

## Methanogenesis and methane oxidation in wetlands. Implications in the global carbon cycle

## Metanogénesis y metano-oxidación en humedales. Implicaciones en el ciclo del carbono global

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### ABSTRACT

Wetlands are important ecosystems on the Earth. They are distinguished by the presence of water, saturated anoxic soils, and different kinds of vegetation adapted to this conditions. Organic matter in these environments is mineralized mainly in the sediments throughout anaerobic processes where sulfate reduction is one of the most important terminal stages of anaerobic decomposition in coastal wetlands, whereas methanogenesis is important in freshwater wetlands.

In this environments, methane, a greenhouse gas, is produced as a result of the activity of a large and diverse group of methanogenic bacteria (Domain Archaea). The generated methane can be diffused to the atmosphere or can be oxidized by several microorganisms under aerobic and anaerobic conditions, such microorganisms intercept and consume this gas diminishing its emission to the atmosphere.

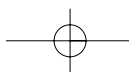
The production and consumption of methane in wetlands involve complex physiological processes of plants and microorganisms, which are regulated by climatic and edaphic factors, mainly soil temperature and water table level. The interaction of these processes with heterogeneous environments results in large variations in the methane fluxes.

Because methane is an important gas that contribute with as much as 15% to the greenhouse effect, several studies had analyzed methane production and its emission from wetlands. These studies established that natural and agricultural freshwater wetlands represent approximately 40% of the sources of atmospheric methane. However, most of the ecological studies assessing the production, consumption, and emission of methane have been performed in boreal and temperate wetlands, yet there are few studies evaluating these activities in tropical wetlands, particularly in Brazil and Panama. In Mexico there are not studies contributing to this respect.

**Key words:** Wetlands, methanogenesis, methane oxidation, methane fluxes.

### RESUMEN

Los humedales son ecosistemas importantes en la Tierra. Se caracterizan por la presencia de agua, suelos saturados anóxicos y diferentes clases de vegetación adaptada a estas condiciones. La materia orgánica en estos ambientes es mineralizada principalmente en los sedimentos a través de procesos anaeróbicos, siendo la



sulfatorreducción la fase terminal más importante de la descomposición anaeróbica en los humedales costeros, mientras que la metanogénesis domina en los humedales dulceacuícolas.

En estos ambientes el metano, un gas invernadero, es producido como resultado de la actividad de un grupo diverso de bacterias metanogénicas (Dominio Archaea). El metano generado puede difundirse hacia la atmósfera o puede ser oxidado bajo condiciones aeróbicas y anaeróbicas por varios microorganismos, los cuales interceptan y consumen este gas disminuyendo su emisión a la atmósfera.

La producción y consumo del metano en los humedales involucra procesos fisiológicos complejos de plantas y microorganismos, los cuales son regulados por factores edafológicos y climáticos, principalmente temperatura y nivel del manto freático. Las interacciones de estos procesos con los ambientes heterogéneos da por resultado grandes variaciones en los flujos del metano.

Se han efectuado estudios en los que se analiza la producción de metano y su emisión a partir de los humedales, debido a que éste es un gas que contribuye aproximadamente con el 15% del efecto invernadero.

Estos estudios establecen que los humedales naturales y agrícolas, representan aproximadamente el 40% de las fuentes del metano atmosférico. Sin embargo, la mayor parte de los estudios relacionados con la producción, consumo y emisión del metano se han llevado a cabo en humedales boreales y templados, existiendo pocos estudios que evalúan estas actividades en humedales tropicales (Brasil y Panamá). En México no hay estudios al respecto.

**Palabras clave:** Humedales, metanogénesis, metano-oxidación, flujos de metano.

## INTRODUCTION

Wetlands are ecosystems with intermediate characteristics between terrestrial and aquatic ecosystems that are usually flooded. They are covered by a great diversity of vegetation, from moss to herbaceous and vascular plants. Their hydrological properties and the abundance of vegetation make them sites with high rates of organic carbon deposition, which is mineralized mainly through anaerobic processes, being methanogenesis the dominant process in freshwater wetlands, whereas sulfate reduction predominates in brackish wetlands.

Because of the large extension of freshwater wetlands in the boreal and temperate regions, methanogenesis is the most important process, being accountable for the release of large amounts of methane ( $\text{CH}_4$ ) into the atmosphere from these ecosystems (Fung *et al.*, 1991; Bartlett & Harris, 1993). However the thin oxic layer and the oxic plant rhizosphere in wetlands promote activity of methane-oxidizing bacteria or methanotrophs. Thus, both  $\text{CH}_4$  formation and consumption are microbiological processes controlled by many factors, and its relationship influences on the magnitude of the flux from wetlands.  $\text{CH}_4$  release has important ecological implications because it is a gas involved in the greenhouse effect related with global climatic change.

Several studies have been made on methanogenesis, methane oxidation, and the emission rate of  $\text{CH}_4$  mainly in the boreal and temperate regions; whereas in the tropical regions there are few studies. In Mexico, where coastal wetlands are abundant, this type of studies are particularly scarce.

In this paper, we review the literature on the activity of microorganisms involved in the production and consumption of  $\text{CH}_4$ , as well as the magnitude of  $\text{CH}_4$  emissions, and the variables influencing its control in natural wetlands. This review focused basically on peat-forming wetlands (bogs, fens, swamps) and some types of non-peat forming coastal wetlands (salt marshes, and mangroves); we also included rice paddy fields because these are responsible of the 20% methane global emissions. We didn't consider littoral sediments of lakes and reservoirs.

## DEFINITION AND CHARACTERISTICS OF WETLANDS

Wetlands are ecosystems with a scarce drainage area that, at least periodically, are saturated or covered by water and represent important constituents of the biosphere, as they perform an indispensable function in the biochemical cycles of carbon, nitrogen, and sulfur (Westermann, 1993b). In Mexico, wetlands are defined like transition areas between aquatic and terrestrial ecosystems, at least periodically, are saturated or covered by water (Carrera & de la Fuente León, 2003).

Wetlands are formed in zones where soil drainage is deficient due to the presence of a bed of impermeable rocks, permafrost, and/or where yearly precipitation exceeds evaporation; or they can be originated by the accumulation of organic matter in the shallow regions of lakes, giving rise to a biological succession phenomenon.

The hydrological characteristics, and the hydroperiod of wetlands produce unique physical-chemical conditions that make them very different ecosystems from the well-drained terrestrial systems, and the deep aquatic systems. The hydroperiod results from the balance between water supplies and their output, the soil and sub-surface conditions. The main water supplies are given by precipitation, superficial run-offs, underground water, tides, and river floods; which originate a transport of energy and nutrients into the wetlands. These supplies influence largely the biogeochemistry of the soils in these environments, and are the main selection force driving richness and composition of species. Hydrology affects primary production, organic matter accumulation and the nutrients cycle. In general, productivity is higher in those wetlands with elevated nutrient flows or in those presenting pulses in hydroperiods. Mineralization of organic matter is slower when there is a stagnant and anaerobic water column than under well drained conditions.

The soil or sediment of wetlands is the zone where many of the chemical transformation of the elements take place; it is often described as a hydric soil for it is poorly drained, it is water-saturated or flooded, and develops anaerobic conditions. Wetland soils are classified as mineral, and organic or peatlands (Table 1) (Mitsch & Gosselink, 1993). The peat covers the superficial strata of wetlands, its constituted by plant materials in diverse decomposition stages. The most important characteristics of peat are its botanical composition and decomposition state.

Botanical composition includes moss, herbaceous, and wood material, and leaves remnants. In most boreal wetlands, the most common moss is *Sphagnum* spp. Peatlands with herbaceous vegetation present freshwater grasslands (*Phragmites* spp., *Carex* spp., *Cladium* spp), wild rice (*Zizania*), brackish

grasslands (*Spartina* spp.), and cattails (*Typha* spp). In the forestry wetlands, peat is formed from the detritus of trees, such as pines (*Pinus* spp.), cypresses (*Taxodium* spp.), or tupelo trees (*Nyssa* sp.).

Regarding the state of decomposition, as it advances the vegetal structure changes physically and chemically until the end product barely resembles the original material. Along the degradation of peat, the amount of large fibers (> 1.5 mm) decreases and the material becomes extremely fragmented. Chemically, the amount of lignin increases, while the cellulose and plant pigments decrease (Clymo, 1983).

**Classification of wetlands.** Classification of wetlands is mainly determined by the hydrological, ecological, and topographic properties, the nutrients regime, as well as the floristic composition and peat structure that constitute them. To establish a classification of the diverse types of wetlands is not easy because the used terminology is complex and often confusing between different countries. A large number of terms have been used depending on the region or continent. In this work, wetlands are grouped mainly based on their salinity characteristics (Table 2) (Clymo, 1983; Matthews & Fung, 1987; Zinder, 1993).

Natural wetlands are concentrated in the high latitudes of the northern hemisphere, where permafrost avoids soil drainage, dominating histosols (95%); as well as in the tropics, where precipitation rates are high, in this regions mangroves and flooding plains are the dominant wetlands.

Mexico possesses barely 0.6% of the worldwide wetlands; most of them are coastal wetlands and these were recently classified according to the Cowardin *et al.* (1979) system, which is used by the National Program of Wetlands Inventory from the Department of Fishing and Wild Life, USA (Table 3) (Carrera & de la Fuente León, 2003).

Table 1. Comparison of mineral and organic soils in wetlands (Mitsch & Gosselink, 1993)

	Mineral soil	Organic soil (peatlands)
Organic content	<20 to 35%	> 35%
pH	Usually circumneutral	Acid
Bulk density	High	Low
Porosity	Low (45-55%)	High (80%)
Hydraulic Conductivity	High (except for clays)	Low to high
Water Holding Capacity	Low	High
Nutrient Availability	Generally high	Often low
Cation Exchange Capacity	Low, dominated by major cations	High, dominated by hydrogen ion
Typical wetland	Riparian forest, some marshes	Northern peatland

Table 2. Types of wetlands (Matthews &amp; Fung, 1987; Bartlett &amp; Harris, 1993; Mitsch &amp; Gosselink, 1993; Zinder, 1993).

