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Diffusion-controlled transport of methane from soil to atmosphere as mediated by rice plants

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Abstract. Methane emission from rice grown in flooded soil was measured in pot experiments using headspaces with different gas composition. The emission rates varied with the atmospheric composition. Based on the kinetic theory of gases the binary diffusion coefficients for methane in various gases were calculated. The ratios of the measured emissions under a certain atmosphere relative to that in air were similar to the ratios of the binary diffusion coefficients showing that plant-mediated CH_4 transport is driven by diffusion. Small deviations from the theoretical ratios of emissions support the hypothesis that mass flow of gas to the submerged parts of the rice plant may depress the upward diffusive CH_4 flux. The results in combination with data from the literature suggest that the rate limiting step in plant-mediated methane transport is diffusion of CH_4 across the root/shoot junction.

Introduction

Methane (CH_4) is an important greenhouse gas that traps part of the thermal radiation from the earth's surface and plays an active role in the atmospheric chemistry (Wang et al. 1976; Bouwman 1990). Methane, produced by strict anaerobes in waterlogged soils, is transported to the atmosphere by diffusion, ebullition or plant-mediated transport. Wetland rice fields are considered a globally important source of methane (Cicerone & Oremland 1988; Bouwman 1990). In rice fields 80–90% of the CH_4 emission is due to plant-mediated transport (de Bont et al. 1978; Holzapfel-Pschorn & Seiler 1986; Holzapfel-Pschorn et al. 1986). Rice can grow in anoxic soil because it possesses a well-developed system of air spaces (aerenchyma) which supplies atmospheric O_2 to the roots for respiration. At the same time this system is an effective vent for the release of CH_4 from the soil to the atmosphere. The transport of oxygen from the atmosphere to the roots depends on diffusion and/or mass flow (Jensen et al. 1967; Armstrong 1979; Raskin & Kende 1985). Transport of O_2 in rice plants may differ from that of CH_4 in several respects. 1) Methane is transported in the opposite direction; 2) respiration of roots and microorganisms form an active sink for O_2 along its way to the soil and 3) diffusive transport will be influenced by the difference in molecular weight between O_2 and CH_4. Because there is a downward mass flow of gas in rice plants (Raskin & Kende 1985), it is unlikely that the upward transport of CH_4 occurs by mass flow. Therefore, CH_4 transport is probably by diffusion, driven by the concentration gradient between the soil (source) and the atmosphere, which acts as an infinite sink due to the low concentration of CH_4 in ambient air. The rate of transport of ethylene through rice plants from the rooting medium to the atmosphere, however, was not proportional to the partial pressure of ethylene around the roots (Lee et al. 1981). This indicates that processes other than diffusion may play a role too.

Clearly, the mechanisms and limitations of plant-mediated CH_4 transport are not fully understood. A proper understanding of the CH_4 transport through the plant is essential for mechanistic modelling of CH_4 emission on a field scale. The aim of the experiments described here is to further elucidate the mechanisms of CH_4 transport through rice plants. Based on the kinetic theory of gases an experiment is designed to test the hypothesis that plant-mediated CH_4 transport is driven by diffusion.

Theory

For the diffusion of a trace gas *i* through any gas mixture the Fickian diffusion coefficient D_{Fi} is independent of the mole fraction of *i* and of the diffusional fluxes of other gases (Jaynes & Rogowski 1983). In this case the D_{Fi} equals the binary diffusion coefficient D_{ij} of gas *i* in gas *j* (Hirschfelder et al. 1964).

$$D_{ij} = c\,\frac{[T^3(M_i + M_j)/(2M_iM_j)]^{1/2}}{p\sigma_{ij}^2\Omega_{ij}} \tag{1}$$

where D_{ij} = binary diffusion coefficient of species *i* in *j* ($m^2.s^{-1}$)
c = constant; 8.42×10^{-24} ($J^3.K^{-3}.mol^{-1}$) (Leffelaar 1987)
T = temperature (K)
M_i = molecular weight of species *i*
p = pressure (Pa)
σ_{ij} = arithmic mean of the collision diameters for species *i* and *j* (m)
Ω_{ij} = collision integral for species *i* and *j*

