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Environmental Controls over Methane Flux from Ecosystems and the Potential for Feedbacks with Climatic Change

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Environmental Controls over Methane Flux from Ecosystems and the Potential for Feedbacks with Climatic Change

by

Margaret Susan Torn

B.S. (University of California, Berkeley) 1984
M.S. (University of California, Berkeley) 1990

A dissertation submitted in partial satisfaction of the
requirements for the degree of
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Committee in Charge:

Professor John Harte, Co-Chair
Professor F. Stuart Chapin, III, Co-chair
Professor John P. Holdren
Professor Pamela Matson

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Abstract

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Margaret Susan Torn

Doctor of Philosophy in Energy and Resources
University of California at Berkeley
Professor John Harte, Co-Chair
Professor F. Stuart Chapin, III, Co-Chair

Ecosystems are the largest source of atmospheric methane, an important greenhouse gas whose atmospheric concentration is increasing 1% annually. My dissertation research on the environmental controls over methane flux suggests that there is the potential for significant feedback between climatic change and methane flux from ecosystems.

From 1991 to 1993, I conducted a variety of field experiments in Alaskan tundra, California annual grasslands, and Colorado montane meadow, measuring methane flux with static chambers. Emission rates from the Alaskan wet tundra averaged 52 mg CH_4 m^{-2} d^{-1} and from California pond margin averaged 38 mg CH_4 m^{-2} d^{-1}. Methane uptake in the Colorado montane meadow averaged -1.2 mg CH_4 m^{-2} d^{-1} and in the California grassland averaged -0.7 mg CH_4 m^{-2} d^{-1}.

Over the annual cycle and across landscape gradients, methane flux was positively correlated with soil moisture and temperature at all three sites. Moisture was the dominant factor, since unsaturated soils took up methane (small negative flux) while saturated soils emitted methane (large positive flux). The response of flux to changes in water level was rapid and direct, rather than occurring via moisture-induced changes in vegetation. Plants

did provide an important pathway for methane emissions, however, by allowing methane to bypass the zone of methane oxidation at the soil or water surface. In the grassland, soil carbon and nitrogen explained 97% of the spatial variation in annually-averaged uptake rates, independent of sheep-grazing.

My research showed that emissions and uptake respond differently to changes in soil micro-climate. An increase in moisture increased emissions but decreased uptake (with an important exception in very dry soils, when further drying decreased uptake rates). Emissions increased exponentially with temperature while uptake showed a weak response to temperature.

A model that takes into account both the differential effect of temperature on emissions and uptake, and the fact that net emissions are the balance of production and consumption, predicts three times more change in global ecosystem emissions in response to a 10°C warming than does a model that ignores these two features and includes only net methane release. Therefore, the magnitude of the feedback generated between methane flux from ecosystems and climate is probably much greater than would be estimated by traditional methane-cycle models, which ignore these two features.

John Harte 8/31/94

Dissertation Co-chair, Professor John Harte Date

F Stuart Chapin, III 8/31/94

Dissertation Co-chair, F. Stuart Chapin, III Date

dedicated to my nieces,
Jessie, Katie, and Shawna
and all the great things they will do

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These have been good years for me. For this, I have many people, places, mysteries, and events to thank, especially those that inspired me to care about our environment and to draw intangible sustenance from it.

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Let me know if I can return the favor some day.

AUTHOR'S PREFACE

A dissertation has two kinds of readers. The first are those who advised or contributed to the research described herein, and who have some expertise in the subject. The second kind of readers are friends and family of the author who graciously open the pages to see what has been occupying the candidate, and who have little or no relevant background to the topic. This preface is a small glossary for the latter, uninitiated reader. Thank you for reading! In the following paragraphs I introduce many of the terms that I used in writing about methane in soil, to try to make the dissertation more comprehensible (sorry I couldn't also make it more exciting).

Methane (CH_4) is formed when dead plant material is decomposed without available oxygen (anaerobically). **Anaerobic decomposition** occurs in the guts of cattle, for example, and also in the **saturated** or flooded soils of wetlands, rice paddies, and landfills. The decomposition process is catalyzed by bacteria (single-celled organisms), which in the case of soil are known as **microbes**. The microbes that catalyze methane formation in soil are known as **methanogens**. Methanogens get energy and cell-building material from methanogenesis, just as humans do from digesting food. Methane formation usually referred to as **methane production** or **methanogenesis**. Methane flux from soil to the atmosphere is called **methane emission, methane release**, or **net methane production**. Methane emissions from soils are a **source** of atmospheric methane.

Methane is oxidized to carbon dioxide by microbes called **methanotrophs**. The process requires abundant oxygen. Methanotrophs get energy from the process, like burning natural gas for energy, and certain types of microbes may also get cell-building material. I refer to methane oxidation as **methane consumption** or, rarely, as methylotrophy. Methane flux from the atmosphere to the soil is called **methane uptake** or **net methane consumption**. Methane uptake by soils is a **sink** of atmospheric methane.

Flux is a term that I use a lot. It's meaning is pretty intuitive. It means the flow of something over/through a given area. For example, the flux of methane from a wetland can be described as the mass of methane that flows to the atmosphere from a square meter of wetland, per day. These units would be abbreviated as: mg CH_4 m^{-2} d^{-1} (milligrams of methane per meter-squared per day). The flux of methane upwards from soil to atmosphere is the emission rate. The flux of methane downwards into the soil is the uptake rate.

CHAPTER 1

INTRODUCTION

Overview

Methane is one of the most important greenhouse gases. Already responsible for 20% of the atmosphere's increase in IR-absorptive capacity above pre-industrial levels, atmospheric methane concentrations are growing at 1% per year (Blake and Rowland, 1988; Steele, et al., 1992). Although soils are known to be the single most important source of atmospheric methane (contributing over 200 Tg/yr), there is substantial uncertainty about the global methane budget, and even more uncertainty about what environmental factors control methane flux (Cicerone and Oremland, 1988). Current uncertainties hinder scientists' ability to predict how much and how fast atmospheric methane concentrations will change in the next century, and thus how climate will be affected. In particular, the ecosystem sources and sinks of methane, which are the most directly controlled by climate of the various budget components, have not been adequately characterized in terms of their current fluxes or response to climate change.

My dissertation investigates the environmental controls over methane flux from soils and the potential for feedbacks between climate and methane flux. In addition, it provides field data on methane fluxes in two ecosystem-types that have not previously been studied, montane meadow and annual grassland. By examining the influence of various environmental factors on soil methane processes I try to elucidate the sensitivity of these processes to environmental changes. The results contribute to our understanding of what controls methane flux from natural soils, and to the modeling of the linkages between soil and the atmosphere. These are essential steps in predicting global atmospheric change.

