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Plants as conduit for methane in wetlands

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Abstract

Next to CO_2, methane is the most important greenhouse gas. Methane is produced by methanogenic bacteria under anoxic conditions, and tropical wetlands are among the most important sources of methane for the atmosphere. In order to cope up with the anoxic conditions the wetland plants have developed morphological features to facilitate oxygen transport to the rhizosphere. This same transport pathway is also utilized for emission of methane produced in the anoxic layers of the habitat to the atmosphere. The methane transport efficiency, however, differs from species to species and depends upon the magnitude of aerenchyma development and root porosity. Methane release site in plants may or may not be stomata.

Carbon dioxide, CH_4, CFC-11, CFC-12 and N_20 are the most important greenhouse gases. Among these, CH_4 is the only gas which directly affects tropospheric chemistry and controls numerous chemical processes and constituents in the troposphere and stratosphere[1]. The infrared spectrum of CH_4 makes it a strong greenhouse gas[2]. The atmospheric concentration of CH_4 has more than doubled during the past 200 years, rising over the past 15 years by an average of 1% per year[3]. Wetlands are significant natural sources of atmospheric methane accounting for about 20% of the current global annual emission of ca 450-550 T[4]. A group of anaerobic bacteria, which occur in a wide variety of habitats, produce CH_4 as a product of their catabolism in strict anoxic conditions. Methanogenesis takes place in environments such as flooded soils, wetlands, estuaries, marine and freshwater sediments and the gastrointestinal tract of animals[5]. Studies conducted on some wetland species indicated that the movement of CH_4 from anaerobic sediments through the shoots of these plants into the atmosphere could provide a significant pathway for the emission of methane[6-8].

In this article we explore the role of plants in CH_4 emission from wetlands.

Methane Production

Methane is produced in saturated soils by anaerobic bacteria called methanogens, which use decomposition products of organic matter as their food source and produce methane as a catabolic product. Methanogens are prokaryotes as they lack a nuclear membrane but in several molecular properties they resemble more closely the eucaryotes than the bacteria[9,10]. They may be rod, coccoid, or spirillum shaped and occur in freshwater and marine sediments, marshes, rice paddies, landfills and sewage digesters, algal mats, geothermal springs, digestive tracts of invertebrates and vertebrates, and even inside the heartwood of living trees. Methanogensis takes place only in strict anoxic conditions and is a complex process, affected by several abiotic and biotic factors[11,12]. In general, flooded condition provides as optimum environment for methane production and emission[13].

The known substrates that methanogens can catabolize are rather limited and include H_2 + CO_2, formate, acetate, methanol methylamines, and methylsulfides[14,15]. Process of methanogenesis may be divided into three major steps - solubilization- hydrolysis, fermentation (or acidogensis) and methanogenesis. Solubilization is concerned with conversion of solid substrate material either into soluble polymeric materials-oligomers or into low molecular weight or monomeric compounds. Soluble organic matter either present initially or originating from solubilization of insoluble organic material consists of proteins and aminoacids, polysaccharides and sugars, lipids, glycerol and fatty acids[16]. Organic anions are released in the fermentation medium by fermenting bateria. Because of the release of organic acid anions the fermentation of soluble organic matter is also referred to as 'acidogenesis'. 'Obligate hydrogen-producing acetogenic' bacteria or OHPA, link the fermentation step with the methanogenic step by metabolizing soluble organic compounds into acetate, H_2 and inorganic carbon. Flooding a soil causes the essential low redox potential and anaerobic decomposition of organic matter and stabilizes the soil pH near neutral. Thus aquatic habitats provide an optimum environment for methane production and emission. A combination of high pH and low redox potential is favourable for CH_4 production[11]. Methane concentration in soil water markedly increased when redox potential attained less than about - 200 mV[17]. According to Parashar et al.[18], pH in the range of 7.5 to 8.5 may be most favourable for methanogenesis.