Eq. (1) shows that a change of the molecular weight of the bulk gas in the atmosphere would influence diffusion of a trace gas from soil to atmosphere. This offers the possibility to test if diffusion controls the emission rate by studying the effect of atmospheric composition on trace gas emission. The dimensionless collision integral (Ω_{ij}) has been tabulated by Hirschfelder et al. (1964) as a function of reduced temperature T_{ij} (= $\kappa T/\varepsilon_{ij}$). Both the arithmic mean of the collision diameters for species *i* and *j* (σ_{ij}) and ε_{ij}/κ are obtained from empirical combining laws (Eq. (2) and (3), Leffelaar 1987).

$$\sigma_{ij} = \frac{(\sigma_{ii} + \sigma_{jj})}{2} \tag{2}$$

$$\frac{\varepsilon_{ij}}{\kappa} = \left[\left(\frac{\varepsilon_{ii}}{\kappa}\right)\left(\frac{\varepsilon_{jj}}{\kappa}\right)\right]^{1/2} \tag{3}$$

where ε_{ii} = Lennard-Jones potential parameter; maximum energy of attraction occurring between molecules of component *i* (J)
κ = Boltzmann constant; 1.3805×10^{-23} (J K^{-1})

Table 1 gives the force constants necessary for calculating the binary diffusion coefficient for CH_4 in several other gasses. Using Eq. (1) through (3) and the data from Table 1 the binary diffusion coefficients for CH_4 in air, N_2, O_2, CO_2 and He are calculated (Table 2).

When applied to CH_4 transport via the rice aerenchyma the binary diffusion coefficients have to be used with caution. If its concentration inside the plant or root aerenchyma would be high, CH_4 would no longer qualify as a trace gas. In that case the Fickian diffusion coefficient D_{FCH4} no longer equals the binary diffusion coefficient D_{CH4j}, but would also depend on the gas mole fraction of CH_4 in the aerenchyma, Y_{CH4}, and on the gas flux ratio f_{jCH4} (Jaynes & Rogowski 1983):

$$D_{F_{CH_4}} = \frac{D_{CH_4j}}{1 - (1 - f_{jCH_4})Y_{CH_4}}. \tag{4}$$

Table 1. Force constants for calculating binary diffusion coefficients for CH_4 in other gasses according to Eq. (1) through (3) derived from tables in Hirschfelder et al. (1964).

Gas	CH_4	Air	N_2	O_2	CO_2	He
σ_{ii} ($\times 10^{10}$ m)	3.822	3.617	3.681	3.433	3.966	2.567
ε_{ii}/κ (K)	137	97	91.5	113	190	10.22
Ω_{CH4j} (T = 30 °C)	—	0.986	0.978	1.008	1.10	0.77

Table 2. Binary diffusion coefficients for CH_4 calculated with Eq. (1) through (3) and the experimental CH_4 fluxes relative to the flux under air derived from Fig. 4.

Gas pair	Binary diffusion coefficient ($D_{CH4\,j} \times 10^5$ $m^2.s^{-1}$)	$D_{CH4\,j}/D_{CH4\,air}$ ($\times$ 100%)	Experimental CH_4 flux relative to air (Fig. 4)
CH_4-Air	2.27	100	99
CH_4-N_2	2.26	99	120
CH_4-O_2	2.29	101	ND
CH_4-CO_2	1.72	76	76
CH_4-He	7.04	310	302

However, up to partial pressures of 10% CH_4 in the aerenchyma (Y_{CH4} = 0.1) and with $0 \leqslant f_{jCH4} \leqslant 2$ the deviation of the diffusion coefficient for CH_4 D_{FCH4}, is within 10% of trace gas values ($0.91\ D_{CH4j} \leqslant D_{FCH4} \leqslant 1.11\ D_{CH4j}$). Furthermore the ratios of the binary diffusion coefficients will all be influenced by Y_{CH4} in the same way. Therefore, by comparing the ratios of the experimental results for two different headspaces, interference of Y_{CH4} can be avoided. So, the hypothesis that the plant-mediated CH_4 flux is driven by diffusion can be tested by comparing the ratio of CH_4 fluxes at different bulk gas compositions with the ratio of the respective relevant binary diffusion coefficients.