In my dissertation research I conducted a field investigation of the environmental factors that control methane flux from soils at sites in Alaska, California, and Colorado. I used experimental manipulations of nutrients and vegetation (Alaska; Chapter 2), incident infra-red radiation (Colorado; Chapter 3), and nutrients and grazing (California; Chapter 4) as well as topographic gradients of soil temperature and moisture at each site. In Chapter 5, I summarize the results from these three sites and synthesize my findings on environmental controls over methane flux. For a description of some important terms in the methane cycle, see the Author's Preface.

Background

Until the present millennium, the history of the earth's atmosphere has been the history of geologic eras, the development of the biosphere, and solar influences. In the past few centuries, however, the history of the earth's atmosphere has become much more a record of the technologies and subsistence patterns of human beings. Among the more noted changes in the composition of the atmosphere have been increases in nitrous oxide beginning in the early 1700s (sources not determined), methane in the early 1800s (rice paddies, grazing, and fossil fuels), carbon dioxide beginning in the 1800s (fossil fuels), and carbon-14 after the 1940s (atomic bomb testing).

Although methane concentrations did oscillate significantly during the last two hundred thousand years--with climatic and ecological consequences--the rise beginning in the early 1700s was unprecedented in its speed and the concentration attained (Figures 1 and 2; Blunier, et al., 1993; Chappellaz, et al., 1990; Stauffer, et al., 1985). Global average methane concentrations now exceed 1700 ppb, well over twice the peak level of the past two hundred thousand years. For the last three decades, methane concentrations have been increasing at around 1% per year (Blake and Rowland, 1988; Khalil and Rasmussen, 1981; Khalil, et al., 1989; Steele, et al., 1992).

The rapid increase in methane has been of particular to concern to environmental scientists because of methane's importance in the energetic and chemical properties of the atmosphere. Methane is an effective greenhouse gas, as are its decay products, carbon dioxide and water vapor. It is second only to carbon dioxide as a contributor to increases in global radiative forcing over the past 100 years (Figures 3 and 4). The major sink of atmospheric methane is oxidation by the hydroxyl radical (OH^-) to CO_2 in the troposphere. In the stratosphere, methane breakdown produces hydrogen which binds chlorine and reduces ozone depletion, and water vapor which warms the stratosphere (Cicerone and Oremland, 1988). Methane's role as a greenhouse gas is emphasized in this dissertation because of the potential for feedback if climate, in turn, influences methane flux to the atmosphere. The potential feedback between ecosystem-methane flux and climate is discussed below.

Soon after it was recognized that methane concentrations were increasing (e.g., by Khalil and Rasmussen, 1981), researchers began to construct a global budget for methane (Cicerone and Oremland, 1988; Hameed and Cess, 1983; Houghton, et al., 1990; Khalil and Rasmussen, 1990). The basic purpose of the methane budget is to quantify the current sources and sinks of methane. The most comprehensive and widely quoted budgets were those compiled by Cicerone and Oremland (1988, Table 1) and Houghton et al. (1990). Both the sink and source terms have been slightly revised in the updated budget of the Intergovernmental Panel on Climate Change (Houghton et al, 1992; Table 2). Soils are still considered the single largest source of methane, with wetlands and rice paddies accounting for over a third of all emissions.

Initially, the only sink for methane included in the budget was oxidation in the atmosphere by hydroxyl radicals (OH^-; e.g., Hameed and Cess, 1983). When soil-uptake of atmospheric methane was first included in the budget, the other budget terms were not adjusted in response to adding a new sink term (i.e., it was not mathematically integrated). This meant that the methane budgets of Cicerone and Oremland (1988) and Houghton et al. (1990) balanced when the soil sink was added, but the budget must be out of balance (sources must be greater than sinks) to explain the observed increase in atmospheric methane. In other words, these budgets predicted the observed annual increase in atmospheric methane only by ignoring the soil sink or by assuming a large unidentified source of methane. In the last 6 years, the volume of literature documenting the soil sink of methane has tripled and this sink has been integrated into the most recent budgets (Houghton, et al., 1992; Reeburgh, et al., 1992). At the same time, the OH^- sink has been revised downward by about 20%[1]. This gives a smaller atmospheric sink term and a longer lifetime for methane in the atmosphere. The methane budget still has large uncertainties and is likely to continue to be revised in response to new empirical data and modeling efforts.

Research Literature and Theory

The methane budget is helpful for understanding why concentrations are increasing, and also for identifying sources that might practically be controlled as a way of reducing global emissions. It does not explain, however, why the different terms have the magnitude they do, and it does not directly address how the strength of sources or sinks have changed in the past, or might change in the future, in response to climate change or other environmental perturbations. While this is true for all components of the methane budget, my focus, in the rest of this introduction and in the dissertation, is solely on the

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[1] The quantity of atmospheric methane oxidized by OH- is calculated from estimates of the atmospheric concentration of these gases and a rate constant for the oxidation reaction. Recent experiments by Vaghijiani and Ravishankara (1991) found that the rate constant for methane oxidation by OH- is 25% slower than previously estimated.

ecosystem and soil components. Understanding the role of soil and ecosystems in the methane cycle is critical to understanding the current budget as well as to understanding past and potential future changes in atmospheric methane concentrations. As described above, ecosystems are the major source of atmospheric methane and, after oxidation by OH^-, the most important sink as well. With respect to ecosystems and the global methane cycle, three kinds of uncertainties are recognized in this dissertation: the magnitude of current sources and sinks of methane, the influence of environmental factors over the seasonal and long-term behavior of these terms, and the appropriate framework for synthesizing this information into an understanding of past and potential changes in the methane cycle. A discussion of these three areas, and how my research relates to them, follows.

Source and sink terms in the budget

The ecosystem-sources of methane in global budgets are estimated from a very limited number of field surveys[2]. The annual contribution from flooded ecosystems and rice paddies has been estimated as the product of the survey values (e.g., expressed as mg C m^{-2} d^{-1}), the areal extent of that ecosystem type, and the number of active days per year. The length of the active season has been only crudely approximated since year-round or full-season measurements have been made in only a handful of sites. Furthermore, with few exceptions, measurements in rice paddies and seasonally-flooded ecosystems have been made only when these areas were saturated and producing methane. Gas fluxes during the dry season, when methane may be consumed by these soils, have been largely overlooked. Areal extent has been estimated from maps by Matthews (1983)

---

[2] Most of the other source terms in the global budgets are also an extrapolation from a relatively small number of site-specific or technology-specific measurements. The methane flux from landfills, livestock grazing, biomass burning, and fossil fuel industries is estimated from a few field samples and literature on area (e.g., of landfill) or activity (e.g., of street paving). Additional information on natural gas emissions and other fossil fuel sources is gathered from industry statistics on lost and leaked product.

and others. Large discrepancies between different researchers' estimates of the methane contribution of a vegetation type often result from classifying a survey site as the wrong vegetation type, measuring at a non-typical site, or using a different total area for that type[3].