Role of Plants in Methane Emission

To cope up with the lack of oxygen in the growth medium, wetland plants have developed morphological features to facilitate oxygen transport to the submerged organs. Such plants are characterized by extensive development of aerenchyma tissue with gas-filled lacunae, in above-as well as in belowground parts (Fig. 1). Through these channels or lacunae atmospheric O_2 is transported to the rhizosphere by diffusion[19,20] or by mass flow[21]. Aerenchyma tissue development is a process caused by cell separation (schizogenous) or cortex breakdown (lysigenous)[22]. Studies on aerenchyma of rice have indicated areas in the root cortex which contained no cells[23-25]. Also, unusually large cells were observed in the cortex of basal tissues of rice roots; the nodal walls of many of these cells extended almost the entire distance from endodermis to epidermis, and longitudinal section revealed an upper empty continuous air passage in the root cortex[25] (Fig. 2). A lack of protoplasm in many of these cells indicated absence of metabolic functions and led to the conclusion

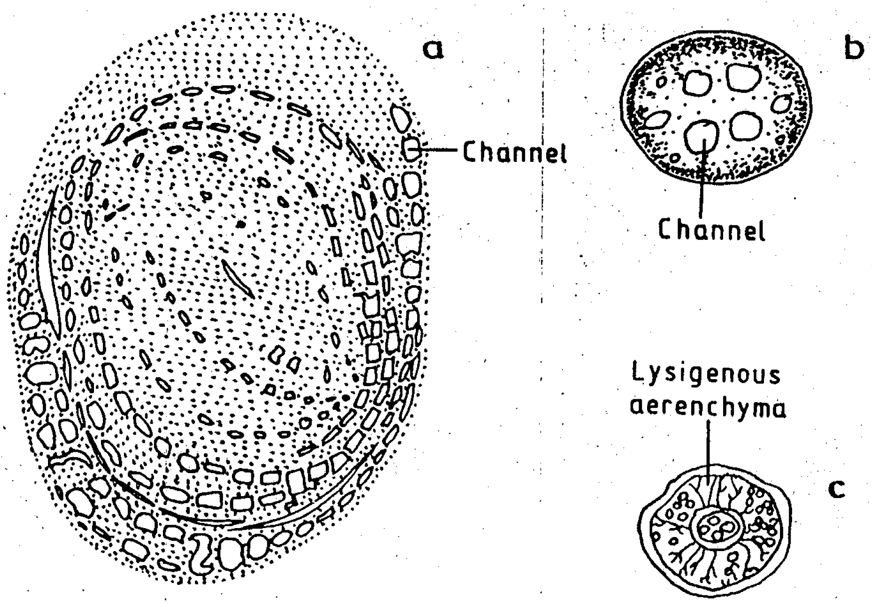

Fig. 1— Cross-sections of wetland plant organs showing ingternal air- spaces. (a) Leaf-stem of *Typha latifolia* showing intercellualr iar spaces which are restricted by thin porous membranes spaced several millimeters apart, (b) Petiole of *Nymphaea odorata* showing intercellular structures as channels, (c) Rice root showing lysigenous aerenchyma. (a and b based on Sebacher et al.[7] and c on Takashashi et al.[53]).