Materials and methods

Maahas clay soil from the IRRI research farm (Block C) in The Philippines was air-dried and sieved. Plastic 5 liter pots were filled with 2.5 kg of soil mixed with 0.27 g urea, equivalent to 100 kg $N.ha^{-1}$. Half of the pots received 6.25 g chopped straw per pot, equivalent to 5 $tons.ha^{-1}$. The soil in the pots was mixed and puddled. The next day, two seedlings (11 days old, variety IR 72) were transplanted into each pot. After transplanting the pots were placed in the greenhouse and a constant floodwater layer of 5 cm was maintained. Approximately 65 days after transplanting the stems of the rice plants were cut approx. 5 cm above the floodwater. Cutting the plants presumably does not influence plant-mediated CH_4 emission (Seiler et al. 1984), but has several advantages: 1) The cover can be smaller making the experimental set-up simpler and the CH_4 detection limit lower because of volume reduction. 2) Photosynthesis is strongly reduced or stopped and does not influence the gas composition of the headspace. 3) The total distance from atmosphere via the leafs, stems and roots to the rhizosphere is reduced, creating a quicker response to headspace composition changes. The assumption that cutting the plants does not influence emission was tested in a separate pilot experiment prior to the main experiment. In the pilot experiment methane emission of rice plants before and approx. 1 hour after cutting the stems above the floodwater was measured.

After cutting, the pots used in the main experiment were moved to a building next to the greenhouse with dim light and with relatively small diurnal temperature variations. A part of the floodwater was removed and a styrofoam disk (∅ = inner diameter of pot) with holes for the stems was placed over the plants and pushed into the pot. The space between stems or rim of the pot and the styrofoam was sealed off with vacuum grease, so that gas transport between soil and atmosphere could take place only via the stems and roots of the rice plants.

The emitted CH_4 was trapped under a cover resting on a water-filled support ring that formed a gas-tight seal separating the inner atmosphere from the outside. The cover was equipped with a small 12 V DC fan to ensure good mixing of the gas phase, and with two septa for sampling or

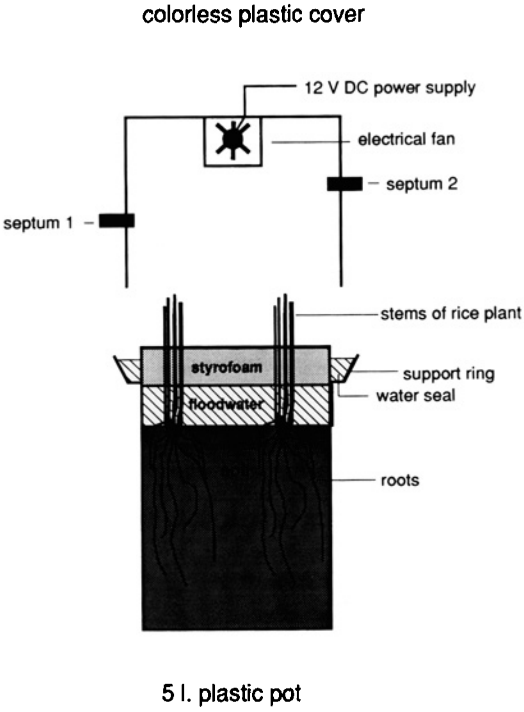

Fig. 1. Experimental set-up for measuring methane emissions.

flushing the headspace (Fig. 1). With a 5 ml disposable syringe 3 ml gas samples were taken from the headspace. The samples were injected immediately into a 2 ml sample loop connected to a gaschromatograph equipped with a Flame Ionization Detector (FID, N_2 as carrier gas, column oven temperature 45 °C). The CH_4 flux was calculated with linear regression from the increase of the CH_4 concentration in the headspace over time. For each flux calculation the headspace was sampled 5 times with an interval of 5—10 minutes. The R-squared of the linear regressions is typically > 0.95.