Wetland	Latitude	Features	Vegetation
Arctic tundra	Arctic regions (>70°N)	Freshwater. Long winter (−10°–24°C). Short summer (july:10°-24°C). 1/3 of the total precipitation like snowfall.	
Bogs or Histosols	Boreal regions (45°-60° N.)	Freshwater. Ombotrophic, precipitation like rainfall. Acid pH (3.5-5.0, average 4.2). < 3% of the total terrestrial area, and content them 30% of the global carbon and nitrogen	Mosses ( <i>Sphagnum</i> , and <i>Chamaedaphne calyculata</i> ). Herbaceous plants ( <i>Eriophorum vaginatum</i> , and <i>E. angustifolium</i> ). Woody plants ( <i>Calluna vulgaris</i> , and <i>Erica tetraliz</i> ).
Fens	Boreal regions (45°-60° N.).	Freshwater. Groundwater, and superficial runoff supplies of water. pH alkaline, neutral or moderately acid. Grow on dolomite with calcium and magnesium, abundance of mineral salts .	Herbaceous plants ( <i>Carex</i> spp.)
Freshwater marshes	Temperate regions (20°-45° N, 30°-50°S)	Freshwater. Mixture of organic and inorganic sedimentary matter. High rates of mineralization. Alkaline or acid pH.	Emergent soft-stemmed aquatic plants: cattails ( <i>Typha</i> spp.), arrowheads, and several species of grasses.
Swamps	Tropical and subtropical regions (20°N-30°S)	Freshwater. Periodically covered by a water column. Water supplies by precipitation or by adjacent streams and rivers. Variety of nutrient concentrations	Woody plants dominated by various species of cypres ( <i>Taxodium</i> ), and gum/tupelo ( <i>Nyssa</i> ).
Alluvial floodplains	Tropical and subtropical regions (20°N-30°S).	Freshwater. They occur along rivers and streams, are are occasionally flooded by those bodies of water. In the growing season several portions are dry.	Diverse vegetation that varies along gradients of flooding frequency.
Rice paddy field	Tropical and subtropical regions (20°N-30°S).	Freshwater. Agricultural wetland, important to global scale (total area:1.43 millions km <sup>2</sup> ). Fertilization with straw rice.	
Salt marshes	Temperate regions (20°N to 30°S).	Brackish. Found along protected coastlines. Temporally or permanently flooded with marine water. In Europe a marsh has a mineral soil and does not accumulate peat	Grasses ( <i>Spartina alterniflora</i> , <i>S. patens</i> and <i>Distichlis spicata</i> )
Mangroves	Tropical and subtropical regions (20°N to 30°S).	Brackish. Found along protected coastlines. Temporally or permanently flooded with marine water.	Salt-tolerant trees: red mangrove ( <i>Rhizophora mangle</i> ), white mangrove ( <i>Laguncularia racemosa</i> ) and black mangrove ( <i>Avicenia germinans</i> ).

Human activity has modified wetlands since the dawn of agriculture. Rubec *et al.* (1988) classified wetland land-use conversions into five categories: agricultural land reclamation, urban and industrial uses, energy development, peat harvesting and forest harvesting. Another wetland land use is the production of rice. Rice paddies account for approximately 20% of all methane emissions (Fung *et al.*, 1991), for this reason they are included in this review.

## BIOGEOCHEMICAL PROCESSES IN THE WETLANDS

Wetlands can be considered systems with three compartments: oxic surface, anoxic soil, and rhizosphere, each one with different physical-chemical conditions that influence the metabolic processes involved in the mineralization of organic matter.

### Oxic zone

The oxic zone (aerobic) of the flooded soils is limited to the water column and the first milli- or centimeters of soil or sediment (King *et al.*, 1990); within this zone, the regions close to the rhizosphere are also considered. The rhizosphere is the zone where the live roots of the plants constituting the wetland are located.

When the plant remnants from the wetlands are covered by water, their soluble substances are lost due to lixiviation. The lixiviate is constituted mainly by amino acids, sugars, volatile, and non-volatile fatty acids; these compounds are metabolized rapidly by the aerobic microflora of the system. The posterior degradation of this vegetal matter depends on the existing relationship among the diverse polymers (lignin, cellulose, and hemicellulose) in the deposits, their structure, and the physico-chemical characteristics of the ecosystem (Moran *et al.*, 1989).

It has been established that fungi are the most important group of organisms involved in the aerobic decomposition of the vegetal matter in marshes, peatlands, and rice fields. Species of *Penicillium*, *Fusarium*, *Alternaria*, and *Helicoon* genera are common (Williams & Crawford, 1983). Likewise, amylolytic, proteolytic, and chitinolytic bacteria are important agents in this process.

### Anoxic zone

When the wetland soils are flooded, oxygen diffusion decreases drastically (oxygen diffuses 10,000 times slower in an aqueous solution than in the air). Because oxygen diffusion is slow and the organic carbon content is high, the oxide-reduction potential (Eh) decreases rapidly with depth, generating chemical gradients that influence the sequence of metabolic reactions occurring during organic matter degradation, as well as the spatial distribution of the microbiota that participates in that process

Table 3. Types of Mexican Wetlands (Carrera & de la Fuente León, 2003)

System	Subsystem	Class
Marine	Subtidal	Open water
	Intertidal	Beach
Estuarine	Subtidal	Open water
		Aquatic vegetation
	Intertidal	Aquatic vegetation
		Coastal floodplain
		Emergent plants. Low littoral
		Emergent plants. Up littoral
		Mangrove
		Modified coastal floodplain
Lacustrine	Limnetic	Open water
		Aquatic vegetation
	Littoral	Open water
		Aquatic vegetation
Palustrine		Open water
		Aquatic vegetation
		Emergent plants
		Emergent modificate
Riverine		Riverine
		Aquatic vegetation
		Artificial
Upland		Agriculture
		Urbanized areas
		No vegetation
		Natural vegetation

(Stolzy *et al.*, 1981; Sweerts *et al.*, 1991). Once oxygen has been depleted, nitrate ( $\text{NO}_3^-$ ) is the first electron acceptor that decreases, followed by manganese (Mn IV), iron (Fe III), sulfates ( $\text{SO}_4^{2-}$ ) and, finally, carbon dioxide ( $\text{CO}_2$ ), giving rise to the anaerobic processes (Fig. 1).

1. Denitrification, is a respiration process in which the electron acceptor is nitrate, it starts when oxygen concentration is  $< 10 \mu\text{M}$ . The resulting denitrification products are molecular nitrogen ( $\text{N}_2$ ) and nitrogen oxide ( $\text{NO}_x$ ). Anaerobic Gram-negative bacteria perform this process; among them, the genera *Pseudomonas* spp., *Clostridium* spp., *Bacillus* spp., and *Alcaligenes* spp. have been reported (Struwe & Kjoller, 1989). It

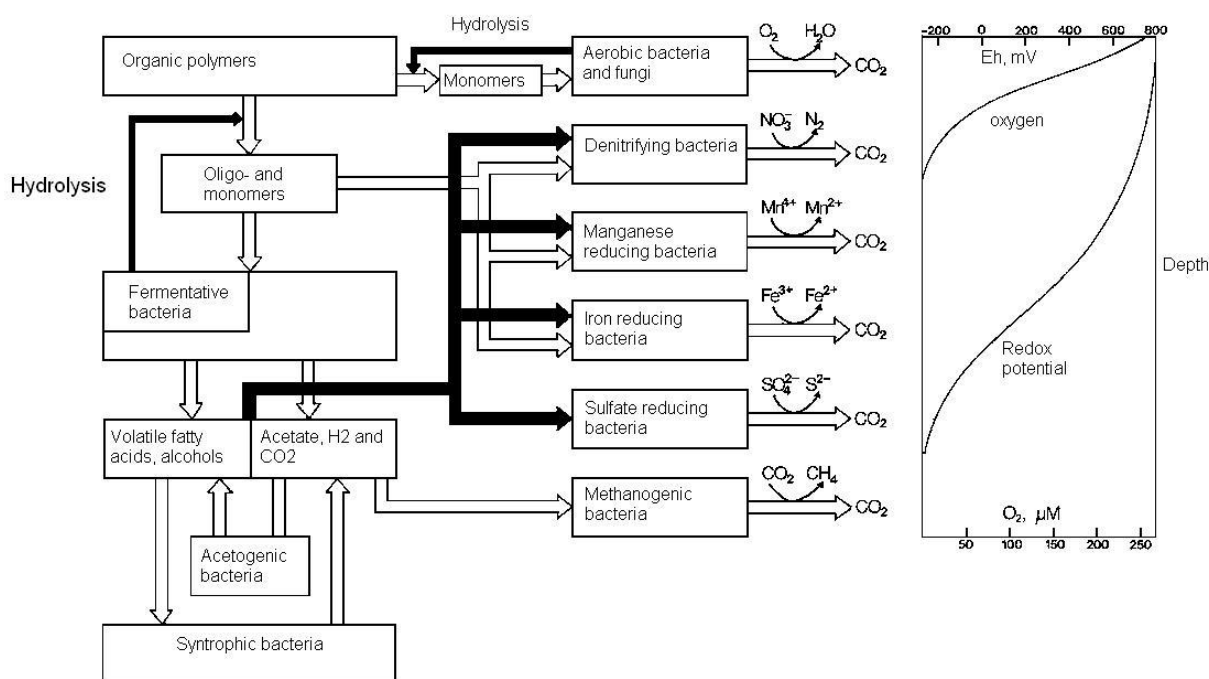


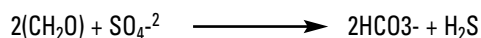
Figure 1. Main pathways in the degradation of organic matter in wetlands (Westermann,1993b).

has been estimated that denitrification is responsible for a 30-40% nitrogen loss from the soil in marshes and rice fields.

2. Manganese reduction, is the transformation of Mn<sup>3+</sup> to Mn<sup>4+</sup>, it starts below +526 mV, and is carried out by a large diversity of facultative bacteria and microfungi.

3. Iron reduction, is a process carried out when the Eh descends to -47 mV. Several groups of facultative and anaerobic bacteria participate in it. Manganese-reduction and iron-reduction are relevant processes in those wetlands with high mineral supplies (Lovley, 1991).