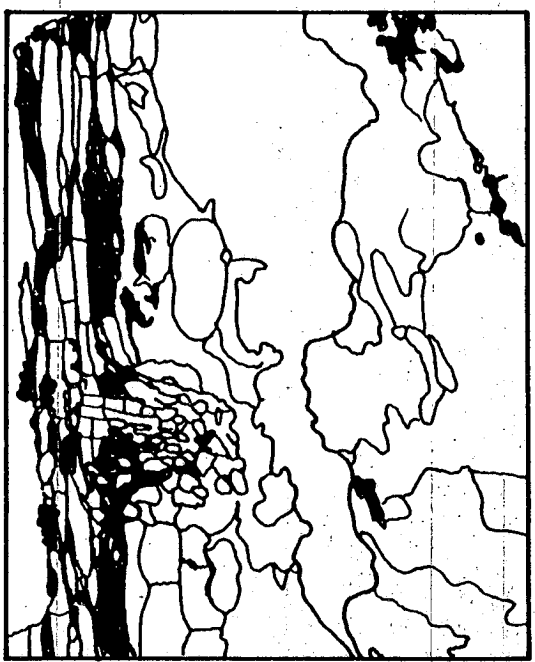

Fig. 2 – Longitudinal section through basal part of rice root showing apparently continuous air space in the cortex (Based on John[25]).

that these structures may constitute a pathway of gas exhange[25]. A well-developed aerenchyma system in a plant would ensure an efficient exchange of gases between the atmosphere and the submerged soil environment[26].

Studies on aquatic habitats demonstrated that the rooted macrophytes such as *Naphur luteum* and *Typha latifolia* act as channel for transport of CH_4 from reduced soil to the atmosphere, and are responsible for the majority of CH_4 emission[6,7,27,28]. The movement of methane from anaerobic sediments through the leaves, stems, and flowers of aquatic plants provides a significant pathway for the methane emission from the aquatic substrates of flooded wetlands into the atmosphere[7]. Bubier and Moore[29] have also reported that aquatic plants can enhance emission by serving as gas conduits, transporting CH_4 from the zone of production below the water table to the atmosphere through aerenchyma. Cutting plant stems below the water surface reduced CH_4 emission to 6-40% of the original rate in fields covered with rice, weed, or reed[30].

Measurements in experimental fields of flooded rice agriculture demonstrated that rice plants also transport CH_4 from soil to the atmosphere[31]. In a subarctic Canadian-fen over 90% of the CH_4 emission was transported by *Carex* species[32]. Plant-enhanced CH_4 emissions have also been reported from Alaskan tundra sites where vegetated borders of ponds and pools had higher fluxes than unvegetated open water areas[33-34].

Sebacher et al.[7] measured methane emission from 22 varieties of hydrophytes in the southern U.S.A. Of these, nine species either emitted no CH_4 or the emitted CH_4 levels were too low to be detected. The methane emissin from hydrophyrtes varied from 14.8 mg CH_4 d^{-1} for *Nymphea odorata* down to 0.1 mg CH_4 d^{-1} for *Zizaniopsis miliacea* (Table 1). In the CH_4- emitting species the CH_4 concentration measured within the stem at the waterline was positively related with the magnitude of CH_4 emission. Those plant species which had soft epidermal layers and outer stem cells where the parenchyma hd developed into elongated tubular structures emitted CH_4 at a rate 1 mg CH_4 d^{-1} (Table 1). The channels in the petiole of *Nymphea odorate* were continuous and unstricted from the rhizome deep in the anaerobic sediments to the floating lily pad exposed to atmosphere. In contrast, the intercellular structures of *Typha latifolia* were restricted by thin porous membranes spaced several millimeters apart[7].

The aquatic plants characterized by relatively hard epidermal layers and outer stem cells as found in the grasses and rushes emitted CH_4 at a rate mg CH_4 d^{-} (Table 1). In these plants, hard outer layers significantly restrict the transfer of gases. The structural and functional differences in the root systems of the above two categories may also affect CH_4 emission from the subaerial parts of these plants. Freshwater floating aquatic plants (not rooted in anaerobic sediments) including *Alternanthera philoseroides*, *Hydrocotyle ranunculoides*, and *Lemma* sp. emitted undetectable amounts of CH_4.

Table 1 – A cross section of values for methane emission from various aquatic plants. Species are arranged in increasing order of CH_4 emission (Source : Sebacher et al. 1985).

