

## Climate Effects on Greenhouse Gas Emissions and Microbial Communities in Wetlands

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### 기후변화가 습지 내 온실기체 발생과 미생물 군집구조에 미치는 영향

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#### ABSTRACT

Global climate changes including elevated CO<sub>2</sub>, drought, and global warming may influence greenhouse gas emissions in wetlands. A variety of microbial communities including denitrifiers and methanogens play a key role in determining such processes. In this paper we summarize current knowledge on the effects of climate changes on CO<sub>2</sub>, CH<sub>4</sub>, and N<sub>2</sub>O production and microbial communities mediating those processes in wetlands. Elevated atmospheric CO<sub>2</sub> and warming generally increase gas emissions, but effects of droughts differ with gas type and drying level. The responses of microbial community to climate changes in terms of composition, diversity and abundance are still in question due to lack of studies in wetlands. Based on the present review, it is suggested that future studies on microbial processes should consider microbial community and relationships between microbial function and structure with diverse environmental factors including climate changes. Such knowledge would be crucial to better understand and predict accurately any shifts in ecological functions of wetlands.

**Key words** : Elevated CO<sub>2</sub>, Drought, Greenhouse gas emissions, Microbial community, Warming, Wetland

#### I. INTRODUCTION

Wetland ecosystems including peat-forming wetland cover only 2-6% of global land surface (Gorham, 1991). However, they play a pivotal role in global biogeochemical cycles. Firstly, peat accumulation over thousands of years has resulted in a vast store of carbon of 455 Pg-C in peatland ecosystems (Gorham, 1991; Roulet, 2000). This represents 20-30% of the world's pool of soil organic carbon and is comparable to the total carbon in the atmosphere as CO<sub>2</sub> (IPCC, 2001). Secondly, wetlands are substantial sources of the radi-

atively active trace gases such as CH<sub>4</sub> and N<sub>2</sub>O (Freeman *et al.*, 1994). For example, natural wetlands and rice paddies release about 40-50% of global emissions of CH<sub>4</sub> which is 25 times more radiatively active than CO<sub>2</sub> on a molar basis (Cicerone and Oremland, 1988). As such, even small changes in gas emissions from wetland soils could significantly influence the balance of carbon flux between the atmosphere and biosphere. This would be of great importance in future trajectory of global warming scenario.

Anthropogenic activities have increased the concentration of atmospheric CO<sub>2</sub> continuously from about

280 parts per million (ppm) at the beginning of the industrial revolution to 382 ppm at the present time (IPCC, 2001). The linear warming trend over the last 50 years (0.13 per decade) is nearly twice that for the last 100 years. Extremely hot and dry summers have also occurred throughout much of the earth. Substantial carbon (C) losses have already been reported in boreal and sub-arctic bogs and fens due to lower water levels during warm and dry summers (Schreuder *et al.*, 1998; Alm *et al.*, 1999; Moore *et al.*, 2002). As such, concerns have been raised that persistent warming and drought could reduce the capacity of wetlands to act as a sink for global C, and may eventually turn it into a source of C to the atmosphere.

Wetland soils undergo intermittent flooding, draining, and dewatering, potentially supporting both aerobic and anaerobic microbial communities. Moreover, chemical characteristics differ substantially among different types of wetlands, ranging from mineral to organic, eutrophic to oligotrophic and saline to freshwater, allowing each wetland to support distinct microbial communities. Those diverse microbial communities may exploit a wide range of electron acceptors during organic matter decomposition. Critical processes controlling CO<sub>2</sub>, N<sub>2</sub>O, and CH<sub>4</sub> production from wetlands are carried out by diverse microbial communities such as denitrifiers, methanogens, and so on. Those microbes potentially influence the balance among anaerobic gas production in soils (Yavitt and Seidman-Zager, 2006).

Climate changes are possible to influence soil microbial processes mediating organic matter decomposition and gas emissions through altering abundance and/or structure of microbial communities inhabiting wetlands. The knowledge on the links between microbial structure and soil functioning is also essential by considering that 80-90% of the processes in soil are reactions mediated by microbes (Nannipieri *et al.*, 2003). However, the effects of climate changes on soil microbial community and activity, and their relationship remain largely unknown in wetlands. The aim of this paper is to summarize current knowledge on the effects of elevated CO<sub>2</sub>, drought, and warming on biogenic gas emissions (CO<sub>2</sub>, CH<sub>4</sub>, and N<sub>2</sub>O) and microbial communities in wetland ecosystems.