Environmental factors controlling flux rates

To quantify the current distribution of sources and sinks globally, scientists need to characterize the relationships between environmental factors, such as soil texture and climate, and flux rates. In addition, to have a better sense of past and potential changes in methane fluxes, we need to understand how flux rates respond to natural and human-caused changes in environmental conditions. In my dissertation, I have given emphasis to the latter question, and in particular, the potential impact of climatic change on methane fluxes.

The existence and potential importance of feedback between natural methane flux and climate is suggested by the close correlation over geologic time between atmospheric methane concentrations and surface temperature (Blunier, et al., 1993; Chappellaz, et al., 1990; Stauffer, et al., 1985). The correlation is beautifully illustrated by the figure from Chappellaz et al. (1990) of methane concentrations and air temperatures over the past 160,000 years based on analysis of the Vostok ice core from Antarctica (Figure 1). The Vostok data are not resolved finely enough to tell whether the curve of methane lags or leads the temperature curve. New data from a core from Greenland, where ice accumulates faster than in Antarctica, should yield a finer, albeit not definitive, analysis of the lead and lag (Blunier, et al., 1993).

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[3] The budget totals have been corroborated by isotope analysis and analytical models that incorporate data from atmospheric monitoring stations and field surveys (Fung, et al., 1991; Khalil and Rasmussen, 1990; Quay, et al., 1991; Tyler, 1991; Tyler, et al., 1988).

One means of studying the mechanisms behind the historical climate:methane correlation is to examine the contemporary influence of climate on methane flux from ecosystems. The climate factors emphasized in this introduction, and by most methane research to date, are soil moisture and temperature. Here I provide a brief summary of the literature. A more detailed discussion appears in the chapters that follow. When my own research results bear on a topic, I have noted the relevant chapter in parentheses. Although not covered here, climate also affects methane fluxes through disturbance regimes (such as fire and hurricanes; e.g., Steudler, et al., 1991; Tate and Striegl, 1993) and the productivity and distribution of ecosystems (e.g., Matthews and Fung, 1987; Chapters 2 and 4).

At the landscape scale, soil moisture is consistently identified as the major determinant of flux rates. This has been a working assumption for the past two decades; saturated ecosystems, such as wetlands and rice paddies, have been counted as high-emission areas, while arid and mesic ecosystems, such as forests, have been categorized as sinks or neutral sites. Survey data confirm these broad generalizations. Within either of these moisture classes--saturated and unsaturated--the effect of moisture is still positive (increasing moisture correlated with higher emission rates) although less pronounced. For example, the depth of the water table below a bog surface is negatively correlated with emission rates (Moore and Roulet, 1993; Roulet, 1991). In sites of methane uptake (arid and mesic ecosystems), soil moisture is usually found to be negatively correlated with uptake (Adamsen and King, 1993).

To a first approximation, the implication for climate feedbacks is that increases in soil moisture would increase the net global flux to the atmosphere by increasing emissions and by decreasing the soil sink. At a more fine scale, modeling trends in emissions in response to changes in moisture requires making assumptions about the importance of the direct effect of moisture on emissions versus the indirect effects of moisture on vegetation, detritus, or microbial communities. There could be considerable time lags between the creation of inundated areas and the onset of emissions, if, for example, aquatic plants (which are important for transporting methane from sediment to atmosphere) are slow to migrate to newly inundated areas. Some insight into the timing of response can be gained by studying ecosystems with seasonal or inter-annual cycles in their moisture regimes (Chapter 4).

A layer of complication is also present in the flux:moisture relationship for the sink term. Specifically, it may not always be correct to assume that reducing soil moisture increases uptake rates. Two different field studies have observed that uptake rates reached their minimum when soils were driest, with rates increasing after moderate rainfall (Mosier, et al., 1991; Striegl, et al., 1992; Whalen, et al., 1990). Neither of these studies presented detailed data on soil moisture and uptake, or statistical analyses of their results. Nevertheless, these observations raise the possibility that methane consumption is related to moisture in a non-linear fashion (e.g., parabolic) and that the feedback to soil drying may not be negative under all conditions or in all soils (Chapter 3).

Temperature is also an important factor in flux rates. Research on emissions consistently reports that increased temperatures are correlated with increased emission rates (Bartlett, et al., 1989; Bartlett, et al., 1988; Bartlett and Harriss, 1993; Dunfield, et al., 1993; King and Adamsen, 1992; Valentine, et al., 1994; Westerman, 1993). In nearly all field studies surveyed the observed temperature effect was probably confounded by effects of season and moisture, since the largest changes in temperatures were due to seasonal cycles or landscape gradients (Bartlett, et al., 1989). In corroboration of the field results, however, laboratory incubations of soil cores, which eliminate most confounding effects, have found a similar magnitude of temperature response. The range of Q_{10} values (the increase in emissions per 10^{o}C increase; i.e., if emissions doubled due to a 10^{o}C warming, the Q_{10} would be 2) is 1.7-4.7 (Conrad, 1989; Schimel, et al., 1993; Valentine, et al., 1994). The implication for climate change is that emissions may generate positive feedback, as warming would lead to more methane release (Chapter 4).

For methane uptake, most field studies do not find a significant influence of temperature (Chapter 3; Schimel, et al., 1993; Tate and Striegl, 1993; Valentine, et al., 1993). In contrast, several--although not all--laboratory experiments do find a temperature response. The explanation may be that methane uptake in the field is usually diffusion-limited (Bartlett and Harriss, 1993; Striegl, 1993) and therefore the temperature response is not operational. Overall, net methane consumption appears neutral with respect to temperature change.

These results for soil temperature and moisture give evidence suggesting that methane fluxes from unmanaged soils will respond to changes in climate of the magnitude predicted for global warming by, for example, Maxwell (1992) and Hansen (1988). In fact, of the major components of the methane budget, soil methane may be the most directly connected to climatic factors[4].