Aquatic plant	Methane emission (mg d^{-1})	Methane instem at water line (mg $m^{''}$)
Zizaniopsis miliacea	0.1	115
Avicennia nitida (Pneumatophores)	0.13	N.A.
Cladium jamaicense	0.15	1824
Nuphar leteum (Lily flower)	0.3	996
Juncus effusus	0.35	749
Glyceria striata	0.64	2952
Eleocharis interstincta	2.05	3475
Peltandra virginica	2.7	538
Sagittaria lancifolia	3.1	3280
Nuphar leteum (Lily pad)	3.3	2501
Pontederia cordata	3.3	7058
Nymphaea odorata (Lily flower)	3.6	5882
Sagittaria gramineae	5.9	3439
Typha latifolia	9.8	1769
Nymphaea odorata (Lily pad)	14.8	1375

N.A. - Not applicable

Root porosity which reflects the extent of intercellular spaces, in an important factor in CH_4 emission. Studies indicate that root porosity and radial oxygen loss increased due to a reduction in redox potential which enhanced methane emission[26]. At-300 mV, roots of rice plant had 35% root air space, compared with 30.7 and 26% at - 200 and 200 mV

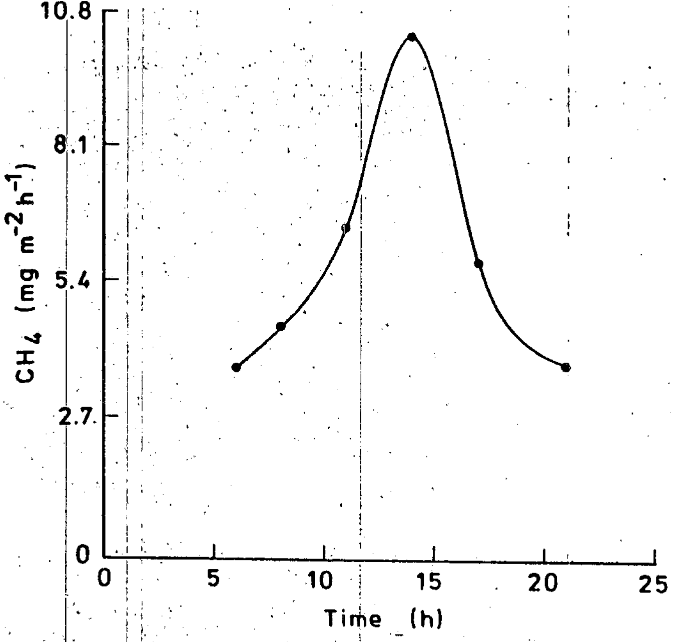

Fig. 3 – Diurnal variation in CH_4 emission from an irrigated rice field at Varanasi.

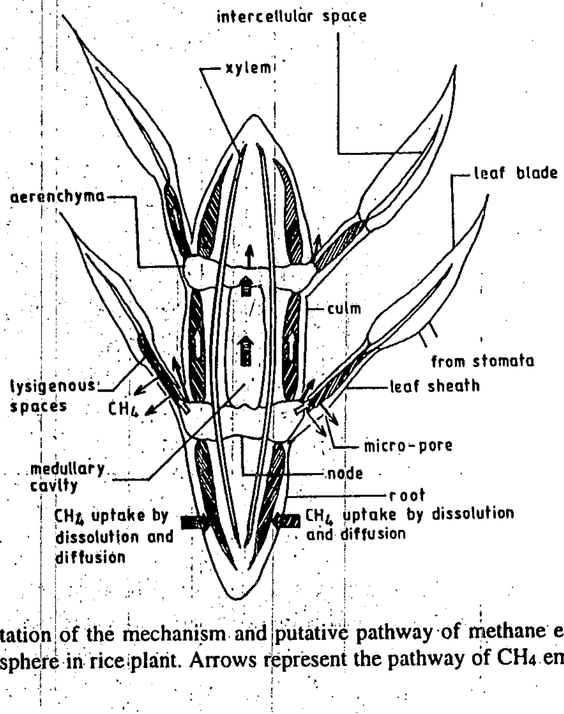

Fig. 4 – A diagramatic representation of the mechanism and putative pathway of methane emission from the rhizosphere to the atmosphere in rice plant. Arrows represent the pathway of CH_4 emission (Based on Nouchi et al.[52]).