4. Sulfate reduction. This metabolism is carried out by sulfate-reducing bacteria (SRB) when the Eh decrease to -120 mV. SRB are anaerobic bacteria and their cells depict a wide range of morphological shapes: bacilli, vibrio, cocci, sarcines, and filaments. SRB use mainly sulfate as their terminal electron acceptor in the anaerobic oxidation of organic substrates, and reduce it to hydrogen sulfide (H<sub>2</sub>S):



Based on their oxidative and metabolic capacities, SRB can be divided in two groups. The first includes those species that metabolize incompletely the long and short chain fatty acids, such as propionate, lactate, and pyruvate, to acetate. Genera *Desulfovibrio* spp. and *Desulfomonas* spp. belong to this group.

The second group comprises those species that carry out a complete oxidation of organic acids, such as lactate, acetate, benzoate, succinate, or fumarate, to CO<sub>2</sub>. The genus *Desulfotomaculum* spp. belong to this group (Pfennig *et al.*, 1981). SRB, are able to use other substrates as electron donors, such as phenolic and indolic compounds, and amino acids (Bak & Widdel, 1986; Gibson *et al.*, 1988)

Many SRB can grow in a syntrophic relation with the methanogenic bacteria that use hydrogen when sulfates are absent (Widdel, 1988). Sulfate reduction is the most important mineralization mechanism in brackish wetlands, representing up to 67-80% of the total respiration in sediments; the main supplies of organic matter for this process are the products from the roots and rhizomes of grasses and mangroves, as well as the excretion of dissolved organic matter during fast-growth periods (Howarth, 1993).

In agricultural wetlands, sulfate reduction is important because the H<sub>2</sub>S released can influence the growth of rice plants. However, it has been observed that, in the oxidative layer near the roots the H<sub>2</sub>S oxidation is stimulated, providing protection to the plant. In most temporally flooded soils, H<sub>2</sub>S rarely accumulates until reaching toxic concentrations because it precipitates mainly as ferrous sulfide (Widdel, 1988).

5. Methanogenesis, is the last stage in the anaerobic degradation and is carried out when the concentration of sulfates decreases. The process requires redox potentials below -244 mV (Lovley & Phillips, 1987; Peters & Conrad, 1996). Methanogenic bacteria (MB) are a unique group of prokaryotes since they produce a hydrocarbon, methane (CH<sub>4</sub>), as the main product of their metabolism. The MB utilize simple organic substrates, such as formate, methanol, methylamines, and acetate (Phelps & Zeikus, 1985).

The importance of metabolic processes in a given wetland depends on the concentration of the specific electron acceptors, and of the availability of organic matter. In coastal wetlands, such as salt marshes, all processes (except methanogenesis) depict high metabolic rates, although they are spatially separated in different strata or microniches (Table 4) (Howarth, 1993).

Because oxygen is present along the oxic-anoxic interface and in the rhizosphere, the electron acceptors regenerate from the re-oxidation of the reduced compounds, contributing to the maintenance of the anaerobic degradation chain.

Anaerobic decomposition in the wetlands is often incomplete, resulted in the accumulation of large amounts of organic carbon (Roulet, 2000). Therefore, the saturated soils of these ecosystems can contain approximately a third of all the organic matter deposited in the soils of the world (Eswaran *et al.*, 1995).

### CARBON CYCLE IN THE WETLANDS

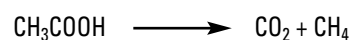
The carbon cycle is controlled by the input of organic matter to the soil. The degradation of the organic matter by means of the aerobic respiration produce CO<sub>2</sub>, and the process is limited by the reducing conditions of the soils or sediments in the wetlands. In anaerobic conditions, the first step involved in the degradation of organic carbon is fermentation, in which the organic matter is the terminal electron acceptor, producing diverse low molecular weight organic acids and alcohols, such

as lactic acid and ethanol, respectively. At the beginning, fermentative bacteria excrete enzymes that hydrolyze polysaccharides. The same group of bacteria converts the resulting monomer into alcohols, fatty acids, and hydrogen (H<sub>2</sub>). In the presence of other electron acceptors, these substrates are completely degraded to CO<sub>2</sub>. When there is a limitation of external electron acceptors, syntrophic bacteria degrade the alcohols and fatty acids to acetate, formate, and CO<sub>2</sub>. An alternative pathway involves the direct conversion of monomers to acetate through the activity of homoacetogenic bacteria. Acetate and H<sub>2</sub> are finally used as substrates by SRB and MB (Fig. 1). In these reactions, 4 mol of H<sub>2</sub> plus 2 mol of acetate are produced for each mole of glucose. In most freshwater wetlands, the concentration of electron acceptors is low as compared to the availability of carbon, hence the predominating process is methanogenesis, which is of great relevance due to the release of CH<sub>4</sub>, a gas related to the greenhouse effect and global climatic change.

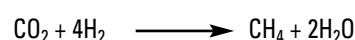
**Methanogenesis.** The analysis of the structure and activity of the methanogenic bacteria (MB) populations in the wetlands is important to understand the global emissions of CH<sub>4</sub>. MB are members of the Archaea domain. They comprise a morphologically diverse group of short and long bacilli, cocci, and several arrangements of the basic forms in large chains or aggregated clumps. All members possess two unique cofactors, factor 420 (F 420) and 2-mercaptoethanesulfonic acid (coenzyme M or CoM) (Mah & Smith, 1981). They are constituted by approximately 50 species grouped in the next genera: *Methanobacterium*, *Methanothermobacter*, *Methanobrevibacter*, *Methanosphaera*, *Methanothermus*, *Methanococcus*, *Methanothermococcus*, *Methanocaldococcus*, *Methanoignis*, *Methanomicrobium*, *Methanogenium*, *Methanoplanus*, *Methanoculleus*, *Methanofollis*, *Methanocorpusculum*, *Methanospirillum*, *Methanolobus*, *Methanococcoides*, *Methanohalophilus*, *Methanohalobium*, *Methanosarcina*, *Methanosalsus* and *Methanosaeta* (Boone *et al.*, 1993).

The MB are metabolically classified in four physiological groups:

I. The genera that use exclusively acetate as substrate, such as *Methanosaeta* spp.:



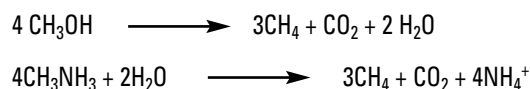
II. The genera that use hydrogen and formate, such as *Methanobacterium* spp., *Methanobrevibacter* spp., and *Methanogenium* spp.:



III. The genera that develop from methylated compounds (methanol and methylamines), among them are *Methanolobus* spp., and *Methanococcus* spp.

Table 4. Respiration rates in two salt marshes in Georgia, USA (Howarth, 1993)

	Sapelo Island g C/m <sup>2</sup> /year	Sippewissett gC/m <sup>2</sup> /year
Aerobic respiration	390	390
Denitrification	10	3
Mn and Fe reduction	nd	Not detected
Sulfate reduction	850	1800
Methanogenesis	40	1-8



IV. The generalists that generate  $\text{CH}_4$  from acetate,  $\text{H}_2$ , and methylated compounds, as occurs in the genus *Methanosarcina* spp. (Garcia, 1990).

In most natural wetlands with neutral pH, methanogenesis from acetate is the predominating pathway implicated in  $\text{CH}_4$  production, followed by reduction of  $\text{CO}_2$  with  $\text{H}_2$ .  $\text{CH}_4$  production by the acetate fermentation pathway is favored in the shallow subsurface, while methanogenesis from the reduction of  $\text{CO}_2$  with  $\text{H}_2$  becomes predominant in less reactive peat (Hornibrook *et al.*, 1997). Methanogenesis from acetate represents 69% in peatlands (0.69-8.54  $\mu\text{M/hr}$ ) and 51% in tidal estuaries (0.40-3.41  $\mu\text{M/h}$ ). However, in mid-latitude wetlands, apparently  $\text{CH}_4$  is not derived from acetate. These compound accumulate to high levels during anaerobic decomposition and is ultimately degraded aerobically to  $\text{CO}_2$  after diffusion into oxic regions of peat (Hines *et al.*, 2001).

In acid wetlands, the reduction of  $\text{CO}_2$  with hydrogen is an important precursor of methane, having quantified a great abundance of hydrogenophilic methanogens in them, around  $3 \times 10^7$  cel/g sediment (Horn *et al.*, 2003). The hydrogenophilic methanogenic bacteria (HMB) are symbiotically associated to anaerobic organisms that produce hydrogen and contribute to maintain low levels of this gas during carbon flux. As a result, low  $\text{H}_2$  concentrations are emitted to the atmosphere. In natural wetlands, HMB belong to the families Methanobacteriaceae, Methanococcaceae, Methanosarcinaceae, and Methanomicrobiaceae.

In a tropical coastal wetland in Mexico (Chiapas State) we quantified a MB density higher than those reported in salt marshes from temperate regions ( $\text{H}_2$ :  $1.3 \times 10^6$ - $3.08 \times 10^{10}$  cells MB/g sediment, and acetate:  $1.53 \times 10^5$ - $1.41 \times 10^{10}$  cells MB/g sediment) (Torres-Alvarado *et al.*, 2005).

Table 5 depicts the amount of  $\text{CH}_4$  produced in several natural wetlands. Matthews and Fung (1987) determined that  $\text{CH}_4$  production rate is higher in tropical zones than in boreal zones, because increases in temperature and net primary production in tropical ecosystems favor the methanogenic process. Hence, wetlands from tropical latitudes dominate global methane production (Fung *et al.*, 1991; Bartlett & Harris, 1993).

In agricultural wetlands, a difference must be made between the rice fields fertilized with straw and those not fertilized. In the first, methanogenesis from acetate represents 84-89% of the released  $\text{CH}_4$ , whereas that from  $\text{H}_2$ - $\text{CO}_2$  represents 11-27% (Glissmann & Conrad, 1999). Production of  $\text{CH}_4$  in fertilized fields starts 8 days after incubation and reaches a stable state after 20 days (Weber *et al.*, 2001). The methanogenic popu-

Table 5. Methane production in several wetlands.