Even without global warming, environmental changes are already affecting the methane cycle. The rapid increase in atmospheric methane concentrations that began two centuries ago reflects in some measure the cumulative impact of incremental land use and development. The expansion of rice cultivation in the last 100 years is certainly implicated in the rising concentration of methane during that time. However, because there has been no coherent research program on the impacts of ecological change, such as grazing, deforestation, or plant invasions on methane flux--e.g., focused on all the activities in a

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[4] Climatic change will have an indirect impact on methane fluxes from grazing, landfills, biomass burning, and fossil fuel use, because the direct impacts will be partially mediated by human responses to global change and many other social actions.

given region--there is as yet no evaluation of how fluxes from unmanaged soils might have changed in the recent past[5].

The existing research has shown, however, that ecosystem-methane fluxes are affected by many different kinds of human activities, including forest-clearing to pastures (Keller, et al., 1990), irrigating rice fields (Neue, et al., 1990), fertilization and grazing (Mosier, et al., 1991; Steudler, et al., 1989), and acid rain (Yavitt, et al., 1993). The mechanisms linking these activities to altered emissions or uptake are not well-characterized. Observational data and a handful of controlled experiments have identified compaction, nitrogen availability, enhanced plant productivity, and pH as important for the activities mentioned. Of these, the impacts of nitrogen content, fertilization, and grazing are subjects of my research (Chapters 2 and 4). My purpose here is to highlight the connection between human activities and methane flux.

With regard to both the climatic and ecological factors affecting methane flux, field manipulations are needed to examine the relative impact of these factors, which are often confounded in correlations developed solely from seasonal or geographic patterns.

A framework for understanding the role of ecosystems in the global methane cycle

In addition to research on the influence of individual environmental factors on methane processes, a framework is needed to extrapolate and analyze these influences on a global scale. Such a framework should relate three factors, methane production, consumption, and transport--and the factors that limit them--to the net flux from ecosystems to the atmosphere. My research considers the factors that influence the individual processes as well as the balance between production and consumption in a given system.

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[5] Khalil and others at the Oregon Graduate Institute are constructing a historical methane budget for the People's Republic of China (1949-present), emphasizing rice paddies.

The balance between methane production and consumption in the soil is a potentially critical control-mechanism over net flux, one that has only begun to be researched. The saturated, carbon-rich sediments of lakes and coastal waters produce extensive methane, yet very little methane escapes to the atmosphere because a large fraction is oxidized in the aerated zone near the water's surface (Galchenko, et al., 1989; King, 1990) and in sediments (Alperin and Reeburgh, 1985). A parallel mechanism may control methane flux from soils. Most saturated, methane-producing soil has a shallow, aerobic surface-layer in which methane consumption may take place. The importance of this mechanism, however, cannot be deduced from measurements of net methane flux at the soil surface[6]. In landfills, it has been documented that the surface soil acts as a filter to the methane produced below, effectively limiting the release of methane to the atmosphere (Whalen, et al., 1990). When I began my research, no one had estimated the atmospheric importance of soils that act as a filter by oxidizing methane that was produced lower in the soil. Recently, however, Reeburgh et al. (1992) estimated the fraction of methane produced that gets oxidized by microbes before it reaches the atmosphere or scavenged from the atmosphere, for different ecosystems and methane sources (Table 3). They estimate that as much as half of all methane produced is oxidized before release to the atmosphere. My dissertation research is not focused on improving upon these estimates, but rather on the implications of this "gross flux model"--in which the net flux to the atmosphere is seen as the difference of methane production and consumption--for human impact on the global methane cycle. The gross fluxes in this model can be vertically layered in the same soil or they can be spatially separate. Within that focus, my dissertation research has two goals: to estimate methane fluxes in different ecosystems and to characterize the influence of certain environmental factors on methane production and consumption at those sites.

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[6] For example, the oxidation of atmospheric methane by soils, roughly estimated to be 10% of the total methane sink, refers only to the net surface flux (Born, et al., 1990).

The underlying hypothesis of my research can be summarized as follows: because the microbial populations responsible for methane production and consumption are active in very different soil environments and have very different metabolic pathways, they respond differently to the same climatic or ecological changes (Yavitt et al. 1990). Thus, the rates of production and consumption of methane by soil should respond differently to the same environmental change. If true, this hypothesis suggests that pollution, changes in land use, or climate change could alter net methane fluxes by affecting sinks and sources differentially. Thus, soils that currently have high gross fluxes but a low net flux could experience a dramatic change in net flux with ecological or climatic change. The global balance of methane fluxes from soils may be altered much more than expected since regions that currently do not show a high net flux may contain areas that are sources and areas that are sinks of methane, or a single area may alternate seasonally between methane uptake and methane emissions. This general hypothesis is derived from consideration of the mechanisms of methane production and consumption. Soils contain populations of micro-organisms that produce methane and populations that oxidize methane. These populations are active in very different environments. Methanogens (methane producers) are found in saturated zones that are penetrated by plant roots or have accumulated organic matter. These microbes require anaerobic conditions and an organic substrate that has been "pre-digested" to very simple compounds by other microbes. Carbon in anaerobic environments is decomposed in a multi-step process leading to methanogenesis. Other microbes, such as fermenting bacteria or homoacetogens, are necessary to provide methanogens with organic substrates they can use. In contrast, methane oxidizers require aerobic conditions and are found near the soil surface. One class of methane oxidizers are obligate methanotrophs. It has been suggested that these are found where methane is produced during some period of the year. Nitrifying bacteria make up the second class of methane consumers. It is thought that nitrifying bacteria prefer ammonium as a substrate but that their enzymes are non-specific; in other words, they manufacture a chemical (enzyme) to catalyze oxidation of ammonium to nitrate, but if that enzyme encounters a methane molecule it will catalyze oxidation of the methane to carbon dioxide. It is likely that the distribution of nitrifiers is linked to an active nitrogen cycle, rather than to the regular presence of the methane substrate.

Research Goals and Questions

My field research has two main goals for contributing to understanding the methane cycle: (1) to measure current methane fluxes in several ecosystems and (2) to characterize the influence of certain environmental factors on methane flux at those sites. I analyze the results of my research in light of the differential controls hypothesis and the development of dynamic models of the global methane cycle.

I worked at three sites in the western United States: California grassland, Colorado montane rangeland, and Alaskan tundra. The three research stations used for these multi-year analyses contain ecosystem types of widespread global distribution. In addition, these are places where I could study the role of many factors in influencing soil-methane processes--including soil moisture, temperature, and nitrogen availability, sheep grazing, biomass, plant species, and soil organic matter.

Each of these sites presented an opportunity to look at a different set of environmental factors, due to the existence of long-term manipulations and unique environmental conditions. Use of field manipulations enabled me to examine the relative impact of several factors that are often confounded in correlations developed solely from seasonal or geographic patterns. In addition, each site had topographic gradients of moisture and vegetation. Accordingly, my research at each location was tailored to the opportunities presented by each, with different hypotheses concerning the environmental controls over methane flux to be addressed at each site.

