing temperature increased both the total seasonal daytime photosynthetic CO_2 uptake and the total seasonal CH_4 emissions of rice (Fig. 8). The dashed line fit of total CH_4 emissions (converted to a common mole basis) versus total photosynthetic CO_2 uptake in this figure had an $r^2 = 0.96$. These results clearly indicate the effect of the combination of CO_2 enrichment and elevated temperature on increasing photosynthetic CO_2 uptake, and subsequent impact of increasing photosynthesis on increasing CH_4 emissions.

DISCUSSION

Seasonal Effects on Methane Emissions

The data agreed with the general findings of a delay between the initiation of flooding of rice paddies and

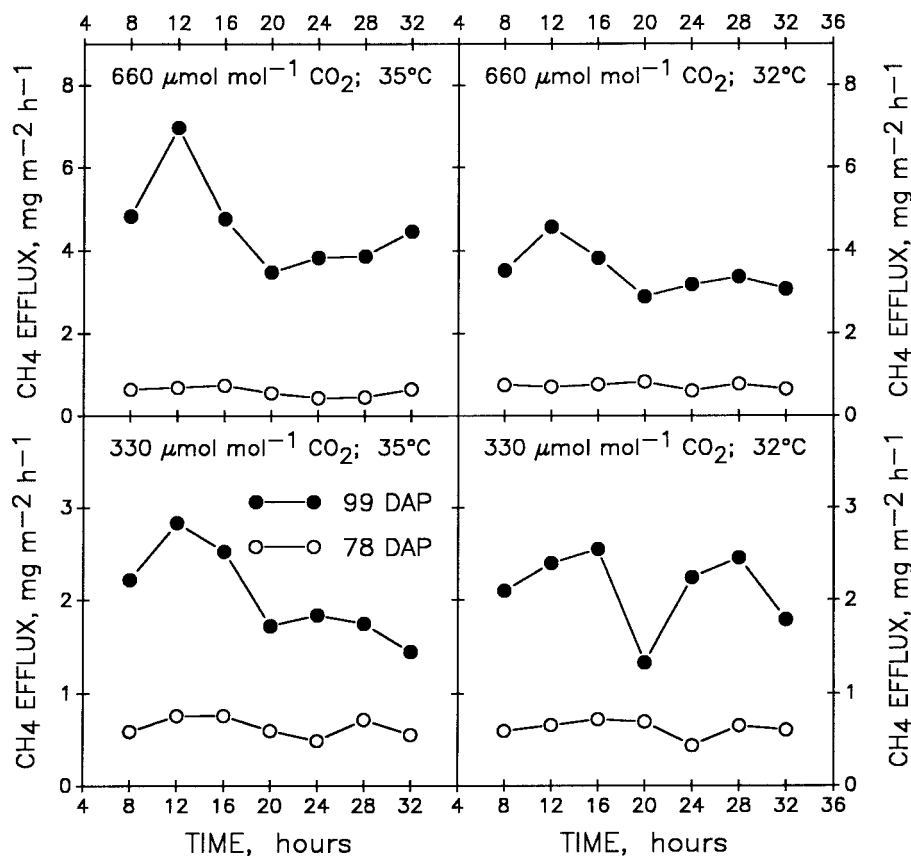


Fig. 4. Diurnal CH₄ emission at 78 and 99 d after planting (DAP) from flooded-soil rice culture at 330 and 660 $\mu\text{mol mol}^{-1}$ CO₂ concentrations and 35/26 and 32/23°C day-night maximum and minimum air temperatures (labeled 35°C and 32°C, respectively).

the onset of CH₄ emissions (Yagi and Minami, 1990; Kimura and Minami, 1995). First, the redox potential has to decrease to low values of at least -150 mv (with respect to the standard hydrogen electrode) for bacterial methanogenesis to begin (Yu et al., 2001). Secondly, sufficient decomposable organic matter must be available. The floodwater was partly drained briefly for application of urea fertilizer at 31 and 63 DAP (Baker et al., 1994), but there was no indication of a change of redox potential of the soil on those dates (Fig. 1). Panicle initiation occurred at about 45 to 50 DAP based on the observed break point of leaf appearance rates between vegetative and reproductive stages of growth (Baker et al., 1994; Allen et al., 1995). The first small peaks in CH₄ efflux density occurred at about 70 to 77 DAP (Fig. 2), probably coinciding with the early stem extension stage. In this experiment anthesis (flowering) occurred at 90 to 100 DAP (Baker et al., 1994). Most sustained increases in emissions until the end of the crop life cycle did not begin until about 90 DAP.