The CH_4 flux was measured at 9:00 on the six days following cutting of the stems. On day 1 and 5 the CH_4 flux was measured every 2 or 3 hours. The pots were temporarily moved on day 5 to a different part of the building where diurnal temperature fluctuations are higher to check for temperature effects on CH_4 emission.

On day 2, 3, 4 and 6, immediately after the flux measurement at 9:00, the headspace composition was changed from air to He, next to CO_2, to N_2 and again to He. The gases were flushed in through septum 1, while a needle through septum 2 connected to a tubing hanging into a beaker with a small layer of water acted as an outlet. To test the efficiency of gas renewal in the system, the headspace was spiked with a high concentration of CH_4. After 45 minutes more than 98.5% of the CH_4 originally present in the headspace was removed. During the main experiments flushing was continued for 1.5 hours before the CH_4 flux was measured at the new headspace composition. The measurements on days 1, 2, 3, 4 and 6 were performed under the same conditions in terms of temperature and light intensity.

The change from air to N_2, CO_2 or He includes a change from an aerobic to an anaerobic system, which might affect the CH_4 source strength by depressing oxidation of CH_4 in the rhizosphere. Therefore a separate experiment was performed consisting of a CH_4 flux measurement at the end of a 15 hour pre-incubation with an N_2 headspace followed by CH_4 flux measurement after flushing with CO_2 for 1.5 and 5 hours.

Results and discussion

The pilot experiment revealed no significant differences in the amount of CH_4 emitted by cut and intact plants, both at high and low levels of emission (Table 3). This confirms the results by Seiler et al. (1984) and shows that cut plants are useful proxis for intact plants in studying factors that determine CH_4 emissions from rice fields. Emission of CH_4 is not influenced by cutting the stems above the floodwater because plant-

Table 3. Methane emission before and after cutting the stems above the floodwater for 6 pots planted with rice plants, 1 month after transplanting.

Pot nr.	Straw addition (g)	CH_4 emission[b] (nmol.s^{-1}.plant^{-1})	
		Intact	Cut
1–3	0	0.243	0.228
4–6	6.25[a]	1.840	2.495

[a] Chopped straw, equivalent to 5 tons.ha^{-1}.

[b] A one sided *t*-test indicated no significant difference at the 95% level between CH_4 emission of intact versus cut plants.

mediated gas transport between soil and atmosphere is independent of transpiration rate or stomatal opening (Lee et al. 1981; Seiler et al. 1984) and takes place mostly via micropores in the leaf sheaths (Nouchi et al. 1990). All further results refer to measurements on cut plants.

Figure 2 shows that the CH_4 emission from cut plants gradually decreased with time over six consecutive days to about 70% of the initial value. To compare the effect of changes in headspace composition on CH_4 emission over a prolonged period, this gradual decrease has to be taken into account. Therefore, the CH_4 emissions fluxes into a headspace with a specific gaseous composition, that were measured on a certain day at