respectively. Radial oxygen loss was 35 μmol O_2 plant^{-1} d^{-1} at - 300 compared with 27 and 20 μmol O_2 plant^{-1} d^{-1} at - 200 and 200 mV respectively. A decrease of redox potential from - 200 to - 300 mV increased CH_4 production 10-fold inthe vegetated treatment and about 9 times in unvegetated plot in a rice field. Kludze and DeLaune[35] conducted an experiment to determine the influence of soil redox intensity on the growth, root porosity radial O_2 loss and methane flux in *Spartina patens* (a perennial flood- tolerant grass). Plants were grown for 50-d in a Mississippi alluvial soil under controlled Eh values of 200, - 200 and - 300 mV. The highest methane emission at - 300 mV occurred on day 30 when the root porosity had attained its maximum level.

More than 90% of methane released from the rice soil to the atmosphere is emitted via the rice plant through aerenchyma[30,36,37]. Seiler et al.[38] reported that the flux rate of methane from paddy soils into the atmosphere may be limited either by transport into the root system or through the aerenchyma system or by the methane production rate within the paddy soil. In an experimental study, Byrnes et al.[39] found that in summer approximately 79-87% methane emission occurred through rice plants, whereas in the winter 61-68% of the total emissions occurred directly from the soils. The cross-sectional area of the individual stalks of the winter-grown plants were about 1/3 those of the summer-grown plants, and the aerenchyma cells of the winter-grown plants were considerably smaller than those of the summer-grown plants. Thus the extent of aerenchyma development was perhaps responsible for the differential emission rates of methane in summer-and winter-grown plants.

A linear relationship occurred between CH_4 emission from *Oryza sativa* and temporal variations in aboveground biomass during a growing season[40]/ A linear relationship between plant biomass and methane emission in a subtropical grassland was also noted by Whiting et al.[8] who reported tht this may be due to a combination of plant-enhanced transport and/or substrate production. Recently a strong predictive relationship was shown between CH_4 flux and net ecosystem production (NEP) across wetlands from Florida to Alaska[41]. NEP may be an integrating variable which incorporates many factors that control methane flux, including substrate availability for methanogenesis associated with recent production, such as root exudation and litter input. This relationship has been demonstrated only where the soil is saturated or flooded throughout the year and the wetland is dominated by vascular species[29].

Mechanism of Methane Emission

Gas transport through aquatic macrophytes may operate either by molecular diffusion[27,43]. Pressurized ventilation is exemplified by *Nuphar* and *Typha*[7,44] *and molecular diffusion by sedges*[45]. *For Typha latifolia,* Sebacher et al.[7] report tht the pressure difference between the new and old leaves results in a gas flow of O_2 from the new leaves to the roots and a pumping of CH_4 from the roots into the brown outer leaves. CH_4 emission rates in plants which exhibit pressurized system were 2-4 times higher during the day time because of the solar heating of leaves[46].

The absorption and release sites of gases are generally considered to be stomata which link the atmosphere with the internal air-space system of the plants. However, Cicerone et al.[47] and Seiler et al.[38] found no change in the rate of CH_4 emission from day to night in rice paddies, which indicated that the CH_4 release was independent of photosynthesis and/or stomatal opening. Methane emission rate in rice paddies may increase form a low value in the pre-dawn hours to a peak in the early afternoon, declining thereafter in the evening. This is exemplified in Fig. 3 for an irrigated rice field at Varansasi. the amplitude of such diurnal variations in CH_4 emission changed with season and reflected the amplitude of the diurnal variation in soil temperatures[48].