## II. EFFECTS OF ELEVATED CO<sub>2</sub> CONCENTRATIONS

Atmospheric CO<sub>2</sub> concentrations have increased

from pre-industrial level of 280 ppm to 382 ppm at present. Considering the long-term average CO<sub>2</sub> increase of 1.5 ppm per year (<http://www.cmdl.noaa.gov/gmd/ccgg/trends>), it is likely to reach approximately 530 ppm by 2100. Previous studies have mainly focused on the effects of elevated CO<sub>2</sub> on wetland vegetation in terms of growth, leaf photosynthesis, evaporation, nutrients and community structure (Jauhainen *et al.*, 1997; Mitchell *et al.*, 2002). Some studies have drawn attention on the response of below-ground processes to elevated CO<sub>2</sub> in terms of dissolved organic carbon (DOC) release, soil enzyme activity, and greenhouse gas emissions (Saarnio *et al.*, 2000; Freeman *et al.*, 2004; Kang *et al.*, 2005).

### 2.1. Gas emissions

Elevated atmospheric CO<sub>2</sub> concentrations increased CO<sub>2</sub> emissions from wetlands via increased root biomass and DOC (Schrope *et al.*, 1999; Kang *et al.*, 2001). CH<sub>4</sub> emissions differently responded to elevated CO<sub>2</sub>. Although many studies showed an increase in CH<sub>4</sub> emissions under elevated CO<sub>2</sub> (Meronigal and Schlesinger, 1997; Wang and Adachi, 1999), no changes or even decrease in CH<sub>4</sub> emissions were also observed in wetlands (Kang *et al.*, 2001; Saarnio and Silvola, 1999; Schrope *et al.*, 1999; Saarnio *et al.*, 2000). It is possible that changes in litter chemistry (Hirschel *et al.*, 1997), nutrient deficiency (Niklaus and Körner, 1996), or heights of water table (Roulet *et al.*, 1992) might change the magnitude and direction of methane emissions in wetland ecosystem under elevated CO<sub>2</sub> conditions.

### 2.2. Microbial communities

In many studies conducted in terrestrial ecosystems, there is an uncertainty in the responses of microbial communities to elevated CO<sub>2</sub>; no change (Griffiths *et al.*, 1998; Deiglmayr *et al.*, 2004; Grüter *et al.*, 2006; Jossi *et al.*, 2006; Chung *et al.*, 2006) and change (Marilley *et al.*, 1999; Montealegre *et al.*, 2000; Janus *et al.*, 2005; Jossi *et al.*, 2006; Lipson *et al.*, 2006) (Table 1). Unfortunately, understanding of microbial communities under elevated CO<sub>2</sub> is still limited in wetland ecosystems. Lee *et al.* (2004) reported a shift of denitrifiers in the marsh incubated at elevated CO<sub>2</sub>.

The lack of consistent results is likely related with analytical tools applied. Most molecular tools (e.g., PLFA, T-RFLP, and DGGE) detect both active and inactive ones in microbial community. More recently, it

**Table 1.** The list of studies reporting the effects of elevated CO<sub>2</sub> on microbial community

Plant type	Molecular methods applied	Responses	Reference
Forest	PLFA <sup>a</sup>	No	Wiemken <i>et al.</i> , 2001
	PLFA	No/changes	Phillips <i>et al.</i> , 2002
	PLFA / DGGE <sup>b</sup>	No	Chung <i>et al.</i> , 2006
	PLFA	No	Zak <i>et al.</i> , 2000
	PLFA / T-RFLP <sup>c</sup>	Change <sup>d</sup>	Janus <i>et al.</i> , 2005
Grassland	TTGE <sup>e</sup> / T-RFLP	No	Grüter <i>et al.</i> , 2006
	PCR-DGGE	No	Jossi <i>et al.</i> , 2006
	Reverse transcriptase-PCR-DGGE	Change	
	PLFA	Change	Montealegre <i>et al.</i> , 2002
	ARDRA <sup>f</sup>	Change	Marilley <i>et al.</i> , 1999
	BOX-PCR	Change	Montealegre <i>et al.</i> , 2000
	PCR-RFLP	No	Deiglmayr <i>et al.</i> , 2004
	DNA hybridization	No	Griffiths <i>et al.</i> , 1998
	%G + C base profiling	No	Niklaus <i>et al.</i> , 2003
Sequencing	Change	Lipson <i>et al.</i> , 2006	
Wetlands	T-RFLP	Change	Lee <i>et al.</i> , 2004
	T-RFLP	No <sup>g</sup>	Kim (unpublished data)

(a) PLFAs (phospholipids fatty acid); (b) DGGE (denaturing gradient gel electrophoresis); (c) T-RFLP (terminal restriction fragments length profile); (d) bacterial and fungal communities; (e) TTGE (temporal temperature gradient gel electrophoresis); (f) ARDRA (Amplified ribosomal DNA restriction analysis); (g) bacterial, denitrifier, and sulphate reducing bacterial communities

has been reported that only “active” species presenting in the rhizosphere responded to elevated CO<sub>2</sub> (Jossi *et al.*, 2006). Additionally descriptive explanation without statistical analysis might attribute to controversial results. It is necessary to apply adequate statistical methods to community composition and structure such as nonmetric multi-dimensional scaling, diversity indices, multi-response permutation procedure and indicator species analysis (McCune and Grace, 2002).