Other studies have shown variations in emissions throughout the life cycle of rice, but not always the same pattern. Schütz et al. (1989) and Sass et al. (1990) reported maximum CH₄ emissions to occur immediately prior to panicle differentiation and just before heading. In a Texas rice field, Sass et al. (1990) reported a second peak during grain filling and maturation. In an Italian rice paddy, Holzapfel-Pschorn and Seiler (1986) found seasonal variation with maximum emission rates be-

tween tillering and flowering. In a California rice field, greatest CH₄ emission rates were reported in the last two to three weeks before harvest (Cicerone et al., 1983). In this study, low emissions early in the season followed by a general increase of emissions is likely due to the lack of initial decomposable organic matter in the soil (despite a total soil organic matter concentration of 43 g kg⁻¹), followed by an increasing availability of root sloughing or exudates with time, dependent on both CO₂ and temperature treatments. Schütz et al. (1989), Yagi and Minami (1990), Kimura and Minami (1995), and Redeker et al. (2000) showed that rice emissions of CH₄ were much greater when rice straw (fresh organic matter) was incorporated in the soil than when mineral fertilizer alone was used (Table 5). Furthermore, early season emissions were much lower without fresh organic matter.

Diel Emission Responses

Holzapfel-Pschorn and Seiler (1986) reported that the highest rice CH₄ emissions occurred in the late afternoon and the lowest in the early morning, which coincides with the temperature variation in the upper soil layer (0–0.10 m). However, the flux boxes used by Holzapfel-Pschorn and Seiler (1986) would have prevented normal transpirational flow of water through the rice plants. The highest CH₄ efflux densities reported in this study occurred earlier at noon (Fig. 3–6). This could be

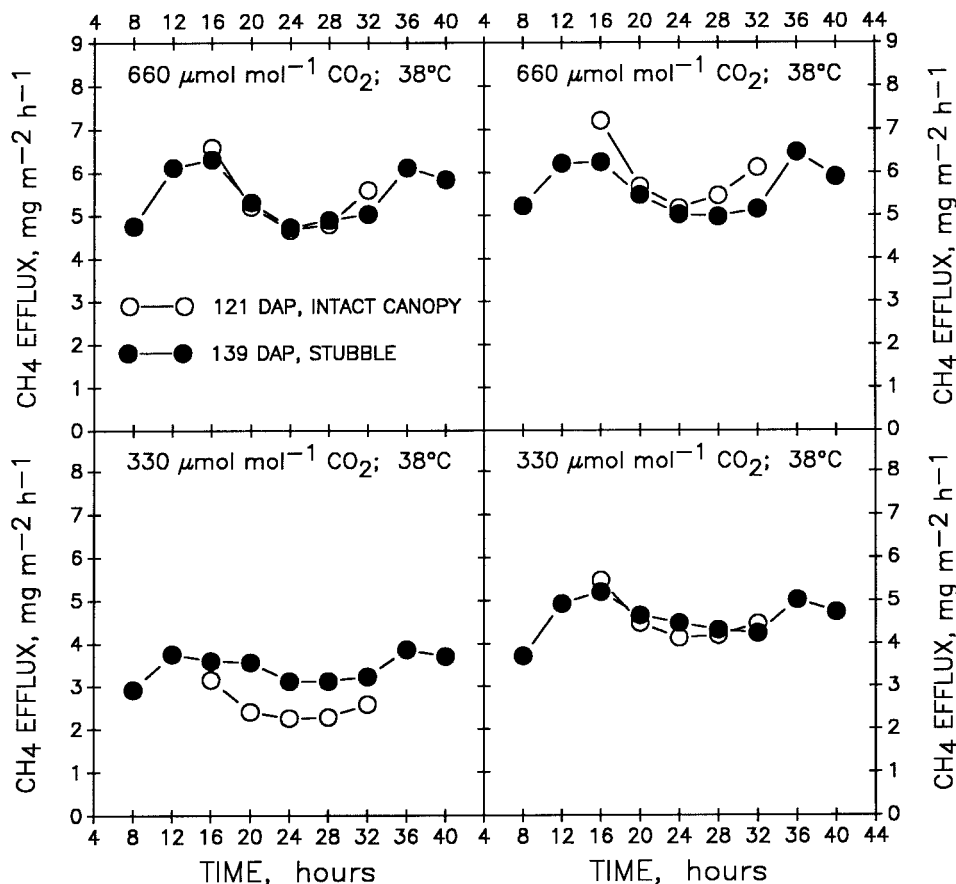


Fig. 5. Diurnal CH₄ emission rates from an intact plant canopy at 121 d after planting (DAP) and from stubble after cutting at 139 DAP at 330 and 660 $\mu\text{mol mol}^{-1} \text{CO}_2$ concentrations and 38/29°C day–night maximum and minimum air temperatures (labeled 38°C). Data are shown from duplicate chambers.