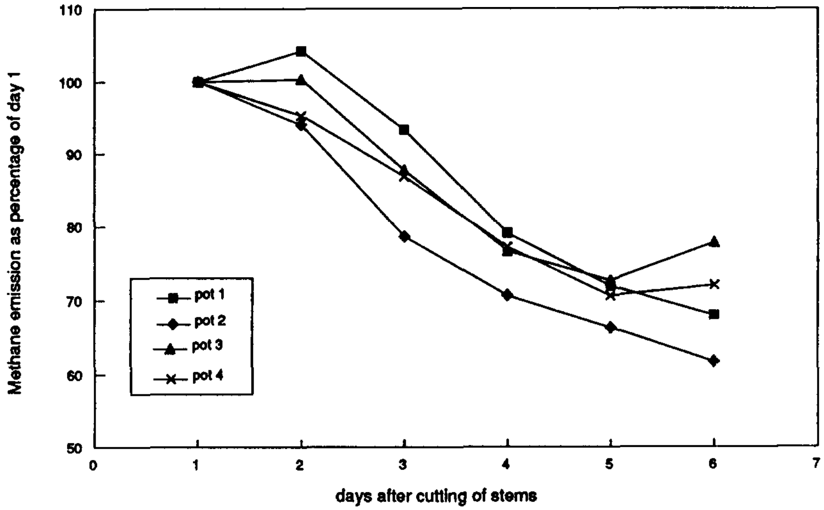

Fig. 2. Plant-mediated methane emission from planted pots measured at 9:00.

11:00 a.m., will always be expressed as a percentage of the CH_4 emission into the same headspace with air, measured at 9:00 a.m. of the same day. This approach carries the risk that emission differences caused by other factors are included. For instance, CH_4 emissions from cut plants into a headspace of constant composition, show a distinct diurnal pattern, with highest emissions around 14:00 (Fig. 3). Similar fluctuations have been observed with intact plants (Schütz et al. 1989, Schütz et al. 1990). Because (1) the diurnal pattern in CH_4 emission parallels that in temperature, and (2) the greatest amplitudes in both CH_4 emission and temperature were observed in the same day (viz. on day 5, Fig. 3), temperature is probably the factor driving the diurnal fluctuation in CH_4 emission. Because the experiments were not thermostated, potential effects of temperature will have to be considered when comparing CH_4 fluxes measured at different times during the day.

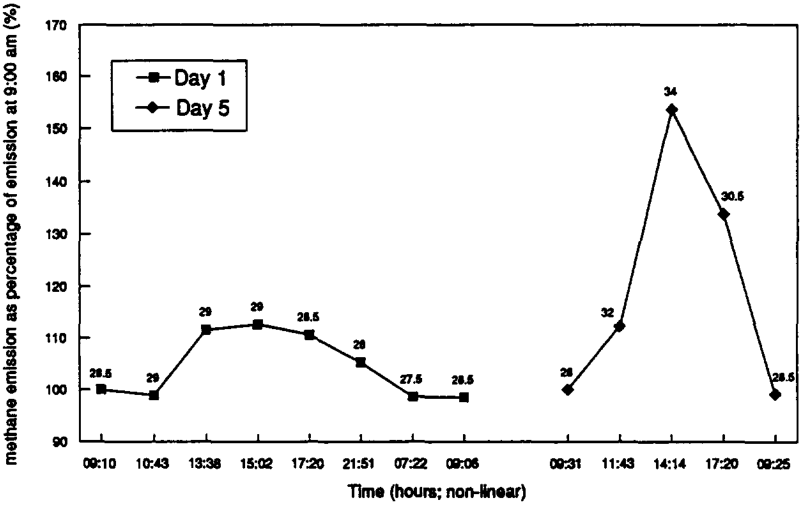

Fig. 3. Diurnal emission pattern from pots with cut plants (Average of 4 pots, air temperature above data point).

Figure 4 shows that replacing air in the headspace by He tripled the CH_4 flux. The effect of He on the relative increase in CH_4 emission was the same on day 2 as on day 6, even though absolute fluxes were lower (by about 30%) on day 6 (Fig. 2). Replacing air by N_2 increased the CH_4 flux by 20%, while replacement of air by CO_2 decreased that flux by 24%. Because the difference in temperature between 9:00 (emission into air) and 11:00 (emission into headspace with variant composition) was too small to markedly affect the CH_4 emission (see Fig. 3, left panel), no attempt will be made to correct for temperature effects in this experiment.