### III. EFFECTS OF DROUGHTS

In the future climate, droughts and floods are expected to be more frequent, severe, and longer-lasting (IPCC, 2001). Persistent droughts are likely to reduce the capacity of wetlands to act as a sink for global carbon, and may eventually turn it into a source of carbon to the atmosphere. Substantial carbon losses have already been reported in various wetlands including temperate, boreal, and sub-arctic peatlands (Shurpali *et al.*, 1995; Alm *et al.*, 1999; Moore *et al.*, 2002) and marsh (Heinsch *et al.*, 2004) during warm and dry summers. After drought wetlands lost their own characteristics in relation with anoxic environments they behaved more like a terrestrial ecosystem (Heilman *et al.*, 2000).

### 3.1. Gas emissions

The main control on a wetland’s ability to retain carbon and to generate trace gases is determined by its ability to remain wet. Partial drying of wetlands significantly increased CO<sub>2</sub> emissions into the atmosphere (Shurpali *et al.*, 1995; Oechel *et al.*, 1998; Heinsch *et al.*, 2004), which is related to the stimulation of hydrolytic enzyme activities (Freeman *et al.*, 1996; Corstanje, 2003). Denitrification and nitrous oxide emissions also increased with drying (Robertson and Tiedje, 1987; Davidsson *et al.*, 2002), because nitrification in the top-soil layers supplied substrates for denitrification (Baldwin and Mitchell, 2000).

Many studies have focused on methane emission in relation with drought (Moore and Knowles, 1989; Freeman *et al.*, 1993; Moore and Roulet, 1993; Ratering and Conrad, 1998). It is generally accepted that droughts reduce the amount of methane emissions from wetlands. Enhanced methane oxidation has been considered as a major reason for the decline in CH<sub>4</sub> emissions. However, recently it has been reported that methane oxidation is unable to completely account for the decreased methane emissions during droughts (Freeman *et al.*, 2002). During drought, suppressed primary production may reduce CH<sub>4</sub> emissions via

**Table 2.** Changes in abundance and diversity of bacteria, methanogens, and denitrifiers amplified bacterial 16S rRNA, *mcrA* and *nirS* genes, respectively, following the drought treatment in riparian, fen, and bog soils. Data were analyzed by t-test at  $p < 0.001^{***}$ ,  $p < 0.01^{**}$ , and  $p < 0.05^*$ ,  $n = 6$  (2-tails).

	Genes	Riparian	Fen	Bog
Abundance	Bacterial 16S rDNAs	-	Decrease*	Increase**
	<i>mcrA</i>	-	-	Decrease***
	<i>nirS</i>	-	Decrease***	Decrease**
Diversity	Bacterial 16S rDNAs	Decrease*	-	Increase(*)
	<i>mcrA</i>	-	-	-
	<i>nirS</i>	Increase(*)	-	-

decreased labile organic substrates which normally drive methanogenesis (Whiting and Chanton, 1993). Additionally, an increased sulphate and ferric iron may allow sulphate and ferric iron reducing bacteria to out-compete methanogenic bacteria on  $H_2$  (Ratering and Conrad, 1998). Although wetlands are restored with rewetting, methane production rates do not recover like before. It is because that rewetting may result in subsequent sulphate releases into surface water, suppressing the recovery of methane emissions via methanogens inhibition (Freeman *et al.*, 1994; Ratering and Conrad, 1998; Dowrick *et al.*, 2006).

### 3.2. Microbial communities

Microbial communities have been assumed to be affected by drought. However, such reports were just based on changes in microbial processes such as enzyme activity, organic matter decomposition, and gas emissions without specific measure of community structure. For example, no release of nutrients following the adding of sulphate into rewetted sediments speculated a loss of sulphate reducing bacteria during droughts (Bayley *et al.*, 1986). Changes in  $CH_4$  emissions may imply a shift in methanogens following droughts (e.g., Boon *et al.*, 1997).