due to the fact that plants were exposed to near-natural light in an atmosphere in which the dry bulb air temperature was controlled to follow a natural, diurnal, sinusoidal type pattern. In this type of system, the flow of transpired water increases in the morning to a maximum at noon or the early afternoon (Baker and Allen, 1993). Therefore, soil water flow to the roots should deliver more dissolved CH₄ to the rice plant during periods of rapid transpiration. Chanton et al. (1997) also proposed that the maximum diel rates of CH₄ emissions were linked to maximum transpiration rate induced bulk flow. Table 2 illustrates that the predominant pathway of CH₄ emission is through the aerenchyma of the rice plant rather than ebullition through the soil and floodwater.

Carbon Dioxide and Substrate Effects

Mayer and Conrad (1990) concluded that CH₄ production was not limited in paddy soils by the number of methanogenic bacteria but by the establishment of a low soil redox potential and the availability of dissolved organic matter. In this study, by 40 DAP all platinum electrodes positioned at 0.20 m below the soil surface registered a low soil redox potential (less than -300 mV with respect to a standard calomel electrode).

Some studies have shown CH₄ efflux density to be linearly related to plant biomass (Sass et al., 1990; Whit-

ing et al., 1991; Sass and Fisher, 1995). Whiting et al. (1991) indicated that the photosynthetic carbon fixation rate may be an important variable controlling CH₄ emissions from vegetated wetlands. The temporal and spatial distribution of CH₄ production was found to be related to root biomass (Sass et al., 1990) and above ground biomass (Huang et al., 1997), determined in part by the type of cultivar. Peak CH₄ emissions during the growing season may be associated with high activity by the rice plants that supplies soil bacteria with fresh organic matter via root exudates or root sloughing (Holzapfel-Pschorn and Seiler, 1986; Schütz et al., 1989; and Yagi and Minami, 1990; Schütz et al., 1991). Root biomass in this experiment was increased about 60% by doubled CO₂ (Table 4), but it was not increased by higher temperature. On average, total above-ground biomass at the final harvest was 18% greater at elevated CO₂ (Baker et al., 1994). In the Philippines, Ziska et al. (1998) also found an 18% increase in total biomass response to 300 $\mu\text{mol mol}^{-1} \text{CO}_2$ enrichment above ambient during the dry season of 1996 but a larger 38% increase during the wet season of 1996. However, since grain yields were decreased substantially (65–80%) at the highest temperature in our study as reported by (Baker et al., 1994), more photoassimilate might have been available as root exudates since it was not being used in seed