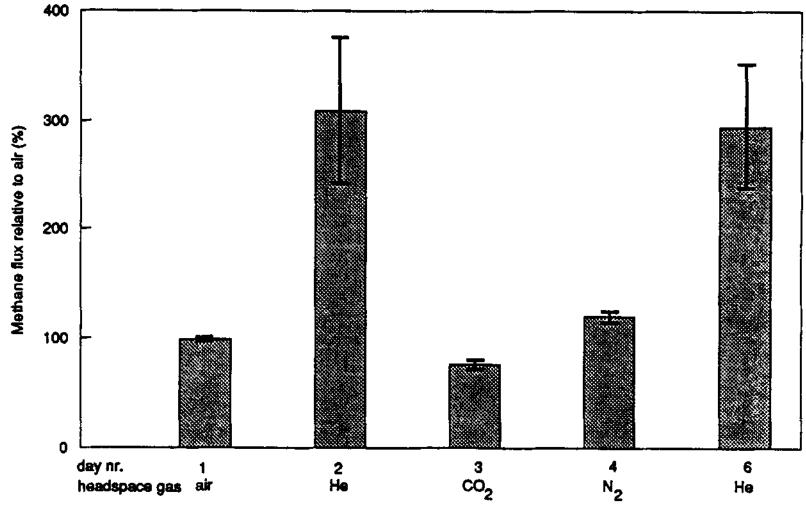

Fig. 4. Mean methane flux from 4 pots with cut plants at 11:00 on successive days. Flux expressed as percentage of flux under air headspace at 9:00 of each day. Error bars indicate positive and negative standard deviation.

The ratios of the CH_4 fluxes into He or CO_2 relative to those into air are very close to the ratios of the corresponding diffusion coefficients (Table 2). This strongly suggests that, on the time scale of the experiments, CH_4 transport is driven mainly by molecular diffusion. However, CH_4 fluxes into an N_2 atmosphere were about 20% higher than expected on the basis of diffusion only, indicating that additional factors are involved.

Two processes in addition to diffusion should be considered. First, by changing the headspace composition from air to any of the other gases considered, the supply of O_2 to the rhizosphere is stopped. Due to respiration of roots and microorganisms the rhizosphere would then become anaerobic. This would suppress CH_4 oxidation by the large number of methane oxidizing bacteria normally present in the rhizosphere (de Bont et al. 1978) and possibly stimulate methanogenic activity in the immediate surroundings of the former oxic rhizosphere. Thus the CH_4 source strength would increase. Methane emission from rice cultures increased by more than 242% after incubation under N_2 for 15—24 hours (Holzapfel-Pschorn et al. 1986) illustrating that a shift from aerobic to anaerobic condition increases CH_4 emission. The 20% higher CH_4 flux after 2 hours of N_2 relative to air may be explained by O_2 depletion, depressing CH_4 oxidation and/or stimulating CH_4 production in the rhizosphere. The relatively low increase in CH_4 emission is probably due to the short duration of the N_2 incubation.

Second, changing the gas composition would lead to a shift in equilibrium between gaseous and dissolved gases in the rhizosphere. Increased dissolution of a gas in the soil solution around the rhizosphere would cause mass flow of that gas from the headspace into the plant. Downward mass flow would, in turn, suppress emission of CH_4. This effect should be particularly important in case of the soluble gas CO_2 (1.713 $l.l^{-1}$ H_2O, Weast 1974): the partial pressure of CO_2 would increase from 0.05—0.2 bar (Ponnamperuma 1972) to almost 1 bar, and much less so for N_2 (shift from about 0.8 to almost 1 bar and low solubility in water; 0.0233 $l.l^{-1}$ H_2O, Weast 1974). The relative increase in partial pressure would be largest for He but, in view of its low solubility in water (0.0105 $l.l^{-1}$ H_2O, Weast 1974), the associated mass flow and its depression effect on CH_4 emission would be small. The expected difference between the effects of CO_2 and N_2 on CH_4 emission was confirmed by a second experiment where a change of headspace composition is not accompanied by a change in aerobic/anaerobic status of the system. To compare the different emission levels the flux for each pot was expressed relative to its flux under N_2 and then averaged for all pots (Table 4). Although emission levels varied among the pots the response to a change from N_2 to CO_2 headspace composition was similar. The CH_4 flux measured at 13:05 and 16:00 under CO_2 headspace is influenced by the diurnal variation in the CH_4 emission (as in Fig. 3). Based on the temperature variation of 2 °C and Fig. 3 it was estimated that, under otherwise unchanged conditions, the flux at 13:05 and 16:00 would be respectively 120% and 115% of the flux at 9:40. This estimate is used for correcting the measured fluxes (Table 4). The change from N_2 to CO_2 resulted in a quick reduction of the CH_4 flux by 35—40%. The flux did not significantly change if the exposure to CO_2 was continued. This reduction is 10—15% lower than expected on the basis of diffusion alone. The additional reduction can be explained by downward mass flow of CO_2. Mass flow of air to the