Recently, DNA-based approaches have been used to measure microbial communities with droughts. We observed the response of eubacteria, denitrifiers, and methanogens to droughts based on abundance, composition or diversity in a bog, a fen, and a riparian wetland (Table 2). The abundance and diversity of microbial communities differently responded to droughts according to the type of wetland and microbial community (Table 2). It has been reported that drying of sediments significantly changed the bacterial community structure in a semi-permanent stream (Rees *et al.*, 2006). However, following rewetting they did not return to their original

structures at pre-drought conditions. As for methanogens, regardless of water regimes, the structure and biomass were relatively stable in rice paddy soil (Mayer and Conrad, 1990; Lueders and Friedrich, 2000). We also found that droughts did not affect the diversity and composition of methanogens in wetlands examined (Table 2).

## IV. EFFECTS OF GLOBAL WARMING

Climate change models predicted that the mean global surface air temperatures will increase by between 1.4 and 5.8°C until the end of the 21st century (IPCC, 2001). Higher temperatures may transform permafrost soils to wetlands and accelerate mineralization in wetlands. Previous studies have demonstrated that warming potentially influenced DOC release (Freeman *et al.*, 2001; Cole *et al.*, 2002), soil enzyme activity (Waldrop and Firestone, 2004; Fenner *et al.*, 2005), and nutrient availability (Fenner *et al.*, 2006) in wetlands. However, the impacts of this projected warming on carbon balance in wetlands are still uncertain.

### 4.1. Gas emissions

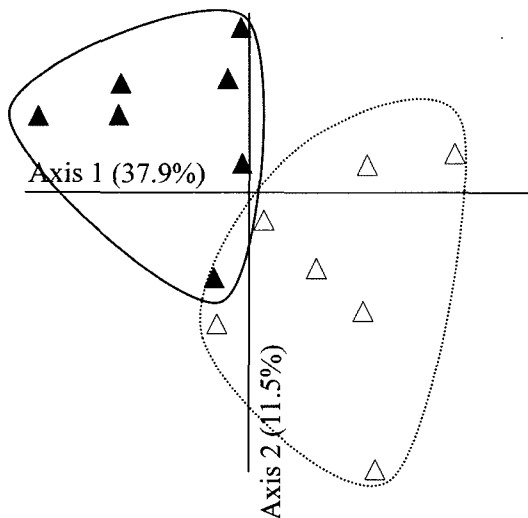
Terrestrial studies demonstrates that  $CO_2$  production is positively related with temperature (Eliasson *et al.*, 2005), which is primarily regulated by enhancement of plant growth (Zhang *et al.*, 2005), dominant soil fauna (Briones *et al.*, 2004) and carbon quality (Fierer *et al.*, 2006). There is also a positive correlation between temperature and  $N_2O$  emission rates (Carnol and Ineson, 1999). As for wetlands, ecosystem respiration (ER) as indicated by  $CO_2$  emission showed a positive relationship with temperature in peatlands (Kim and Verma, 1992; Updegraff *et al.*, 2001; Lafleur *et al.*, 2005). However, little attention has been given to possible

effects of warming on N<sub>2</sub>O emissions from wetlands.

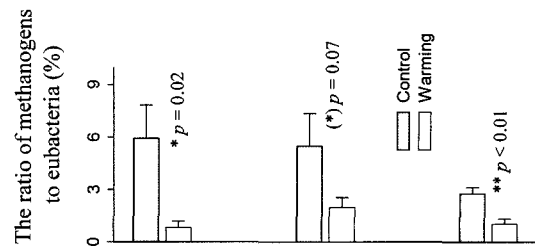
CH<sub>4</sub> efflux is positively correlated with soil temperature (Hutchin *et al.*, 1995; Kim *et al.*, 1999; Updegraff *et al.*, 2001). CH<sub>4</sub> production rates in anaerobically incubated rice field soil increased with temperature ranging from 10 to 37°C (Fey and Conrad, 2000). The optimum temperature and the lower limit for methanogenesis were 25 and -5°C, respectively, in acidic peats (Metje and Frenzel, 2005). It is consistent with a study showing that a marked increase in CH<sub>4</sub> emissions from peat soils between 6 and 15 (Fenner *et al.*, 2006). Temperature sensitivity of methanogenesis is potentially influenced by substrate quality, wetland type, and soil nutrient dynamics (Updegraff *et al.*, 1995, 2001). Global warming would also influence a shift in growth stages of wetland vegetation, resulting in altered plant mediated CH<sub>4</sub> and CO<sub>2</sub> transport (Kim *et al.*, 1998, 1999). Additionally, warming may increase CH<sub>4</sub> emissions possibly at the global scale via increases in newly formed peatlands as a result of melting of the permafrost (Gorham, 1991).