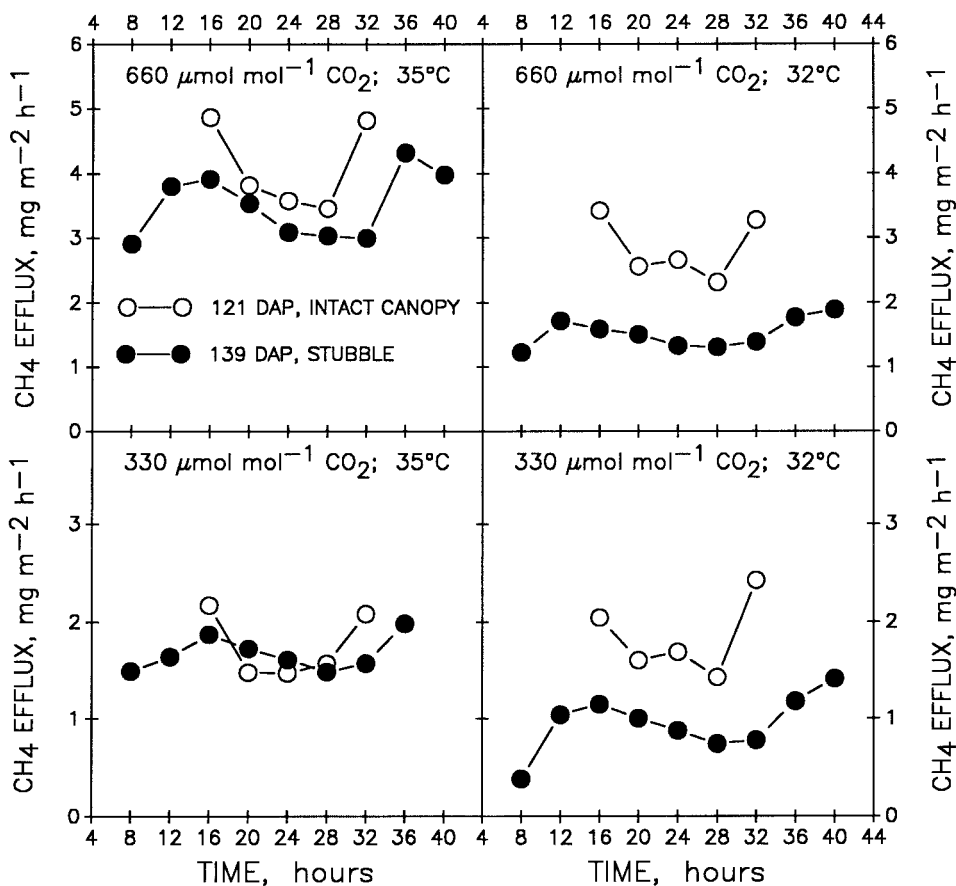


Fig. 6. Diurnal CH₄ emission rates from an intact plant canopy at 121 d after planting (DAP) and from cut stubble at 139 DAP at 330 and 660 $\mu\text{mol mol}^{-1}$ CO₂ concentrations and 35/26 and 32/23°C day-night maximum and minimum air temperatures (labeled 35°C and 32°C, respectively).

production during the later stages of plant development. Subsequent research by Snyder (2000) documented considerable nonstructural carbohydrates and nitrogen (i.e., protein) in rice culms under elevated temperatures (40/30°C) that limited flower fertility and grain yield to nearly zero. These carbohydrates have no sink but roots after shoot expansion ceases.

Baker and Allen (1993) and Allen et al. (1995) reviewed a series of studies of rice responses to atmospheric CO₂ and temperature. Carbon dioxide enrichment to 660 $\mu\text{mol mol}^{-1}$ increased rice photosynthesis by 32%. Total above ground biomass, root biomass, tillering, and final grain yield were all increased with CO₂. Since root exudates can represent more than 1.7% of the total photosynthate (Feldman, 1988), the increase in CH₄ efflux densities observed in this study was probably due to higher soil substrate levels obtained directly under the high CO₂ treatment and indirectly under the highest temperature treatment.

Not all studies of elevated CO₂ in rice have shown increased CH₄ emissions. Schroppe et al. (1999) found lower CH₄ emissions in rice exposed to CO₂ concentrations 350 $\mu\text{mol mol}^{-1}$ above ambient levels despite the fact that shoot and especially root biomass was greater under elevated CO₂ treatments. They suggest that greater root density in the rice containers may have allowed greater O₂ transport to the soil and thus decreased CH₄ emissions.

Temperature Effects

Schütz et al. (1990) and Khalil and Rasmussen (1990) found CH₄ efflux density to be influenced by soil temperature. Our study showed that CH₄ emissions were increased significantly in elevated air temperature treatments (Table 2). However, Schroppe et al. (1999) generally observed a decrease of emissions with increasing temperature. Flood-water temperatures tracked the controlled air temperatures closely during the early season when there was little shading of the water surface by rice vegetation (Baker et al., 1994). However, by 57 DAP after complete vegetative cover had developed (Baker et al., 1994), the midday maximum water temperatures decreased almost 10°C below maximum air temperatures (attributable to shading and evaporative cooling of the water). Therefore, the temperature effect on CH₄ emissions might have been more related to temperature effects on the above-ground components of rice than on the soil bacteria via the following mechanism. Total seasonal daytime CO₂ uptake was increased by increasing temperature at both levels of CO₂ exposure; however, grain yield was decreased considerably by increasing temperature as reported by Baker et al. (1994), while nonstructural carbohydrates and N in culms remained high or increased concurrently with similar high temperatures (Snyder, 2000). Therefore, more photoassimilates were available for translocation to roots and

Table 2. Methane emission from the tube cuvette experiment at 53, 63, and 100 d after planting (DAP) taken from the cylinder covering a hill containing four plants and from the cylinder covering bare soil only (0.04 m²).