Wetland	Production mg $\text{CH}_4/\text{m}^2/\text{day}$	Reference
Freshwater		
Michigan swamps	110	(Baker-Blocker <i>et al.</i> , 1977)
Great Dismal Swamp	1-15	(Harris <i>et al.</i> , 1982)
Marshes in Louisiana (USA)	440	(Smith <i>et al.</i> , 1982)
Brackish		
Marshes with <i>Spartina</i> spp. (Georgia, USA)	0.8-109	(Wiebe <i>et al.</i> , 1981)
Marshes in Louisiana (USA)	14	(Smith <i>et al.</i> , 1982)

lations that colonize the rice straw belong to the families Methanosaetaceae, and Methanomicrobiaceae, being the genera *Methanobacterium* spp., and *Methanosarcina* spp. the most representative ones. However, the calculated diversity indexes (equitativity=0.29) are low as compared to the indexes reported for soils without fertilizers (0.54-0.85); this is due to the fact that the rice straw is predominantly an habitat for fermentative bacteria, whereas MB are more abundant in the soil around the fertilizer, where the products resulting from fermentation concentrate and serve as substrate.

In non-fertilized soils, it has been observed that acetoclastic methanogenesis represents 51-67% of the produced  $\text{CH}_4$ , whereas  $\text{H}_2$ - $\text{CO}_2$  contributes with 17-31% of the total (Liesack *et al.*, 2000). In rice fields, from  $2.0 \times 10^6$  to  $2.3 \times 10^7$  cell/g dry soil abundance of HMB has been quantified, and around  $5.1 \times 10^5$  to  $1.3 \times 10^6$  cell/g dry soil of acetoclastic methanogenic bacteria (AMB). The MB localized in the rice plants roots differs from that found in the anoxic soil, resulted in different pathways to  $\text{CH}_4$  formation between these two environments. In the roots of the rice plant (*Oryza sativa*, var. *roma*, type *japonicus*), the AMB belonged the species of *Methanosarcina*, and *Methanosaeta* genera. Because the *Methanosarcina* species have a greater affinity for acetate, these are more abundant at the roots with high acetate concentration; in contrast, in the anoxic soil, where acetate concentration decrease, the *Methanosaeta* species are more abundant because their affinity for acetate is lower. HMB are represented by the family Methanomicrobiaceae in the roots (Chin *et al.*, 2004).

Global methanogenesis has increased due to the increment of the agricultural areas used for rice cultivation, these are,



currently, responsible for half of the global production of CH<sub>4</sub> and the microbiota located at the roots of the rice plants supplies 50% of the total production from the degradation of vegetal photosynthates excreted by the roots and for 3-6% of the CO<sub>2</sub> photosynthetically fixed (Anastasi *et al.*, 1992).

**Methane oxidation.** Wetlands are the main ecosystems that emit CH<sub>4</sub> to the atmosphere due to the large amount of organic matter (generated during primary production) degraded during methanogenesis. However, the amount of released CH<sub>4</sub> depends on the existing ratio between its production and consumption by diverse organisms. There are different microbial groups that carry out methane oxidation, in both aerobic and anaerobic conditions.

#### Aerobic conditions

Aerobic oxidation of CH<sub>4</sub> is carried out by methane oxidizing bacteria (MOB), and nitrifying bacteria. These strict aerobic microorganisms oxidize CH<sub>4</sub> to CO<sub>2</sub> using oxygen as the electron acceptor, releasing methanol as intermediate product. Oxidation of CH<sub>4</sub> demands about 14-29% of the total oxygen contained in the sediment.

MOB are non-mobile Gram-negative Proteobacteria that oxidize CH<sub>4</sub> as the sole carbon and energy source generating bacterial biomass. The reaction is catalyzed by the mono-oxygenase enzyme (MMO). There are two MMO forms, a cytoplasmic soluble form and a particulate form associated to the cellular membrane.

Phylogenetic studies indicate that there are two groups of MOB. Type I assimilates carbon through the ribulose monophosphate pathway, represented by genera *Methylomonas*, *Methylobacter*, *Methylococcus*, and *Methylosinus*, the latter two are the most active ones in histosols (Edwards *et al.*, 1998). Type II use the serine route for carbon assimilation (Bowman *et al.*, 1995). MOB inhabit peat and sediments, depict a notable capacity to survive in anoxic conditions and rapidly consume CH<sub>4</sub> when oxygen is re-introduced into the ecosystem. MOB obtained from pure cultures are neutrophils, however, histosol communities are moderately acidophilic, with an optimal growth at pH between 4.5 and 5.5. Species *Methylococcus capsulatus*, and *Methylosinus trichosporium*, as well as the genus *Methylocystis* have been identified in these ecosystems (Dedysh *et al.*, 1998).

In peatlands, 10<sup>3</sup>-10<sup>4</sup> cell/ml of MOB have been quantified, whereas their abundance is higher in rice fields (2-18x10<sup>6</sup> cel/g dry soil) (DeBont *et al.*, 1978). In peatlands Yavitt and Lang (1990) reported a CH<sub>4</sub> oxidation rate of 80% of the total production, while King *et al.* (1990) demonstrated a consumption of 91% of the total CH<sub>4</sub> produced in the Everglades (Florida, USA). It has been estimated that 80% of the produced methane is oxidized in rice fields.

Nitrifying bacteria also have a high affinity for CH<sub>4</sub>, oxidizing it under nitrogen limiting conditions of the soil (Chan & Parkin, 2001). In freshwater wetlands, this microbial group can compete for the available oxygen with the MOB (Megraw & Knowles, 1987).

The CH<sub>4</sub> oxidation depends on the availability of oxygen, therefore this process occurs mainly in freshwater wetlands during the dry periods, when the level of the water table descends and the soil of the wetland is exposed to air (Harris *et al.*, 1982; Yavitt & Lang, 1990). Likewise, CH<sub>4</sub> oxidation is higher in the roots and rhizome regions, where there is oxygen available coming from the atmosphere that is transported from the leaves to the roots (King, 1994). In peatlands, CH<sub>4</sub> oxidation is accomplished in the first 7 mm as a function of oxygen penetration (Moore & Knowles, 1990; Moore & Roulet, 1993).

The aerobic oxidation of CH<sub>4</sub> is influenced by changes in plant activity produced by their senescence in the autumn and new growth in the spring, which modify the superficial area available for colonization by MOB and by the organic matter supply for methanogenesis. Hydrogen concentration is also a factor related to CH<sub>4</sub> oxidation; in alpine tundra soil, it has been observed that high H<sub>2</sub> and CO<sub>2</sub> concentrations stimulate CH<sub>4</sub> oxidation up to 70 pmol/g/h, vs. 20 pmol/g/h, in soils not enriched with H<sub>2</sub> and CO<sub>2</sub> (West & Schmidt, 2002).

#### Anaerobic conditions

Anaerobic oxidation of methane (AOM) is carried out mainly in brackish water wetlands, participating in it at least two phylogenetically different groups of Archae, the ANME-1 and ANME-2. These bacteria generally form consortia with SRB, and the metabolism of its involves a syntrophic relationship based on inter-species electron transfer (Valentine, 1991; Orphan *et al.*, 2002). Apparently, Archaea oxidize the CH<sub>4</sub> and the resulting products are used by SRB (Table 6) (Blair & Aller, 1995; Valentine, 2002).

The ANME-1 Archae can oxidize methane without necessarily coupling oxidation with a syntrophic member (Orphan *et al.*, 2002). The ANME-2 Archae, in contrast, couple to a syntrophic member. This group is related with *Methanosarcina* genus. The sulfate-reducing consortium comprises species of *Desulfosarcina*, and *Desulfococcus* genera, which are characterized by the capacity to accomplish complete oxidation of fatty acids to CO<sub>2</sub>.

The AOM is carried out in the transition zone between sulfate reduction and methanogenesis, since CH<sub>4</sub> produced at deeper layer diffuses upwards where sulfate is available. The AOM inhibited gas transport to the atmosphere.

Among the factors related with AOM are organic matter content, supply rate of CH<sub>4</sub>, depth of sulfate penetration, tem-

Table 6. Chemical potential reactions in the anaerobic oxidation of methane (Valentine, 2002)

Oxidation of CH <sub>4</sub> by Archaeas:	
CH <sub>4</sub> + 2H <sub>2</sub> O	→ CO <sub>2</sub> + 4H <sub>2</sub>
CH <sub>4</sub> + 4HCO <sub>3</sub> <sup>-</sup> + 2H <sup>+</sup>	→ CO <sub>2</sub> + 4HCOOH + 2OH <sup>-</sup>
CH <sub>4</sub> + CO <sub>2</sub>	→ CH <sub>3</sub> COOH + 4H <sub>2</sub>
2CH <sub>4</sub> + 2H <sub>2</sub> O	→ CH <sub>3</sub> COOH + 4H <sub>2</sub>
Chemical reactions effectuated by sulfate reducing bacteria (syntrophic relation)	
SO <sub>4</sub> <sup>2-</sup> + 4HCOOH	→ S <sup>2-</sup> + 4CO <sub>2</sub> + 4H <sub>2</sub> O
SO <sub>4</sub> <sup>2-</sup> + 4H <sub>2</sub>	→ S <sup>2-</sup> + 4H <sub>2</sub> O
SO <sub>4</sub> <sup>2-</sup> + CH <sub>3</sub> COOH	→ 2HCO <sub>3</sub> <sup>-</sup> + H <sub>2</sub> S

perature, pressure, mineralogy, sediment porosity, and seasonal changes, as well as anthropogenic activities that generally induce a decrease in CH<sub>4</sub> consumption activities, as occurs with the change in use soil to agricultural purposes and the use of fertilizers (Ojima *et al.*, 1993).

There is a relation between oxidation mechanisms and CH<sub>4</sub> emission determined mainly by the speed of the internal gas fluxes within the ecosystem. This means that a fast displacement of CH<sub>4</sub> from the soil avoids significant oxidation by oxidizing microbiota, inducing important gas emissions to the atmosphere.

## EMISSION OF METHANE

The loss of CH<sub>4</sub> through the surface of soils or sediments is determined by the balance between its production in deep layers and its oxidation after it diffuses to zones with a positive redox potential. It has been estimated that global CH<sub>4</sub> production rate from wetlands is 20% higher than the rate of its release (Reeburgh *et al.*, 1993).