#### 4.2. Microbial communities

Warming changes substrate quality and quantity in belowground (Hooper *et al.* 2000; Biasi *et al.*, 2005), which is likely to affect microbial community. We observed changes in bacterial community following warming treatment (+3°C) over three years (Kim,



**Fig. 1.** Non-metric multidimensional scaling (NMS) ordination of bacterial 16S rRNA genes in control (  $\triangle$  ) and warming (  $\blacktriangle$  ) treatments. The percent variation explained by each axis is shown in parentheses.



**Fig. 2.** The ratio of methanogens to eubacteria based on abundance with depth at warming and control treatments (2-tails).

2007) (Fig. 1). The diversity and composition of nitrogen-fixing microbial communities changed with warming (1-3°C) in an arctic ecosystem (Deslippe *et al.*, 2005). However, increased temperatures did not change methanogens in a rice field soil (Chin *et al.*, 1999) and a bog (Metje and Frezel, 2005). Warming relatively increased the relative contribution of fungi to soil microbial community (Thormann *et al.*, 2004), whereas warming decreased that of methanogens to eubacterial community in peatlands (Kim, 2007) (Fig. 2).

## V. SUMMARY AND CONCLUDING REMARKS

In order to better understand and predict more accurately future C dynamics in wetlands, we suggest several future directions of research. First, the combined effects of climate changes should be considered. Interactions of elevated CO<sub>2</sub>, drought, and warming may be different from separate effect. For example, elevated CO<sub>2</sub> treatment increased the temperature sensitivity of soil CO<sub>2</sub> emissions through an increase in substrate availability (Tingey *et al.*, 2006). In contrast, rising temperature down-regulates CH<sub>4</sub> emissions via an increased O<sub>2</sub> availability caused by droughts.

Secondly, effects of climatic changes on wetlands should be considered in various geographical regions, because wetlands located in different latitudes and locations exhibit substantial differences in geology, litter chemistry, carbon pool size, and future scenario of climate change. In fact, the effects of elevated CO<sub>2</sub> on CH<sub>4</sub> emissions have been reported to be slighter in northern peatlands (Saarnio and Silvola, 1999; Saarnio *et al.*, 2000; Kang *et al.*, 2001) compared to those in temperate or subtropical wetlands. Furthermore, sensitivity to rainfall patterns differed in northern and southern Europe (Sowerby *et al.*, 2005), depending on

previous exposure to moisture stress (Fierer *et al.*, 2003). Another example is differences in litter chemistry (Thormann *et al.*, 2004) and labile carbon pools (Eliasson *et al.*, 2005), which affect sensitivity of SOM to warming effects (Knorr *et al.*, 2005).

Lastly, the relationship between microbial community structure and their ecological functions should be interpreted with caution, because differences in microbial communities may lead to no changes in microbial functions. Measuring whole microbial community does not represent microbial groups involved in critical processes measured. Therefore, understanding of functional groups like denitrifiers, methanogens, and sulphate reducing bacteria subjected by climate changes would be essential to predict wetland C cycling.

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## 적 요

대기 중 이산화탄소 농도 및 온도 증가와 강수 패턴 변화에 따른 가뭄 정도 및 횡수의 변화는 습지에서 발생하는 온실가스의 양에 영향을 미칠 수 있다. 습지에 존재하는 다양한 미생물 군집(탈질세균 및 메탄생성세균)이 온실가스 생성에 있어 중요한 역할을 담당한다. 본 논문은 지금까지 전지구적 기후변화가 습지에서의 온실가스 발생과 관련 미생물 군집에 미치는 영향에 관한 다양한 연구를 정리하는 데 그 목적이 있다. 대기 중 이산화탄소 농도와 기온 증가는 일반적으로 온실가스 생성을 증가시켰다. 반면, 가뭄의 영향은 기체 종류와 가뭄 정도에 따라 다양한 결과가 보고되었다. 기후변화에 따른 미생물 군집의 변화는 습지 시스템에서 보고된 연구의 부족으로 인해 특정한 결론을 도출할 수 없었다. 본 총설은 습지에서 미생물을 매개로 한 반응을 연구함에 있어 관련 미생물 군집구조의 특성을 파악하고, 다양한 환경인자에 대한 그들의 반응을 알아내는 것과 미생물 반응과 군집구조간의 상

관 관계를 도출하는 것의 중요성을 제안한다. 이는 향후 전지구적 기후 변화가 습지의 생태학적 기능에 미칠 영향을 더 잘 이해하고 예측하는데 있어 매우 중요할 것이라 사료된다.

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