[CO ₂] μmol mol ⁻¹	Air temperature (maximum and minimum) °C	Methane emission (mean ± SE)	
		Hill	Bare soil
53 DAP			
330	32/23	1.5 ± 0.3	0.1 ± 0.1
330	35/26	1.2 ± 0.3	0.0 ± 0.0
330	38/29	0.9 ± 0.4	0.1 ± 0.0
330	38/29	1.2 ± 0.3	-0.4 ± 0.1
660	32/23	0.7 ± 0.3	0.0 ± 0.0
660	35/26	0.6 ± 0.0	0.0 ± 0.0
660	38/29	2.3 ± 0.7	0.3 ± 0.1
660	38/29	0.8 ± 0.3	1.2 ± 0.7†
63 DAP			
330	32/23	2.2 ± 0.2	0.0 ± 0.0
330	35/26	0.9 ± 0.3	-0.1 ± 0.1
330	38/29	2.6 ± 0.4	0.0 ± 0.1
330	38/29	3.6 ± 2.1	0.4 ± 0.6
660	32/23	1.9 ± 0.2	0.0 ± 0.1
660	35/26	2.0 ± 0.2	0.0 ± 0.0
660	38/29	8.0 ± 1.0	0.1 ± 0.1
660	38/29	4.2 ± 0.4	0.2 ± 0.1
100 DAP			
330	32/23	7.1 ± 0.3	0.2 ± 0.7
330	35/26	2.9 ± 0.7	0.0 ± 0.1
330	38/29	3.8 ± 0.3	0.0 ± 0.0
330	38/29	3.1 ± 0.2	0.0 ± 0.0
660	32/23	6.5 ± 0.7	-0.1 ± 0.0
660	35/26	7.8 ± 0.4	0.0 ± 0.0
660	38/29	11.8 ± 0.8	0.0 ± 0.1
660	38/29	14.8 ± 0.4	0.0 ± 0.0

† Value is probably due to ebullition of a methane gas bubble.

potentially provide more root exudation to support CH₄ production (Watanabe and Kimura, 1998). Alternatively, aerenchyma might have been modified such that it supported more rapid gaseous diffusion and emissions of CH₄.

Means of Methane Escape

Various studies have convincingly demonstrated that the principal means of CH₄ transport from the rice paddy to the atmosphere is by diffusion through stems of the plants (Cicerone and Shetter, 1981; Holzapfel-Pschorn and Seiler, 1986). Sass et al. (1990) recorded low CH₄ emission from bare soil throughout a 75-d

Table 3. Methane emission from the tube cuvette experiment at the end of the rice life cycle (136 d after planting [DAP]) taken from a hill containing four plants and from the same hill immediately after the plants were cut 0.05 m above the water level (stubble).

[CO ₂] μmol mol ⁻¹	Air temperature (maximum and minimum) °C	Methane emission (mean ± SE)	
		Plants	Stubble
mg m ⁻² h ⁻¹			
330	32/23	4.4 ± 0.2	4.7 ± 0.7
330	35/26	4.1 ± 0.3	3.9 ± 0.6
330	38/29	9.7 ± 2.0	9.4 ± 2.9
330	38/29	8.7 ± 1.5	6.8 ± 0.8
660	32/23	3.2 ± 0.2	3.7 ± 0.5
660	35/26	12.6 ± 1.0	9.8 ± 2.1
660	38/29	14.3 ± 2.0	13.6 ± 1.9
660	38/29	17.9 ± 3.7	16.7 ± 2.8

growing period. Mariko et al. (1991) stated that CH₄ transport capacity of rice plants depends mainly on plant size. They reported greater emissions from a plant with nine tillers compared to a plant with three. In the present study, the number of viable tillers per plant did not change with CO₂ or temperature treatments, but ranged from 12 at 40 DAP to 6 at final harvest (Baker et al., 1994).

Nouchi et al. (1990) provided strong evidence that CH₄ release to the atmosphere from rice occurs through micropores discovered in the leaf sheath and not through stomatal pores in the leaf blade. They also demonstrated that bubbles formed on the rice leaf sheath occur with CH₄ emissions. In a 5-h light switching (on-off) study of a rice plant in the laboratory, Nouchi et al. (1990) also found no correlation between transpiration rates (which requires open stomata on the leaf blades) and CH₄ emission rates. Since there is no aerenchyma in leaf blades of rice (only intercellular air spaces) there is little reason to expect CH₄ emissions to be governed by stomatal conductance, which certainly governs transpiration rates and is directly related to leaf photosynthetic rates. Nouchi et al. (1990) suggested that CH₄ dissolved in the soil water surrounding the root diffuses into the cell-wall water of the root cells and then gasifies in aerenchyma channels of the root cortex, and they diagrammed the aerenchyma channel system that would allow CH₄ to diffuse from roots into the leaf sheaths.

Table 4. Root biomass per pot (0.0141 m³) and root length density (length of roots per unit volume of soil) of rice grown at two carbon dioxide concentrations and three day–night maximum and minimum temperatures sampled at various days after planting (DAP).