I applied the same basic methodology at each field site. I measured methane flux between the soil and atmosphere with small chambers, and sampled methane concentration in the soil with metal "straws". At each site I characterized ancillary ecosystem properties and on each sampling day I measured soil temperature and moisture. The timing of measurements, for example every 4 hours over 28 hours or once each season over a year and a half, was tailored to address site-specific questions. Next I outline my research at each site and how it addresses the two goals described above.

Arctic Tundra, Alaska

My research from Alaska (Chapter 2) was the first experimental study published on the environmental controls over methane flux in the Arctic. The mechanisms controlling methane flux from arctic tundra are particularly important to understand, since tundra is estimated to produce a third of all soil methane (Cicerone and Oremland 1988) and climate change is expected to be most pronounced in the polar regions (Hansen et al. 1988). The research in Chapter 2 addressed this gap using field experiments to investigate the influence of nutrient availability, plant biomass, and photosynthetic rate. Specifically, Toolik Lake Field Station had a long-term nutrient manipulation and a topographic gradient of vegetation types associated with high methane-emission rates. Results of the nutrient additions, on vegetation and soil properties, were described by Chapin and Shaver (Chapin and Shaver, 1985; Shaver and Chapin, 1986). In addition, my work in Alaska contributes to a current revision of the estimate of methane flux from tundra soils.

The questions I address with my research in Alaska are:

1. How does net methane flux change across a topographic and physiognomic gradient in Alaskan tundra?
2. How do soil temperature and soil moisture influence rates of methane flux across this gradient?

3. Does nitrogen fertilization affect methane flux from tussock tundra?
4. What is the role of plants in flux from tussock tundra?
5. What is the role of plants in flux from wet-meadow tundra (arctic wetlands)?

Montane Meadow, Colorado

My research in Colorado offers the first analysis of methane fluxes from a montane meadow ecosystem[7]. This was an excellent site to investigate the influence of soil microclimate on methane flux. Because soil-moisture conditions vary from saturated during snowmelt to less than 10% moisture in mid-summer, the meadow is a good site to investigate the effect of soil moisture on methane flux. In addition, the Colorado research site has a meadow-warming experiment in which the soils are warmed by over-head infra-red lamps. The warming also manipulates soil moisture, indirectly. There is only one other soil-warming field experiment in which methane fluxes are being measured (Peterjohn, et al., 1993), but no data have yet been published from it. Located in a hardwood forest in Massachusetts, it uses heating tapes placed under the soil.

The questions I address with my research in Colorado are:

1. Is the montane meadow a sink or source of atmospheric methane, and what are flux rates from this system?
2. How do soil temperature and soil moisture influence rates of methane flux from the meadow?
3. Do soil temperature and moisture have the same influence over flux at different time scales (comparing a diurnal cycle with seasonal effects)?
4. Does the warming treatment effect methane flux, and if so, is the effect independent of changes in soil temperature and moisture.

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[7] Mosier et al.(1993) recently published survey data from a sub-alpine meadow, a similar ecosystem except that it has a cooler, moister summer and no sagebrush (artemisia).

5. What is the role of plants in flux (Do plant species or plant biomass have an effect on methane flux from the montane meadow)?
6. Does substrate transport limit methane flux at this site and is it the only limiting factor?

Annual Grassland-Pond System, California

My research in California is the first analysis of methane fluxes from annual grassland. The U.C. Hopland Research and Extension Center, in oak savanna, has maintained nitrogen fertilization and grazing manipulations for the past 40 years. A pond surrounded by annual and perennial species provides a topographic gradient of positive- to negative-flux soils. To investigate the relationship between soil organic content and soil nitrogen content and methane uptake, I measured methane uptake in grasslands across a natural gradient in soil carbon and nitrogen content as well as across a combination of long-term fertilization and sheep-grazing treatments manipulations.

The questions I address with my research in California are:

1. Is the annual grassland a sink of atmospheric methane, and what is the annual cycle of flux rates from this system?
2. Is the pond a source of atmospheric methane, and what is the annual cycle of flux rates from this system?
3. How do soil temperature and soil moisture influence rates of methane flux from these ecosystems?
4. What is the annual cycle of methane flux from the pond-grassland system, and how is it influenced by temperature and moisture?
5. How does grazing by sheep affect rates of methane flux in the grassland?
6. How are soil carbon and nitrogen content correlated with rates of methane flux in the grassland, and is this relationship different for fertilized soils?

Trail Map to the Dissertation

My dissertation research consisted of three field-based inquiries into the influence of environmental factors (temperature, moisture, grazing, soil nutrients, vegetation) on release and uptake of methane by natural ecosystems. Chapter 2 summarizes research conducted in arctic tundra at Toolik Lake, Alaska. Chapter 3 is based on my research in montane meadow at the Rocky Mountain Biological Laboratory, Colorado. Chapter 4 presents my research in annual grassland-oak savanna and a pond at the U.C. Hopland Research and Extension Center, California. In Chapter 5, I conclude by summarizing the results of my field research in light of the differential controls hypothesis.

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Table 1. Global Budget of Atmospheric Methane by Cicerone and Oremland (1988).

(a) Annual Methane Release Rates for Identified Sources

Identity	Annual Release Tg CH_4	Range Tg CH_4
Enteric fermentation (animals)	80	65-100
Natural wetlands	115	100-200
Rice paddies	110	60-170
Biomass burning	55	50-100
Termites	40	10-100
Landfills	40	30-70
Oceans	10	5-20
Freshwater	5	1-25
Methane hydrate destabilization	5?	0-100 (future)
Coal mining	35	25-45
Gas drilling, venting, transmission	45	25-50
Total	540	400-640

Natural wetlands includes forested and unforested bogs, forested and unforested swamps, tundra and alluvial formations.

Table 1. Continued

(b) Summary of Data for Atmospheric Methane Concentrations, Atmospheric Residence Time, and Budget Data

Parameter	Value
Tropospheric mole fraction, ppm	
Global average	1.68
Northern hemisphere average	1.72
Southern hemisphere average	1.64
Total atmospheric burden	3×10^{14} mol or 4.8×10^{15} g
Residence Time, years	
Computed value	9.6
Range	8.1 to 11.8
Quasi-steady state source (or sink), g/yr	
Computed value	500×10^{12}
Range	$(405 \text{ to } 595) \times 10^{12}$
Rate of increase	14 to 16 ppb/yr or $(40 \text{ to } 46) \times 10^{12}$ g/yr or 0.8 to 1.0 %/yr
Modern biogenic portion of source	70% to 90%

Global average mole fraction is for September 1987 from Blake and Rowland (1988). Residence times are from Prinn et al. (1987). Rates of increase are from Blake and Rowland. The quasi-steady state source figure is derived from 1980s data on methane amounts and residence time.