The deep layers of wetlands contain trapped CH<sub>4</sub> due to the hydrostatic pressure of the overlying water layer, and also because this gas is barely soluble in water (23-40 mg/l at 0-20°C). A large amount of CH<sub>4</sub> trapped in sediments must be released periodically depending on the hydrostatic and atmospheric pressures, which means that CH<sub>4</sub> can escape through the sediment to the atmosphere. There are three different routes involved in vertical transfer of CH<sub>4</sub> to the atmosphere from the wetlands: diffusion, emergence in the form of gas bubbles, and transport controlled by vegetation (Fig. 2) (Cicerone & Oremland, 1988; Whiting & Chanton, 1992).

By diffusion CH<sub>4</sub> molecules move from higher concentration regions (deep layers of the soil or sediment) to regions of

lower concentrations. However the largest loss of CH<sub>4</sub> towards the atmosphere is produced when the concentration in the interstitial water of the soil or sediment is higher than the hydrostatic pressure of the overlying water layer forming gas bubbles than can escape to the surface by ebullition (Yavitt & Knapp, 1995).

Transport of CH<sub>4</sub> in tidal wetlands and peatlands located in the state of Michigan (USA) is given by ebullition and diffusion. Chanton and Martens (1988) quantified an ebullition flow of 20.8 g CH<sub>4</sub>/m<sup>2</sup>/year and Kelley *et al.* (1990) determined a diffusion flow corresponding to 56% of the total emission.

Transport by vegetation is a response to the anoxic conditions of the soil, plants developed an adaptation strategy to aerate their submerged organs in the water by creating an internal ventilation system with gas localized in the stems, roots, and rhizomes, this space corresponds to the aerenchyma and acts as a gas channel, among these O<sub>2</sub> and CH<sub>4</sub>.

Wetland plants present two diffusion gradients, one of them produced by the oxygen flux from the atmosphere to the roots and rhizomes located in the anoxic peat where CH<sub>4</sub> is generated. The second one is produced by CH<sub>4</sub> diffusion from peat to the atmosphere, which is facilitated by the introduction of CH<sub>4</sub> to the aerenchyma of the roots. The transport of CH<sub>4</sub> through plants includes its diffusion inside the root, conversion of the dissolved form to the gaseous form in the root cortex, diffusion through the cortex and aerenchyma, and, finally, release to the atmosphere through the micropores of the stems and the stomata of the leaves. It has been observed that CH<sub>4</sub> flux reduces with closure of stomata because ventilation is stopped (Morrissey *et al.*, 1993); however, emission can continue through the cuticle or the micropores present in the petiole and stems of plants, as occurs in *Eriophorum angustifolium* (Schimel, 1995).

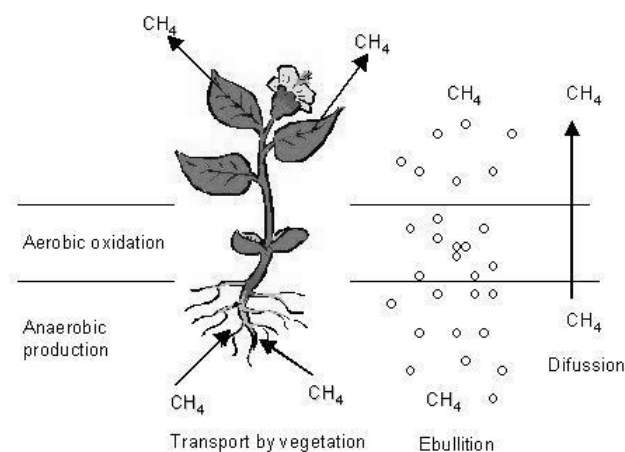


Figure 2. Routes involved in the emission of methane from wetlands to the atmosphere.

Vascular plants exert a double effect on emission fluxes. On one side, penetration of roots into anoxic soils contributes to oxygen transport to these regions, creating oxic conditions near the rhizosphere that induce inhibition of methanogenesis and, hence, a decrease in  $\text{CH}_4$  production. The presence of aerobic sediments near the roots also stimulates  $\text{CH}_4$  oxidation by methanotrophic bacteria (King, 1994; 1996).

Aquatic vegetation is an important  $\text{CH}_4$  channel, in some cases, more than 80% of the total  $\text{CH}_4$  flux occurs through leaves and stems (Dacey, 1980; Whiting *et al.*, 1991; Muller *et al.*, 1994). In marsh peat with *Typha latifolia* and *Sagittaria eurycarpum*, a  $\text{CH}_4$  emission rate of 53-178  $\text{mg}/\text{m}^2/\text{day}$  and an oxidation rate of 9.6-97.6  $\text{mg}/\text{m}^2/\text{day}$  were calculated at the laboratory level, representing 8.8-43.2% of the produced  $\text{CH}_4$  (King, 1996). The importance of vegetation in  $\text{CH}_4$  transport has been demonstrated by Torn and Chapin (1993), who by removing vascular plants from a saturated tundra observed a reduction in  $\text{CH}_4$  emissions (Fig. 3).

The physiological state of plants affects the emission flux, principally in those plants with an active transport of gases through the stomata than in those presenting diffusion transport through the micropores (Nouchi *et al.*, 1990). Gaseous exchange is also related with environmental variables, such as temperature, solar radiation, and relative humidity.

Wetlands are the largest natural sources of  $\text{CH}_4$  to the atmosphere, accounting for about 20% of the current global annual emission.  $\text{CH}_4$  emissions have been quantified in different types of wetlands (Table 7). The fluxes among wetlands of the same latitude are very variable due to differences in organic matter supplies, depth of water column, exposition to air, type of vegetation, salinity, wetland area, and the method used to quantify these fluxes.

Out of the total amount of  $\text{CH}_4$  emitted, northern wetlands contribute with 34%, because of the large areas covered by these ecosystems (Wang *et al.*, 1996). Histosols emit 3-7% of the total atmospheric  $\text{CH}_4$  and shows lower methane fluxes than those emitted by minerotrophic fen, this is usually due to a lower level of water table (Sebacher *et al.*, 1986). In temperate regions, wetlands contribute with a minor proportion of the total and the salt marshes have very variable emission rates.

There is little information on the emissions from wetlands flooded during ephemeral periods, as those found in regions dominated by monsoons or in semi-arid zones, where precipitation is very low. From the information available on temporal wetlands, it has been determined that  $\text{CH}_4$  emissions are higher during summer floods than during winter because fermentative and methanogenic bacteria depend largely on temperature. In these wetlands, emissions become faster, once the wetland has been flooded as compared to rice fields. This behavior is caused

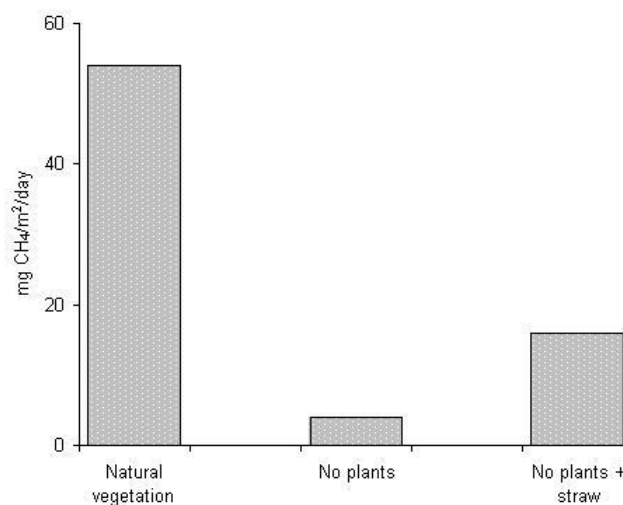


Figure 3. Comparison from methane flux from saturated wet-meadow tundra (Torn & Chapin, 1993).

by the fast decomposition rate of the organic matter coming from emerging macrophytes as compared to the rice straw. Ephemeral wetlands can consume atmospheric  $\text{CH}_4$  during the dry season, hence acting as  $\text{CH}_4$  sinks (Boon *et al.*, 1997).

Bartlett & Harris (1993) performed an extensive review on the available information about  $\text{CH}_4$  fluxes from different natural wetlands and, by relating the emissions with the surface area occupied by these environments as established by Matthews and Fung (1987), obtained global  $\text{CH}_4$  emission values (Fig. 4). Based on their results, they determined a total emission of 109 T/year, where boreal and arctic wetlands contribute with 34% to the total, temperate wetlands with 5%, and tropical wetlands with 60%.

A significant proportion of the present increase of atmospheric  $\text{CH}_4$  concentration could be due to the increase in worldwide surface used to cultivate rice. Besides, most rice fields are located in tropical regions, where emissions are higher due to a higher methanogenic rate, considering also that the hollow stems of the rice plants favor  $\text{CH}_4$  transport to the atmosphere (Anastasi *et al.*, 1992).

The contribution of the diverse transport processes of total emission of  $\text{CH}_4$  from the rice fields varies according to seasons. The ebullition process is the dominant mechanism during the first stages of the cultivation period. Along the growth period of the rice plants, ebullition rates decrease and transport by vegetation becomes the dominating process. It has been estimated that transport through the aerenchyma represents 70% of the annual  $\text{CH}_4$  flux; the percentages attributed to the ebullition and diffusion fluxes are 25%, and 5%, respectively (Schütz *et al.*, 1989a).

Table 7. Methane fluxes from several wetlands.