[CO ₂] μmol mol ⁻¹	Temperature °C	29 DAP		70 DAP		122–126 DAP	
		Biomass g	Density cm cm ⁻³	Biomass g	Density cm cm ⁻³	Biomass g	Density cm cm ⁻³
330	32/23	0.12	0.09	1.95	1.07	2.22	1.32
	35/26	0.16	0.12	1.56	0.88	1.51	0.90
	38/29	0.20	0.15	1.53	0.82	1.85	1.02
660	32/23	0.36	0.21	3.36	1.71	3.74	1.80
	35/26	0.13	0.10	2.79	1.47	2.49	1.38
	38/29	0.25	0.16	2.15	1.14	2.41	1.33
<i>F</i> values							
Temperature		4.47NS	4.93NS	3.22NS	9.20†	6.18NS	13.16NS
[CO ₂]		5.78NS	7.29NS	20.65*	38.40*	75.01†	34.88NS
[CO ₂] × Temperature		2.33NS	9.10†	2.33NS	1.75NS	25.41NS	0.64NS

* Significant at the 0.05 probability level.

† Significant at the 0.10 probability level.

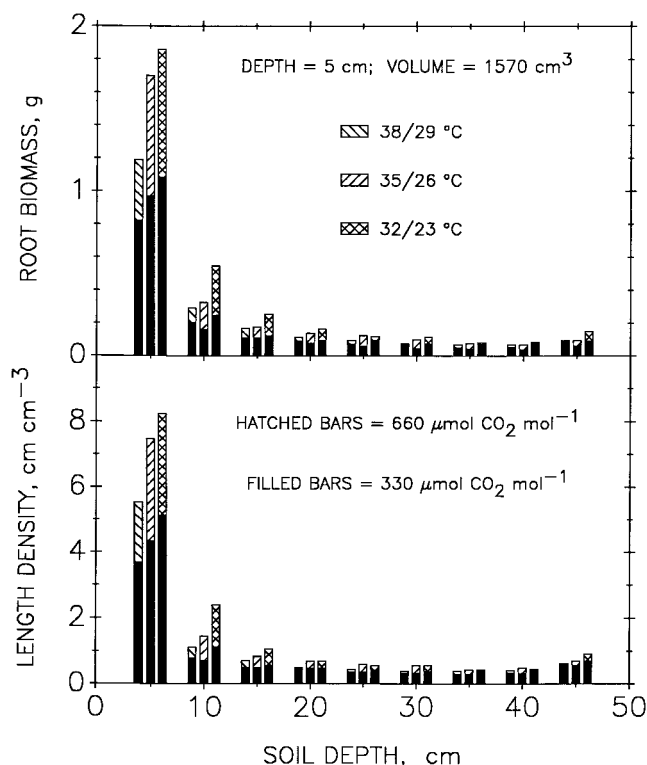


Fig. 7. Rice root biomass (top panel) and root length density (bottom panel) at 5-cm depth increments sampled at 70 d after planting from a cluster of four plants growing in 20-cm-diameter cylindrical pots in the Soil-Plant-Atmosphere Research (SPAR) chambers at two CO₂ concentrations and three temperature regimes. Values for 330 μmol mol⁻¹ in solid bars are plotted over values for 660 μmol mol⁻¹ in hatched bars. Across three samplings during the season, root length density (cm cm⁻³) at the 0- to 5-cm soil depth = 0.264 + 4.32 × root biomass (g); r² = 0.99.

The emissions of CH₄ presumably occur by molecular diffusion since pressurized convective throughflow that exists in wetland plants such as *Typha* spp. and *Phragmites* spp. has not been reported for rice (e.g., review

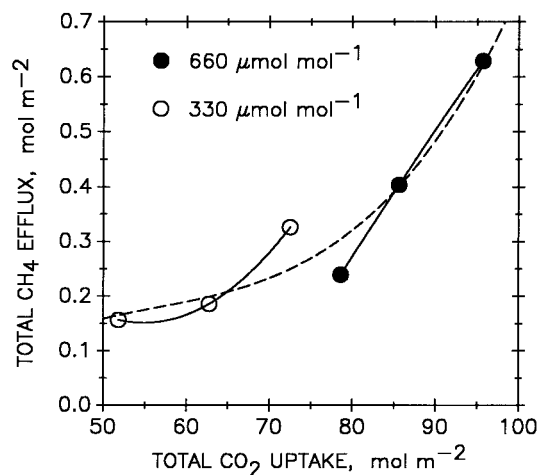


Fig. 8. Total seasonal CH₄ emissions versus total seasonal photosynthetic CO₂ uptake of rice for two CO₂ and three temperature treatments. Within each CO₂ treatment, the data points increase in magnitude within increasing temperature treatments of 32/23, 35/26, and 38/29°C, respectively.

by Allen, 1997). Chanton et al. (1997) found that CH₄ emission through rice was dominated by molecular diffusion and not convective through-flow.

Our results on CH₄ efflux densities of the intact plant canopy versus stubble (Fig. 5 and 6) confirm the fact that neither top biomass nor transpiration rates control CH₄ emissions directly. On the other hand, the number of tillers, photosynthetic rates, and root biomass seem more likely to exert a significant role in governing CH₄ emissions.