Table 2. Global Budget of Atmospheric Methane by Houghton et al. (1990).

Estimated Sources and Sinks of Methane (Tg CH_4 per year)

	Value Tg CH_4 per year	Range Tg CH_4 per year
Sources		
Natural		
Wetlands	115	100-200
Termites	20	10-50
Ocean	10	5-20
Freshwater	5	1-25
CH_4 hydrate	5	0-5
Anthropogenic		
Coal mining, natural gas, and petroleum industry	100	70-120
Rice paddies	60	20-150
Enteric fermentation	80	65-100
Animal wastes	25	20-30
Domestic sewage treatment	25	?
Landfills	30	20-70
Biomass burning	40	20-80
Sinks		
Atmospheric (tropospheric + stratospheric) removal	470	420-520
Removal by soils	30	15-45
Atmospheric increase	32	28-37

Table 3. A Global Atmospheric Methane Budget that Includes Microbially-Mediated Methane Oxidation (Reeburgh et al., 1992).

	P	**- C**	**= Net**
Source/Sink Term	Global production	Global consumption	Net Atmospheric Budget Tg CH_4
Animals	80	0	80
Natural wetlands	142	27	115
bogs/tundra	50	15	35
swamps/alluvial	92	12	80
Rice paddies	577	477	110
Biomass burning	55	0	55
Termites	44	24	40
Landfills	62	22	40
Oceans, Freshwater	85.3	75.3	10
Hydrates	10	5	5?
Coal production	35	0	35
Gas venting, flaring	10	0	10
Gas distribution leaks	48	18	30
Total Sources			500
Chemical destruction			-450
Soil consumption	40[a]	40	-10
Total Sinks		688.3	-460
Total Production	1188.3		

[a] Soil consumption of atmospheric methane is added to the gross budget as an equivalent production term.

Figure Captions

Figure 1. Atmospheric concentrations of methane and carbon dioxide over the last 160,000 years based on the Vostok ice core (Houghton, et al., 1990). The 5-7°C temperature swings between glacial and interglacial periods were partially caused by the changes in concentrations of methane and carbon dioxide (Houghton, et al., 1990).

Figure 2. Atmospheric methane concentrations from 3000 years ago to the present based on analysis of ice cores as published in (a) Cicerone and Oremland (1988); and (b) Houghton et al (1990).

Figure 3. Contributions to radiative forcing due to increases in methane and other greenhouse gases over the past 215 years. Methane contributes 15-20% in each time period, counting only the direct effect of methane (Houghton, et al., 1990).

Figure 4. Contributions to radiative forcing due to increases in methane and other anthropogenically released greenhouse gases from 1980 to 1990 (Houghton, et al., 1990).

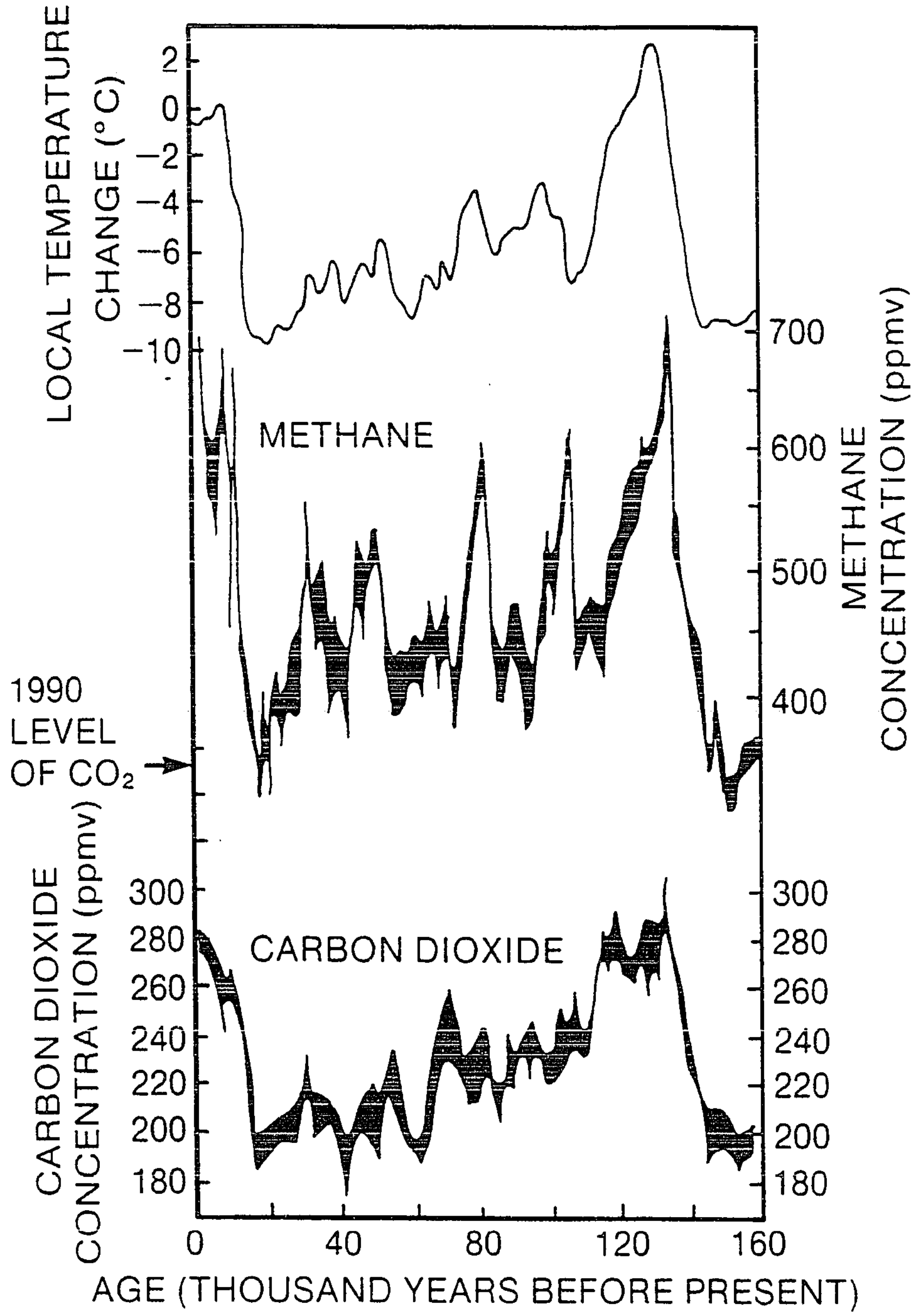
LOCAL TEMPERATURE CHANGE (°C)
2
0
−2
−4
−6
−8
−10
METHANE
700
600
500
400
METHANE CONCENTRATION (ppmv)
1990 LEVEL OF CO₂
CARBON DIOXIDE
CARBON DIOXIDE CONCENTRATION (ppmv)
300
280
260
240
220
200
180
0
40
80
120
160
AGE (THOUSAND YEARS BEFORE PRESENT)