Latitude	Wetland	Range mgCH <sub>4</sub> /m <sup>2</sup> /day	Average mgCH <sub>4</sub> /m <sup>2</sup> /day	Reference
Tropical 20°N a 30°S	Central Amazon floodplain	0 - 2997	192	(Bartlett <i>et al.</i> , 1988)
	Orinoco floodplain	0 - 2736	248	(Smith & Lewis, 1992)
	Congo River basin (swamp)	9.9 - 550	106	(Tathy <i>et al.</i> , 1992)
	Swamp (Panama)	0 - 2600	379	(Bartlett <i>et al.</i> , 1988)
Temperate and Subtropical 45° - 20° 30° - 50°S	Coastal wetlands of South India	3.10 - 21.56		(Purvaja & Ramesh, 2001)
	Great Dismal Swamp (United States)	1-20 (wet season)		(Harris <i>et al.</i> , 1982)
	Salt marsh in Sapelo Island (USA)	0.24 - 1920	145	(King & Wiebe, 1978)
	Short <i>Spartina alterniflora</i>	0.02 - 144	15.8	
	Tall <i>Spartina alterniflora</i>			
	Salt marsh in Tree Bay			(Bartlett <i>et al.</i> , 1985)
	Short <i>Spartina alterniflora</i>	0 - 13.9	3	
	Tall <i>Spartina alterniflora</i>	-1.1 - 16.2	5	
	Freshwater marsh in Mississippi delta	0 - 2600	587	(DeLaune <i>et al.</i> , 1983)
	Histosol	- 6.7 - 29.6	-1.14	(Yavitt <i>et al.</i> , 1990)
	Minerotrophic fens	7.7 - 748	-1.14	
	Cypress swamp floodplain	4.6 - 21.8	9.9	(Harris & Sebacher, 1981)
	Swamps in Quebec (Canada)	1 - 4		(Knowles & Moore, 1990)
Mangroves (Everglades)	1.9 - 7.7	4	(Harris <i>et al.</i> , 1988)	
Boreal 45° - 60° N	Freshwater marshes (Sanjiang Plain, China)	25.7-35.6		(Ding <i>et al.</i> , 2002)
	Nonforested bogs	18-866	199	(Crill <i>et al.</i> , 1988)
	Minerotrophic fens (Minnesota)	152 - 711	348	(Williams & Crawford, 1984)
	Bogs (Germany)	0.02 - 15		(Horn <i>et al.</i> , 2003)
	Minerotrophic fens (Canada)		30	(Joabsson <i>et al.</i> , 1999)
Arctic 60° - 70° N	Freshwater marsh	-0.1 - 1.2	1.2	(Roulet <i>et al.</i> , 1992)
	Coastal tundra (Alaska)	34-266	119	(Sebacher <i>et al.</i> 1986)
	Wet coastal tundra (Alaska)	0-265	90	(Whalen & Reeburgh, 1990)

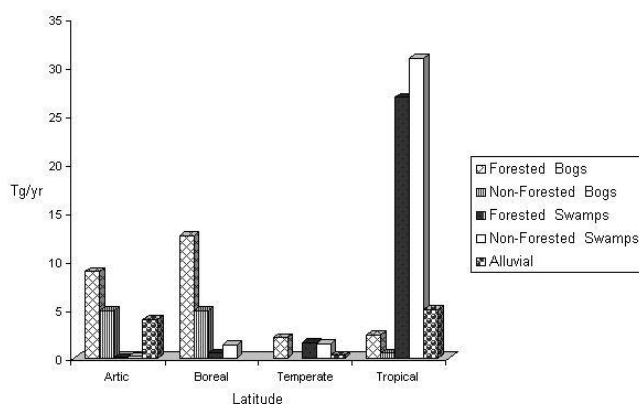


Figure 4. Global methane emissions at different latitudes (Dates from Bartlett & Harris, 1993).

**Relation of environmental variables with methane emissions.** The net  $\text{CH}_4$  flux from the wetlands results from diverse environmental variables that influence, in a complex manner, its production (methanogenesis), consumption (methanotrophy), and transport.

The relation between  $\text{CH}_4$  emission and environmental variables is difficult to understand for several reasons, for example, the episodic fluxes occurring in the subarctic wetlands (minerotrophic fens), mainly during spring, release the  $\text{CH}_4$  trapped in the ice during the winter. However, it is possible to establish some general aspects that influence  $\text{CH}_4$  flux to the atmosphere.

1. Temperature. From diverse studies it has been possible to establish that  $\text{CH}_4$  emissions are related to soil temperature, due to its influence on microbial metabolism. There is a direct relation between the increase in temperature and growth of MB (Westermann, 1993a). This relationship produces an exponential increase in  $\text{CH}_4$  flux while soil temperature increases (Hargreaves & Fowler, 1998). Hence, there are large emissions from the marshes and alluvial floodplains located in tropical regions. In this regions the optimal temperature of decomposition was  $35^\circ\text{C}$  and methanogenesis did not proceed at  $45^\circ\text{C}$  (Miyajima *et al.*, 1997).

The temperature-emission relationship also explains the increase in methanogenic activity in wetlands from mid and high latitudes during high temperature seasons. Similar results have also been obtained experimentally, in which increases in temperature induce an exponential increase in the acetogenic, and hydrogenophilic methanogenic activity (Fig. 5) (Brooks Avery *et al.*, 2002). Increases in temperature also produced an increase in  $\text{CH}_4$  consumption by methanotrophs (Krumholz *et al.*, 1995).

An important aspect related with temperature is the use of substrates by MB in the rice fields, as it has been observed that a decrease in temperature (from  $30^\circ\text{C}$  to  $15^\circ\text{C}$ ) induces a decrease in  $\text{CH}_4$  production and a change in organic matter degradation pathways. When temperature diminished, a decrease in hydrogen partial pressure occurs with an accumulation of acetate, propionate, caproate, lactate, and isopropanol; hence,  $\text{CH}_4$  production from hydrogen decreases and the use of acetate increases (Conrad *et al.*, 1987).

Besides, it has been observed that fermentation processes, related with the supply of organic substrates for methanogenesis, are more sensitive than even MB to temperature changes. Thus, temperature dependence of *in situ*  $\text{CH}_4$  production is also a reflection of the impact of this variable on the microbial processes involved in the production of substrates.

Soil temperature not always explains the differences in  $\text{CH}_4$  fluxes among the different wetlands, although some authors have reported an accurate statistical relation between emission rate and temperature (Harriss *et al.*, 1985). According to Morrissey and Livingston (1992), temperature helps to explain 90% of the seasonal variation in  $\text{CH}_4$  production and emission.

2. Water table level. Its determines the depth at which aerobic and anaerobic conditions occur in wetlands, these conditions, in turn, control the methanogenic and methanotrophic processes (Kelley *et al.*, 1995). The methanogenesis is a strict anaerobic process, and it will be stimulated during flooding periods, when the water table level increases (Reddy & Graetz, 1988). In contrast, with a decrease in flooding periods,  $\text{CH}_4$  production decreases. An inverse relation is observed with  $\text{CH}_4$  oxidation.

The mean position of the water table level is the best indicator of  $\text{CH}_4$  emissions; apparently a critical depth exists at which maximal emissions occur (Moore & Roulet, 1993; Moore & Dalva, 1993). It has been determined that depths of the water table greater than 18 cm do not produce high emissions, since  $\text{CH}_4$  production (methanogenesis) decreases and its consumption increases (methanotrophy). In contrast, when the water table level is 12 cm below the surface of peat, or exceeds it, emissions are high. Bubier *et al.* (1993) and Daulat and Clymo (1998) indicated that  $\text{CH}_4$  flux to the atmosphere from hollows is 5-60 times higher than that produced in hummocks, because the first have a lower water table depth than the hummocks (Fig. 6). The variables influencing directly or indirectly the water table level are very important to make regional extrapolations.

The water table level not only influences the amount of  $\text{CH}_4$  emitted to the atmosphere, but also its atmospheric removal. Harris *et al.* (1982) determined that peat from the Great Dismal Swamp contributes to remove the atmospheric  $\text{CH}_4$  when the water table level is below the surface of the peat during dry

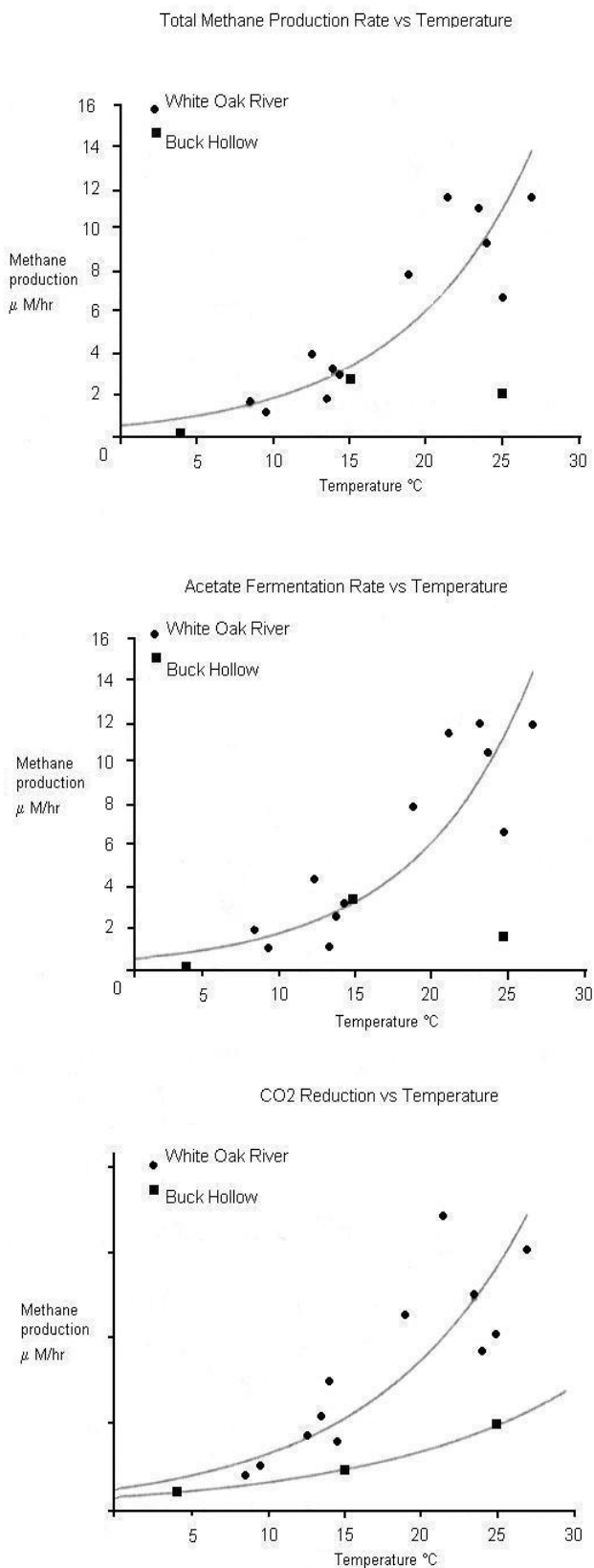


Figure 5. Methane production versus temperature (Brooks Avery, *et al.*, 2002).

periods; in contrast when peat is well saturated with water it becomes an important  $\text{CH}_4$  source to the atmosphere.