Absence of stomatal control of CH_4 emission was also indicated in *Spartina alterniflora*[49] and in *Cladium jamaicense*[8]. Kludze and DeLaune[35] studied methane emission from *Spartina*

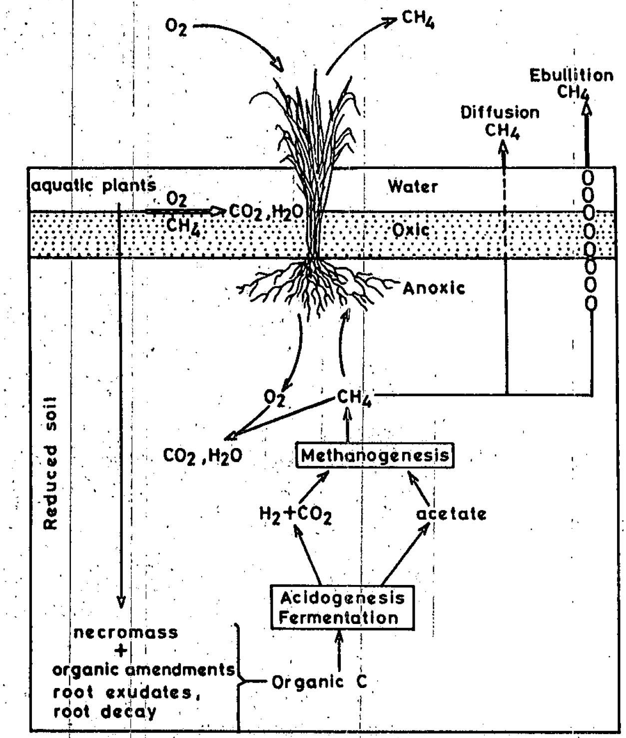

Fig. 5 – Diagramatic representation of production, reoxidation and transport of methane in rice field (Based on Conrad[54] and Schutz et al.[48]).

patens in light and dark conditions; no significant differences existed between emission in light and in the dark which suggested a lack of stomatal influence on methane emission. The stomatal control of CH_4 emission is controversial and may vary with plant species; Chanton et al.[46,50] have discounted its importance in *Peltandra, Cladium* and *Typha,* while Morrissey et al.[34] and Knapp & Yavitt[51] have argued for its importance in *Carex* and *Typha.*

According to Nouchi et al.[52], methane was mostly released fromthe culm of the rice plant, which is an aggregation of leaf sheaths, but none or little from the leaf blades. Examination of the surface structure of rice leaf-sheath through scanning electron microscope revealed hook-shaped micropores, 4 µm in diameter and about 80 µm apart from each other. These were arranged regularly on 50 µm wide vein[52]. Althrough most of the CH_4 was emitted through these micropores, there was no evidence that micropores were linked to the lysigenous intercellular space[52]. Eviently furtehr anatomical work is needed to ascertain whether the micropores are indeed the main site of methane release from rice plants.

For flooded rice field Nouchl et al.[52] suggested that methane dissolved in the soil water surrounding the rice root diffuses into the cell wall water of the root cells, gasifies in the root cortex, transported in the gaseous state to the shoots via the aerenchyma and then is released mostly through the micropores in the leaf sheaths (Fig. 4).

Fig. 5 summarizes the relationships between methane production and emission in wetlands.

Conclusions

Methane is produced in the submerged soil of the wetland under anaerobic condition as catabolic product of methanogenic bacteria. Wetland plants have a well developed internal airspace system for transporting oxygen to the rhizosphere. This system also serves as conduit for CH_4 emission. Studies on rice plants indicate that CH_4 dissolved in soil water diffuses into the root cells, gasifies in the root cortex, and is then transported to the shoots through the aerenchyma. In certain plants gas transport operates through molecular diffusion and in others by a thermally p0ressurized ventilation system. The later plants exhibit marked diural variation in CH_4 emission. The principle release sites for methane may or may not be stomata. In rice micropores located on veins of leaf sheath appear to be responsible for the majority of CH_4 release.

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