Figure 1

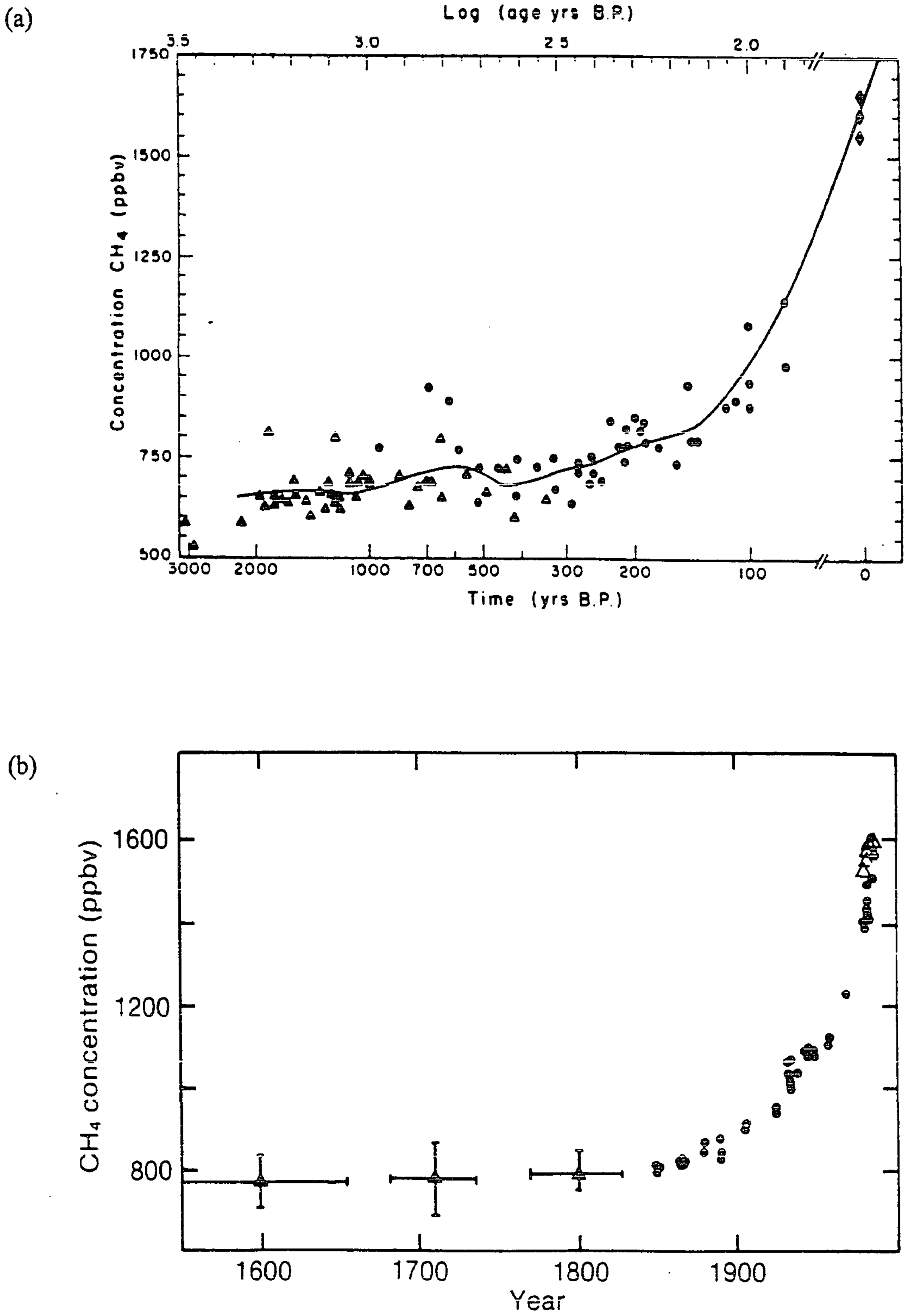
(a)
Log (age yrs B.P.)
3.5
3.0
2.5
2.0
1750
1500
1250
1000
750
500
Concentration CH$_4$ (ppbv)
3000
2000
1000
700
500
300
200
100
0
Time (yrs B.P.)
(b)
1600
1200
800
CH$_4$ concentration (ppbv)
1600
1700
1800
1900
Year