3. Net production. The magnitude of emissions depends on the amount of organic compounds released by plants from the net primary production process, since this represents the substrate for MB (Chanton & Dacey, 1991). Most of the carbon assimilated by the plants from the wetlands during photosynthesis is deposited in the root tissues, so that in this zone a great potential for easily degradable carbon exists, which contributes to the development and proliferation of MB. Consequently, the photosynthesis rate exerts a great impact on methanogenesis because a high carbon assimilation implies necessarily a greater concentration of available labile carbon in the roots that will be used by MB when it enters to the rhizosphere (Whiting & Chanton, 1993). Whiting and Chanton (1992) determined a positive relation between  $\text{CH}_4$  emission and net primary production of a minerotrophic fen dominated by *Carex* spp, these authors attribute the high  $\text{CH}_4$  emission rates to methanogenesis stimulation by the supply of labile organic substrates derived from the photosynthetic process, as well as to the fact that plants act as gas conductors. It has been estimated that approximately 3% of the net production of wetland ecosystems escapes to the atmosphere in the form of  $\text{CH}_4$ .

The relationship of the primary production process with  $\text{CH}_4$  emission also influences the diurnal variations of the emissions. Thomas *et al.*, (1996) demonstrated an increment in  $\text{CH}_4$  flux from peat during the day and a decrease during the night. During the day, photosynthesis products contribute to the increase in root exudates that promote formation of  $\text{CH}_4$  by MB, which is transported through the vascular system of plants and released through the stomata. In addition, during the day, photosynthesis releases oxygen that displacement the oxic zone below the peat surface and around the roots, increasing  $\text{CH}_4$  oxidation. Therefore the emissions dynamics, during a short period, depends on the circadian physiology of the wetlands flora (Lloyd *et al.*, 1998).

4. Supply of labile organic matter. In wetlands, availability of labile organic carbon susceptible to be used during the methanogenesis process depends, besides net production, from the amount of flooded vegetal matter. When the water column depth increases, decomposition of vegetal matter is greater under anaerobic conditions and, since these processes are slower, the generated organic substrates are of better quality (carbohydrates and proteins). In the other hand, with a lower water column depth, there is a smaller amount of flooded vegetal cover, favoring the aerobic mineralization processes, which are faster and, hence, generate substrates difficult to degrade as humic substances, biologically inert (Cicerone *et al.*, 1992).

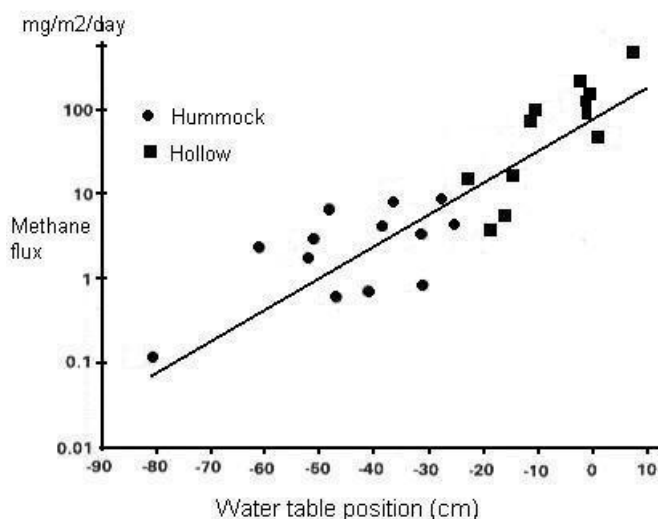


Figure 6. Methane emissions and water table level (Bubier *et al.*, 2002).

To this respect Miyajima *et al.* (1997) demonstrated a negative correlation between methanogenic rate with the lignin and fiber contents of the substrate plant materials. However in freshwater wetlands the presence of high concentrations of labile organic carbon increases the amount of total  $\text{CH}_4$  produced (Crozier & DeLaune, 1996). In marshes with *Deyeuxia angustifolia*, a  $\text{CH}_4$  content of  $0.72 \text{ g/m}^2$  with  $0.68 \text{ mM}$  of labile organic carbon was determined, whereas, in marshes with *Carex lasiocarpa*, a concentration of  $1.61 \text{ g CH}_4/\text{m}^2$  and  $1.86 \text{ mM}$  of labile organic carbon was found (Ding *et al.*, 2002).

5. Substrates concentration. A high acetate concentration promotes the growth of *Methanosarcina* spp., which requires  $0.2\text{-}1.2 \text{ mM}$  acetate, whereas *Methanosaeta* spp. needs  $< 10 \mu\text{M}$ . In fertilized rice fields where acetate concentrations up to  $24 \text{ mM}$  have been evaluated, *Methanosarcina* spp. dominates (Lovley & Klug, 1983; Lovley & Klug, 1986). It has been observed that MB can tolerate up to  $100 \text{ mM}$  of volatile fatty acids (acetate among them) at neutral pH; however at acidic pH bacteria become extremely sensitive to acetate concentrations. In acidic conditions, with an extracellular pH lower than 4.7, the non-dissociated acetic acid is abundant and can diffuse through the cellular membrane towards the interior of the cell, that remains at a neutral pH; once inside, the acid dissociates and induces uncoupling of the membrane protons producing cell death (Russell, 1991).

Finally, since at the beginning of the mineralization processes there is no available substrate for the MB, this bacterial population does not establish; therefore, fermentative activity limits methanogenesis (Shannon & White, 1996).

6. Vegetal cover and distribution.  $\text{CH}_4$  flux is not related with the total vegetal cover area but flux is related with the floristic composition. Bryophytes are more sensitive to changes in water table levels than vascular plants, hence they are better indicators of  $\text{CH}_4$  emission (Gignac & Vitt, 1990). In a smaller scale, the presence of certain species in the humid zones is a good indicator of the flux. *Carex rostrata*, *C. limosa*, and *Cladopodiella fluitans* are indicators of high  $\text{CH}_4$  emissions (higher than  $100 \text{ mg/m}^2/\text{day}$ ). The bryophytes *Scorpidium scorpioides*, and *Limprichtia revolvens* are associated to low emissions ( $9\text{-}14 \text{ mg/m}^2/\text{day}$ ) (Bubier, 1995). Emissions magnitude is also related to the distribution of bryophytes in histosols, since in hollows when *Sphagnum majus*, *S. cuspidatum*, *Cratoneuron filicinum*, and *Warnstorfia exannulatus* dominate,  $\text{CH}_4$  flux is  $156 \text{ mg/m}^2/\text{day}$ ; in contrast in hummocks, with *S. fuscum*, emissions decrease to  $5 \text{ mg/m}^2/\text{day}$  (Bubier *et al.*, 1993).

In freshwater marshes,  $\text{CH}_4$  flux increases linearly with the increment in the density of stems from *Deyeuxia angustifolia* ( $25.7 \text{ mgCH}_4/\text{m}^2/\text{hr}$ ), *Carex meyeriana* ( $31.1 \text{ mgCH}_4/\text{m}^2/\text{hr}$ ), and *Carex lasiocarpa* ( $35.6 \text{ mgCH}_4/\text{m}^2/\text{hr}$ ). Emissions reached maximal levels in the area where root growth was more abundant (Ding *et al.*, 2002). In nutrients-poor wetlands, characterized by the presence of *Oxycoccus* spp. and *Andromeda* spp., emissions increase (Sundh *et al.*, 2000).

7. Sulfates concentration. In brackish wetlands characterized by constant supply of sulfates, was determinate a negative correlation between sulfate concentration and  $\text{CH}_4$  emission (Purvaja & Ramesh, 2001). In this environments the sulfate reduction process is favored in contrasting with the methanogenesis since SRB compete more efficiently for the available substrates, mainly acetate and hydrogen, as compared to MB (Lovley & Klug, 1986). In consequence,  $\text{CH}_4$  production decreases and methanogenesis is restricted to deep areas of sediments where sulfate supply decreases (Sinke *et al.*, 1992). In a coastal wetland of Mexico (Chiapas) we observed that methanogenesis was higher in months associated to the rainy season when the sulfate concentration diminished (Torres-Alvarado *et al.*, 2005).

Senior *et al.* (1982) demonstrated that  $\text{CO}_2$  reduction is the only mechanism for  $\text{CH}_4$  production in sediments from salt marshes where sulfate supply is high. The capacity of HMB to produce  $\text{CH}_4$  in the presence of competitive processes, such as sulfate reduction, allowed methanogenesis continue in this type of wetlands. In addition to the use of hydrogen, MB are able to use less competitive substrates, such as methanol and methylamines. Lovley and Klug (1983) determined that  $\text{CH}_4$  formation from methanol represents  $2.8\text{-}4.0\%$  of the total production and helps methanogenic bacteria to maintain their populations when sulfate is being supplied to the environment.

A complete inhibition of methanogenesis by addition of sulfate also been observed in rice fields (Achnich *et al.*, 1995). In this wetlands the activity of SRB is higher directly at the root of the rice plant (500 nmol/cm<sup>3</sup>/day) as compared to the rhizosphere (310 nmol/cm<sup>3</sup>/day) and the oxic-anoxic interface (100 nmol/cm<sup>3</sup>/day). The presence of two different physiological types of SRB has been suggested in these wetlands. The rhizosphere region is colonized by SRB that oxidize incompletely the substrates and have fast growth, such as species from the genus *Desulfovibrio*, whereas the soil is the habitat of those SRB that oxidize completely the substrate, belonging to the slow growth spore forming bacteria, such as species from the genus *Desulfotomaculum* (Liesack *et al.*, 2000).

An important aspect related to the rate of CH<sub>4</sub> emission is the effect of acid rain. In regions affected by this phenomenon, atmospheric deposition of sulfates occurs in the aquatic ecosystems and wetlands that might reduce the magnitude of CH<sub>4</sub> flux (Nedwell & Watson, 1995). Watson and Nedwell (1998) demonstrated that in histosols of the Great Dun Fell, methanogenesis is inhibited by 250 μM sulfate concentrations supplied by the acid rain in England that favors the sulfate reduction process.