Table 4. Average CH_4 flux from six planted pots in CO_2 relative to the flux in N_2 headspace composition, after correction for diurnal variation.

Exposure to CO_2 (hr)	T (°C)	Correction factor[a]	Average CH_4 flux (%)[b]
1.5	32	1.20	58 (8)
5	30	1.15	54 (6)

[a] Correction factor based on temperature and Fig. 3.

[b] Relative flux is first calculated per pot than averaged, standard deviation in brackets.

submerged parts of rice plants driven by solubilization of CO_2 was previously observed by following changes in headspace volume of a leaf chamber (Raskin & Kende 1985). Mass flow can also be induced by temperature or barometric fluctuations but it is unlikely that this will be of any great significance in the overall plant-mediated gas transport process (Armstrong 1979). Mass flow of gas to the submerged parts of the plants would be especially important for O_2 transport to the roots but may also play a role by reducing the upward diffusive CH_4 flux. In such a case CH_4 has to diffuse against the downward flow of gas.

That a change from air to CO_2 headspace composition did not show the additional flux reduction due to downward mass flow (Table 2) can be explained if the flux reduction due to mass flow was balanced by the enhanced CH_4 flux resulting from a shift from aerobic to anaerobic conditions. Indeed, the decrease in CH_4 flux due to downward mass flow of CO_2 is in the same order of magnitude as the increase in CH_4 flux from changing air to N_2. Figure 5 presents a schematic overview of the processes influencing the plant-mediated CH_4 emission as a function of the change in headspace gas explaining all our observations and which is in accordance with the findings of Jensen et al. 1967, Lee et al. 1981 and Raskin & Kende 1985.

The quick reaction of the CH_4 emission to a change of headspace (at least within 1.5 hours) indicates a limiting step for diffusive transport close to the atmosphere. A possible source of internal diffusive resistance is the root/shoot junction. Experiments assessing total pore space resistance prior and after excision of the root/shoot junction indicated that the effective porosity across the junction is low compared to that in roots, stems or leaves (Armstrong 1979). That the root/shoot junction acts as a barrier for gas transport is further supported by; 1) Cutting the stems did not influence the emission rate proving that the rate limiting step in plant-mediated CH_4 transport is not located in the cut-off part of the plants. 2) The observation that the transport rate of ethylene from the rooting medium via the rice plant to the atmosphere was not proportional to the partial pressure of ethylene in the rooting medium (Lee et al. 1981). Lee et al.'s (1981) finding appears to be in conflict with diffusive transport since diffusion is driven by a concentration gradient. However, the concentration in the root aerenchyma of the dissolved gases present in the rooting medium may become so high that changes in partial pressure outside the roots do not significantly influence the concentration in the root aerenchyma. Then the concentration gradient across the root/shoot junction is no longer influenced by increasing partial pressures in the rooting medium and diffusive transport across the junction would not increase.