Comparisons with Other Studies

Table 5 summarizes some of the measurements of CH₄ efflux densities from other studies. The report of Kahlil et al. (1991) from Chinese rice fields showed the highest average CH₄ efflux densities of 58 mg m⁻² h⁻¹. Yagi and Minami (1990) and Schütz et al. (1989) demon-

Table 5. Average methane efflux density from rice measured at several locations around the world.

Reference and location	Conditions	Efflux density mg m ⁻² h ⁻¹
Khalil et al. (1991), China		58
Cicerone and Shetter (1981), California	no fertilizer	1.3
	mineral fertilizer	6.3
Cicerone et al. (1983), California	mineral fertilizer	9–12
Holzappel-Pschorh and Seiler (1986), Italy	no fertilizer	6–11
	mineral fertilizer	8–24
Schütz et al. (1989), Italy	no fertilizer	6–16
	mineral fertilizer	5–16
	rice straw, 3–6 Mg ha ⁻¹	10–28
Seiler et al. (1984), Spain	sea water sulfate	4
Yagi and Minami (1990), four diverse paddy fields in Japan	mineral soil, Tsukuba-Ryugasaki	0.2–2.9
	compost, Mito-Ryugasaki	1.9–3.8
	rice straw, Tsukuba-Kawachi	0.4–16.3
Kimura and Minami (1995), Thailand	range of sites and conditions	1–33
Sass et al. (1990), Texas	vegetated plots	2.5–8.8
	bare plots	0.1–0.6
Wang and Shangguan (1995), China	range	8–59
	national weighted average	16.7–21.8
Sass and Fisher (1995), Texas		11.6 ± 6.0 (mean ± SD, n = 49)
Huang et al. (1998), China	model average of irrigated rice	13.3
Denier van der Gon (1999), China	estimated from total emissions	14.5
Redeker et al. (2000), California	vegetated plots with rice straw	2.5–11.2
	vegetated plots with burnt straw	0.7–5.0
	bare flooded plots	0.3–2.2

Table 6. Average methane efflux density from wetlands or rice culture grown at ambient and elevated CO₂ concentrations.

Reference and location	[CO ₂] μmol mol ⁻¹	Efflux density mg m ⁻² h ⁻¹	Average or ratio
Dacey et al. (1994), Maryland marsh	360	0.22–4.59	1.32
	690	0.39–5.72	2.36
	ratio	2.36/1.32	1.8
Hutchin et al. (1995), Wales mire	355	1.2–6.4	
	550	2.9–15.6	
	ratio		>2.0
Ziska et al. (1998), Philippine rice	360	5.9–10.4	8.15
	660	9.5–16.1	12.8
	ratio	12.8/8.15	1.9
	360 + 4°C	5.0	
	660 + 4°C	15.7	
ratio	15.7/5.0	3.1	
Schrope et al. (1999), Florida greenhouses	360	0.6–4.1 (maximum)	
	710	0.1–1.0 (maximum)	
	ratio	1.1/4.7	0.23

strated the importance of presence and type of soil organic matter on CH₄ emissions. Incorporation of compost increased CH₄ emissions slightly, but incorporation of uncomposted rice straw raised CH₄ emissions considerably (Table 5), presumably by adding readily decomposable organic matter with a high C to N ratio to the flooded soil.

Elevated CO₂ has also been found to raise CH₄ emissions from a brackish marsh (Dacey et al., 1994) in Maryland (factor of 1.8), a mire (Hutchin et al., 1995) in Wales (>2.0) and in flooded rice (Ziska et al., 1998) in the Philippines (1.9–3.1) (Table 6). In this present study, the ratio of CH₄ emissions in elevated compared with ambient CO₂ increased from 1.4 to 2.3 across the range of 32/28 to 38/29°C temperature treatments. The elevated CO₂ effect and the elevated temperature effect (660 μmol mol⁻¹ at 38/29°C vs. 330 μmol mol⁻¹ at 32/23°C) jointly increased the CH₄ emission ratio to 4.0, a quadrupled effect (Table 7).

Baker et al. (1997a,b) conducted a subsequent study in rice (cv. IR72) grown at CO₂ concentrations of 350 and 700 μmol mol⁻¹ and lower, constant day and night temperatures of 28/21°C. Methane emissions during this ensuing study showed a minor peak at 40 DAP of about 1.0 mg m⁻² h⁻¹ for both CO₂ treatments, and then emissions decreased for several weeks (data not shown). At about 90 DAP emissions began increasing again and rose to maximal values at 110 DAP of about 5.6 mg

m⁻² h⁻¹ in 700 μmol mol⁻¹ CO₂ but only 0.8 mg m⁻² h⁻¹ in 350 μmol mol⁻¹ CO₂ (Table 7). This sevenfold ratio of CH₄ emissions for a doubling of CO₂ is the largest that has been observed.