8. pH. In laboratory studies it has been demonstrated that CH<sub>4</sub> production by MB depends on the pH, with optimal values between 5 and 7; however tolerant strains to the acid conditions of histosols have been reported (Williams & Crawford, 1984; Dunfield *et al.*, 1993).

9. Phosphates. It has been observed that the acetoclastic methanogenic activity in the roots of rice plants is inhibited by phosphates concentration. In laboratory experiments with acetate, a CH<sub>4</sub> production of 40% was obtained without phosphates and this production decreased to 20% with phosphates in the medium (Chin *et al.*, 2004). In contrast, CH<sub>4</sub> production increased with a carbonate buffer solution.

10. Soil texture. Soil and sediments texture is also a factor related to CH<sub>4</sub> emissions. Soils with high clay content and high supply of organic matter have the highest CH<sub>4</sub> production, whereas sandy soils are characterized by a low production potential (Neue *et al.*, 1990). In clay soils average CH<sub>4</sub> emission rates of 209 mg/m<sup>2</sup>/day were quantified, whereas in sandy slightly acid soils the average emission was 59.7 mg/m<sup>2</sup>/day.

11. Peat harvesting. The peat is an important CH<sub>4</sub> source. Draining activities and peat harvesting to be used as oil, natural gas, and in medicine mainly in Canada, Russia, Ireland, and Nordic cities, alter CH<sub>4</sub> flux. Before peat harvesting starts, the water table level where it is located, has decreased considerably due to draining processes. Because the superficial layer is more oxidized, a decrease in CH<sub>4</sub> emission is produced; however, during the harvesting, peat becomes an important source

of CH<sub>4</sub> emission (15-93 mg/m<sup>2</sup>/hr) than drained peat (0.11 mg/m<sup>2</sup>/hr) (Roulet & Moore, 1995).

12. Alteration of river beds. River flows worldwide have been modified by human development, causing a decrease in fluvial volume and changes in its distribution. Fluctuations in water level affect flooding periods of wetlands, and this influences the production/consumption of CH<sub>4</sub>, changing the gas emission rate. In adjacent wetlands to Murria River (Australia), maximal CH<sub>4</sub> emissions occurred in winter (rainy season) or spring (ice melting). However when the course of the river was changed, maximal emissions were quantified during the summer with the flooding period (Boon *et al.*, 1997).

## METHANE AND GREENHOUSE EFFECT

Global methane sources to the atmosphere range between 10<sup>12</sup> to 10<sup>14</sup> g CH<sub>4</sub>/year, producing a 1.75 ppm concentration of this gas in the atmosphere, with a mean life span of 7 to 11 years; however in the last decades this concentration has increased at a rate of 0.5-0.8% annually. Atmospheric CH<sub>4</sub> is recognized as one of the most important gas involved in the greenhouse effect (Pearman & Fraser, 1988; Karl & Tilbrook, 1994).

Gases found in the atmosphere such as CO<sub>2</sub>, CH<sub>4</sub>, nitric oxide (N<sub>2</sub>O), and ozone (O<sub>3</sub>), entrap solar radiation when this is reflected by the earth surface (greenhouse effect), helping to maintain the earth warm with a global average temperature of 15°C, which induces development of biophysical processes. The warming effect produced by a gas is related to its concentration and permanence in the atmosphere, as well as with its radioactive force. In this sense, although CH<sub>4</sub> has a considerably lower atmospheric concentration (1.7 ppm) than CO<sub>2</sub> (345 ppm), it has a greater capacity to absorb infrared radiation, therefore addition of 1 kg CH<sub>4</sub> to the atmosphere blocks better the heat emitted by the terrestrial surface than 1 kg CO<sub>2</sub>. Therefore, CH<sub>4</sub> as a molecule is 30 times more effective to absorb heat during the greenhouse effect than CO<sub>2</sub> (Tyler, 1991). For this reason, CH<sub>4</sub> is the second gas of importance, after CO<sub>2</sub>, involved in the greenhouse effect; contributing approximately with 25% to atmospheric warming.

**Methane emissions and global climatic change.** The increase in concentrations of the main gases with greenhouse effect in the atmosphere in the last years has promoted an increase in the average temperature of the earth. This phenomenon is known as Global Climatic Change due to the effects produced on the earth's weather.

There are different factors affecting the climatic system, however many scientists claim that emission of gases CH<sub>4</sub> and CO<sub>2</sub>, coming mainly from anthropogenic activities and wetlands,



could be a key factor in the increase of temperature and the global climatic change. The increase in atmospheric temperature produces a greater activity in the hydrological cycle, changes in the distribution of rainfall and in climatic patterns, alterations of terrestrial ecosystems and of migration species patterns (EPOMEX, 1998). A loss of biodiversity is being forecasted, particularly in the tropical regions, as well as a fusion of the polar caskets that will increase the level of water in oceans (Masera, 1992).

It has been anticipated that the effects of the Global Climatic Change will be more pronounced in the continental regions of the Northern Hemisphere because they contain most of the wetland ecosystems, where the flow of gases with greenhouse effects is relevant, producing between 22 to 70 Tn/year, (Anselmann & Crutzen, 1989). Likewise, tropical regions, due to their high biological activity, have the potential to emit large amounts of gases to the atmosphere. If an increase in Global Warming is produced, a change in peat saturation of wetlands could be induced, modifying CH<sub>4</sub> fluxes (Conrad *et al.*, 1987).

It is expected that Global Warming be more pronounced at high latitudes, calculating that, in the Arctic, the average temperature will increase approximately 3°C. As a consequence, in boreal wetlands, the rate of evapotranspiration will increase reducing the area of the saturated ecosystems, decreasing CH<sub>4</sub> production and increasing its consumption through bacterial oxidation processes, hence, the increase in temperature would have a negative feedback control on atmospheric CH<sub>4</sub> (Arah & Stephen, 1998). In contrast, in tropical regions, increase in temperature could be accompanied by an increase in methanogenesis and CH<sub>4</sub> emissions from wetlands (Cao *et al.*, 1998).

**Management and mitigation measures.** Although recent environmental regulations recognize the fundamental relevance of wetlands as natural habitats and center of biogeochemical activity, not clearly mitigation measures have been established to attenuate the flux of CH<sub>4</sub> emissions to the atmosphere. This is particularly difficult with natural wetlands where management measures require diverse studies before their implementation. Despite this, there have been some proposals to this respect.

Plants growth in wetlands produce a larger supply of organic matter for methanogenesis, incrementing the production and emission of CH<sub>4</sub>. In consequence, removal of vegetal residues could contribute to diminish methane fluxes. In Sweden, where harvest of peat is practiced, a regular cleaning of the dikes from which peat is extracted has been established as a mitigation measure to help maintain low emission levels (Sundh *et al.*, 2000).

Several mitigation strategies have been established for rice paddy fields. One of the most drastic measures proposed has been the transition of the wetland to up-land regions without

flooding. This measure is not simple to implement in the agricultural practice mainly for production reasons. Most of the uplands used for rice cultivation produce 1-4 Ton/ha, whereas the flooded rice fields produce more than 7 Ton/ha (Institute, 1988).

A more promising measure involves a modification in the irrigation pattern to include short dry periods, since rice plants can recover after short dry periods once the flooding conditions are reestablished. An additional measure refers to the implementation of an internal drainage system in the cultivated fields that might facilitate oxygen introduction to increase CH<sub>4</sub> oxidation. This measure would have a particular positive effect on saline and alkaline soils (De Datta, 1981).

The use of different types of fertilizers has been another of the analyzed measures; however, the results obtained until now have been contradictory. The use of ammonium sulfate in some regions in Italy has reduced CH<sub>4</sub> emissions (Schütz *et al.*, 1989b). However, its use in rice paddies from California did not attenuate methanogenesis (Cicerone & Shetter, 1981). Another proposal refers to the addition of enough amounts of iron (III) to the rice fields to promote development of iron-reducing microbiota, which competes more effectively for the available substrates, both for sulfate reduction and methanogenesis, which could decrease CH<sub>4</sub> production in rice fields (Nouchi *et al.*, 1990; Wassmann *et al.*, 1993). This phenomenon also was observed in natural wetlands where incubation experiments demonstrated that microbial Fe(III) oxide reduction suppressed sulfate reduction and methanogenesis in surface sediments, whereas in rhizosphere sediment the Fe(III) oxide reduction accounted for 65% of total carbon metabolism, compared to 22% for methanogenesis (Roden & Wetzel, 1996).

## CONCLUDING REMARKS

This review has outlined some aspects of methanogenesis and CH<sub>4</sub> oxidation in wetlands, and its relation with CH<sub>4</sub> emissions from this environments. CH<sub>4</sub> is considered one of the most important greenhouse gases in the atmosphere. Because of the strict anaerobic conditions required by CH<sub>4</sub> generation by microorganisms, natural wetland ecosystems are one of the main sources of biogenic CH<sub>4</sub> and tropical wetlands are one of the largest natural sources in the global methane budget due to high biological activities.

Increases in atmospheric CH<sub>4</sub> and other greenhouse gas concentrations are predicted to rise global mean temperature with several implications. The only way by which the magnitude of climatic changes at a global scale can be assessed is by performing several quantifications of the production, oxidation, and emission of CH<sub>4</sub> in a large variety of wetlands and characterize their response to environmental parameters, since the available database on CH<sub>4</sub> emissions to the atmosphere is insufficient in

regard to the large variety of climatological and edaphological factors that would allow to reliably extrapolate data at a global scale and to design more precise models on the impact of the Global Climatic Change leading to a better prediction of future scenarios. In Mexico is particularly important because there aren't studies to respect.

The increase in rice demands due to the growing human population could lead to further increases in the areas used for its cultivation and, therefore, would contribute to higher CH<sub>4</sub> emissions. As a result, rice cultivation will have a large impact on future Global Warming. By these reason, the research on rice cultivation must be addressed to a better analysis of CH<sub>4</sub> production, its oxidation and to the development of possible mitigation strategies to diminish and/or suppress emissions of this hydrocarbon.

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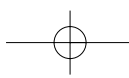
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