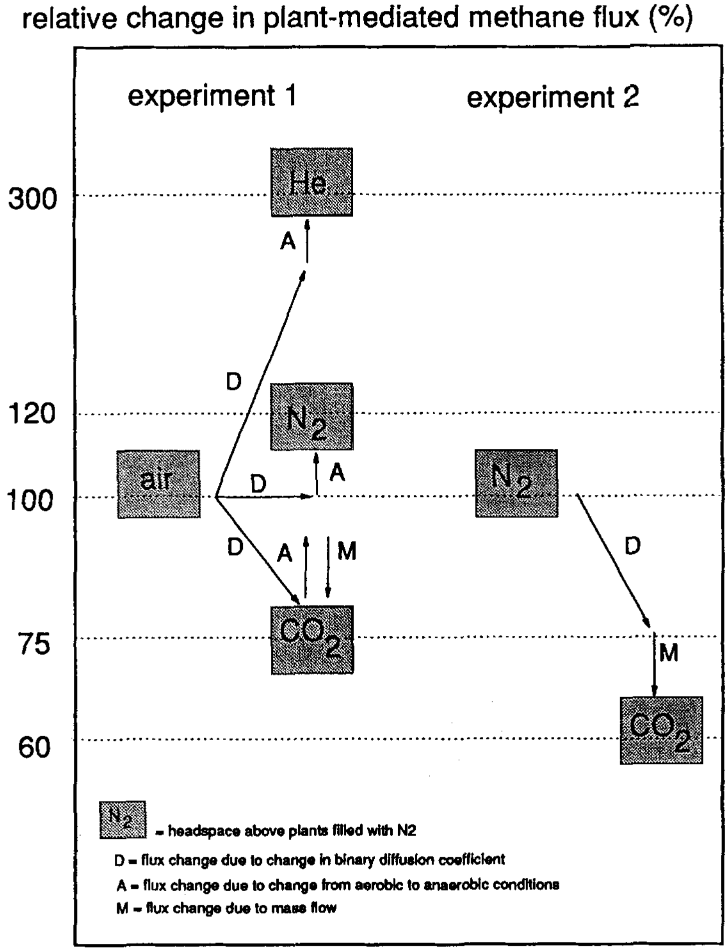

Fig. 5. Schematic model indicating the changes in plant-mediated methane flux induced by various processes, when changing the headspace gas from air to He, N_2 or CO_2 (experiment 1), or from N_2 to CO_2 (experiment 2).

The model presented in Fig. 5 is only valid for lowland rice varieties because gas transport mechanisms differ among plants. Aquatic plants such as the waterlily *Nuphar luteum* (Dacey 1981), cattail *Typha latifolia* (Sebacher et al. 1985) or some trees *Alnus glutinosa* (*L.*) (Schröder 1989) possess an active thermally driven ventilation system that largely controls gas transport in these plants. Such a ventilation system is absent in rice *Oryza sativa* (Chanton & Dacey 1992). Furthermore, gas transport in deepwater rice and floating rice may differ substantially from Fig. 5 since physiology of these rice varieties differs from lowland rice.

Diurnal variation patterns of methane emissions from rice fields differ substantially among locations e.g. Italy (Schütz et al. 1989) and China (Wang et al. 1990). The combination of mass flow and diffusion in rice plants is part of the processes necessary to come to a mechanistic understanding of methane emissions from rice fields.

Conclusions

The response of the plant-mediated CH_4 flux to a headspace with a variable gas composition corresponds with the change in binary diffusion coefficients of CH_4 in these headspace compositions. Deviations from this pattern can be explained qualitatively by increased CH_4 emission due to decreased CH_4 oxidation and/or enhanced CH_4 production in the rhizosphere when replacing air by an anaerobic gas, and by downward mass flow of the bulk gas if that would dissolve to an appreciable extent in the soil solution (CO_2). The results indicate that diffusion is the rate limiting step in plant-mediated CH_4 transport to the atmosphere. Therefore in a field situation factors that enhance diffusion rates will enhance CH_4 emission (e.g. temperature increase, concentration gradient). The results in combination with literature data suggest that, as soon as the partial pressure of CH_4 in the rhizosphere reaches a threshold value, diffusion across the root/shoot junction becomes the rate limiting step in plant-mediated CH_4 transport.

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