Not all studies have reported an increase of CH₄ emissions with increasing CO₂ concentrations. Schrope et al. (1999) found lower CH₄ emissions in rice grown under elevated CO₂. They attributed the lower emissions to greater rooting density, which would have allowed greater oxygen penetration to the soil through the aerenchyma of the plants and roots, and thereby provided opportunity for methanotrophic bacteria to consume CH₄ before it could be emitted. In 3.8-L pot studies of bulltongue arrowhead (*Sagittaria lancifolia* L.), Schipper and Reddy (1996) found that CH₄ emissions from plants were inversely related to newly accumulated plant biomass. Furthermore, CH₄ production from soil sampled immediately after the plant measurements decreased with increasing plant biomass. They also observed that when the larger plants were removed from the containers that the root system appeared to be pot bound. This observation supports the concept that a dense root system can supply sufficient O₂ to the rhizosphere to oxidize CH₄ and/or limit methanogenesis.

CONCLUSIONS

Results of this study provide convincing evidence that both elevated CO₂ and higher temperatures cause in-

Table 7. Average methane efflux density from rice culture grown at ambient and elevated CO₂ concentrations and various day–night maximum and minimum temperatures.

Reference and location	[CO ₂] μmol mol ⁻¹	Temperature °C	Efflux density mg m ⁻² h ⁻¹	Ratio
This study, Florida rice	330	32/23	0.9	
	660	32/23	1.3	
	660 to 330 ratio	32/23		1.4
	330	35/26	1.0	
	660	35/26	2.1	
	660 to 330 ratio	35/26		2.1
	330	38/29	1.5	
	660	38/29	3.5	
	660 to 330 ratio	38/29		2.3
		330	38/29 to 32/23 ratio	
	660	38/29 to 32/23 ratio		2.7
	660 at 38/29°C to 330 at 32/23°C ratio			3.9
Baker et al. (1997a,b), Florida rice	350	28/21	0.8 (maximum)	
	700	28/21	5.6 (maximum)	
	ratio			7.0

creased CH₄ emissions in flooded rice culture. Moreover, the combination of the two factors caused a four-fold greater emission in this experiment. The effect is probably due to greater root exudation or root sloughing mediated by increased seasonal total photosynthetic CO₂ uptake (Fig. 8), coupled with decreased partitioning of biomass to seed production (Baker et al., 1994). Thus, the hypothesis that increased photosynthetic CO₂ uptake (due primarily to elevated CO₂ concentration) would cause an increase of CH₄ emissions, and that elevated temperature might modify the CO₂ uptake and emissions response (perhaps because of less CH₄ oxidation in the soil water since O₂ solubility decreases with temperature), was substantiated.

Greater biomass productivity under elevated CO₂ could also lead to increased yield of rice straw. If the additional rice straw were incorporated into the soil, this could potentially increase CH₄ emissions earlier after flooding and increase CH₄ emissions throughout the crop life cycle.

The greater CH₄ emissions of rice grown at elevated temperatures (at either CO₂ concentration) than at lower temperatures imply a greater amount of root exudation or a greater rate of root sloughing, since root biomass was not greater in high-temperature treatments at any of the sampling dates. Because root length density of cv. IR72 was tightly related to root biomass across all treatments and DAP, the pattern for O₂ permeation into the flooded soil was likely to be very similar. Since much of the CH₄ that is produced in wetland soils may actually be oxidized by methanotrophic bacteria before it escapes through the plant (Epp and Chanton, 1993; Schipper and Reddy, 1996), overall CH₄ emissions should be a balance between substrates available for methanogenesis and O₂ available for methanotrophy (i.e., substrate availability to O₂ transport ratio).

Natural wetlands could behave like flooded rice culture in terms of CH₄ emission responses to elevated CO₂ and temperature. With the combination of doubled CO₂ and predicted temperature changes, natural wetland emissions might become two to four times greater, which could mean that CH₄ could rival CO₂ as a greenhouse effect gas. The currently estimated emissions by natural wetlands might increase from current estimates of 120 Tg yr⁻¹ up to 240 to 480 Tg yr⁻¹. Unless other unidentified feedback factors exist, the combination of both rising CO₂ and anticipated global warming would thus appear to enhance CH₄ emissions and tend to stimulate further global warming. If CH₄ emissions from wetland systems are enhanced by this combination, the global warming potential of CH₄ could become more important, rather than less, as currently predicted (Lelieveld et al., 1998).

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