Figure 2

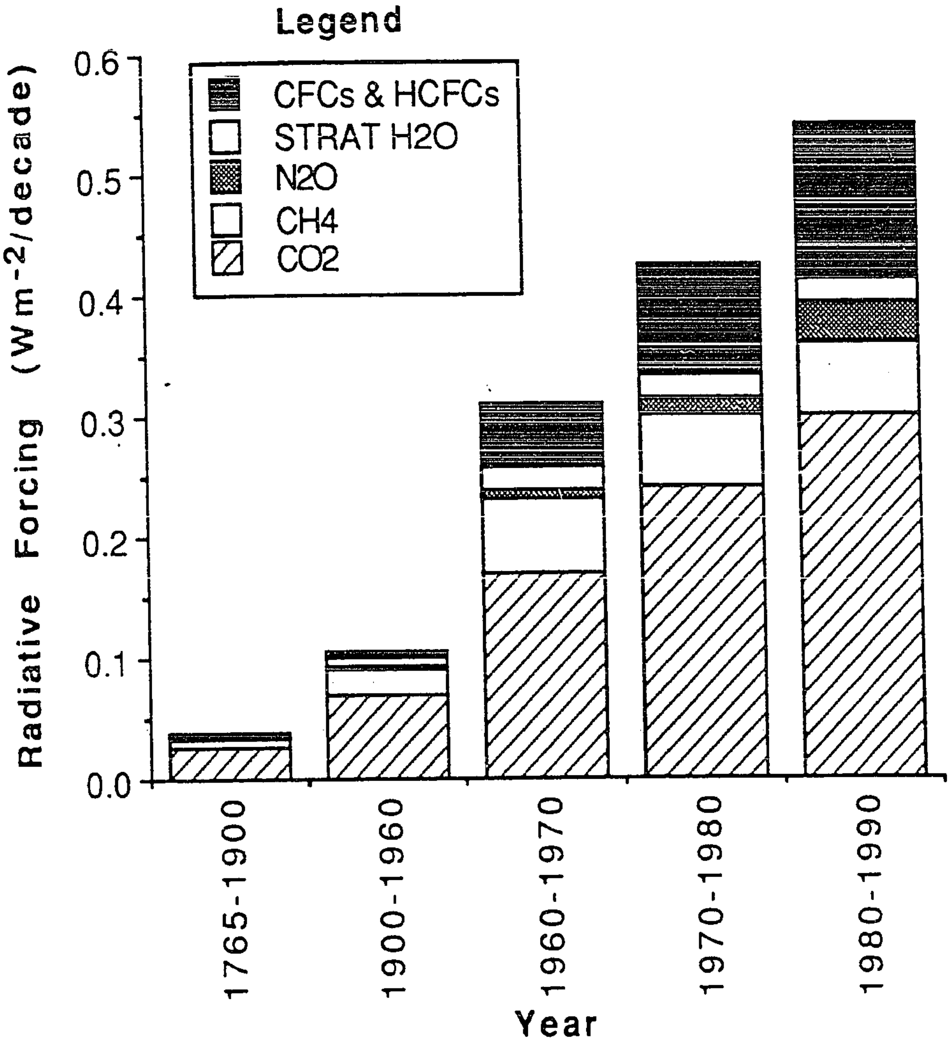
Legend
CFCs & HCFCs
STRAT H2O
N2O
CH4
CO2
Radiative Forcing (Wm-2/decade)
0.6
0.5
0.4
0.3
0.2
0.1
0.0
1765-1900
1900-1960
1960-1970
1970-1980
1980-1990
Year

Figure 3

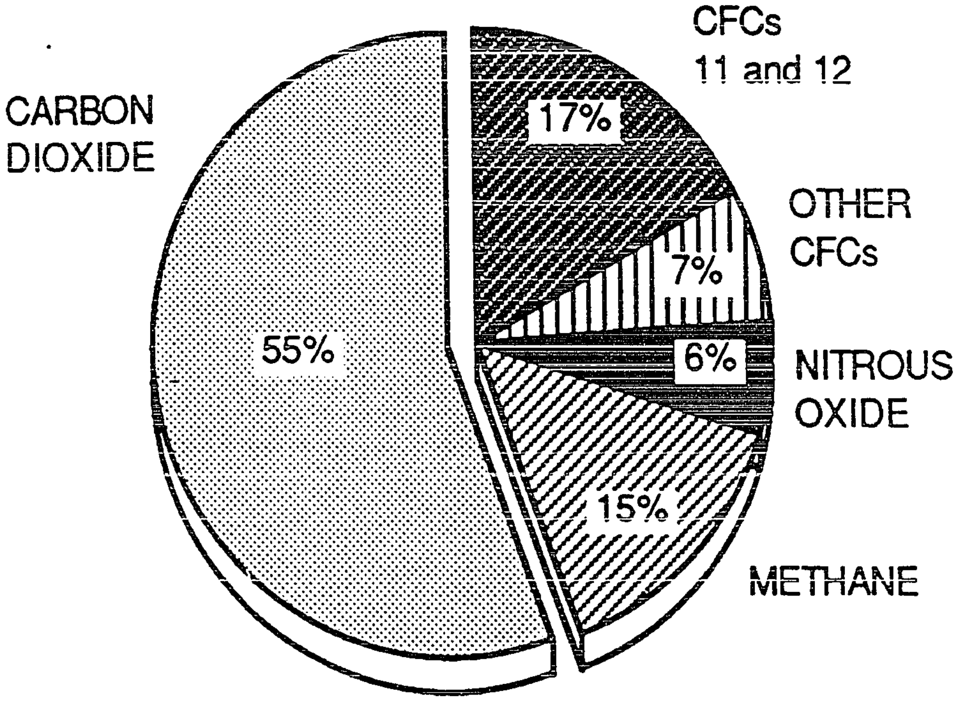
CFCs
11 and 12
17%
OTHER
CFCs
7%
6%
NITROUS
OXIDE
15%
METHANE
CARBON
DIOXIDE
55%

Figure 4

CHAPTER 2

ENVIRONMENTAL AND BIOTIC CONTROLS OVER METHANE FLUX FROM ARCTIC TUNDRA

Introductory Notes

This chapter was previously published as: Torn, M.S. and F.S. Chapin, III. 1993. Environmental and Biotic Controls over Methane Flux from Arctic Tundra. Chemosphere 26(1-4): 357-368[1].

Abstract

On the arctic slope of the Brooks Range, Alaska, we conducted a series of field experiments and observations to determine the major environmental and biotic controls over methane flux. Methane flux was more strongly influenced by long-term gradients in soil moisture and vegetation than by plant biomass, species composition, or nutrient availability. Soil temperature and moisture explained 75% of the variance in flux across the vegetation gradient. In wet meadow, where fluxes were high, plants provided the dominant transport pathway for methane, independent of photosynthesis or light levels, and allowed methane transport past the zone of surface oxidation in these submerged soils. In moist tussock tundra, where fluxes were low, soil-methane profiles indicated soil consumption of atmospheric methane, and the presence of plants had negligible influence on methane flux. The low methane fluxes that we and others have recently measured in

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moist tussock tundra are 10- to 30-fold lower than published values, leading to 20 Tg yr^{-1} discrepancy in estimates of global methane sources, equivalent to 17% of net methane flux attributed to global wetlands. These site differences in methane flux emphasize the need for a more comprehensive data base on methane fluxes from natural ecosystems if we are to better understand the current methane budget.

Introduction

Northern-latitude wetlands contribute about one-third of the global wetland emissions of methane (Matthews and Fung, 1987; Khalil and Rasmussen, 1983) and 8% of total global emissions (Cicerone and Oremland, 1988; Ehhalt and Schmidt, 1978). Atmospheric methane concentrations are increasing at close to 1% per year (Blake and Rowland, 1988; Khalil and Rasmussen, 1981). The causes of increases in this important greenhouse gas remain obscure. Over long time scales, warming periods are correlated with increasing atmospheric methane concentrations (Chappellaz et al., 1990; Stauffer et al., 1985). Despite low temperatures in the Arctic, methane fluxes from this region are high and responsive to inter-annual variation in weather conditions (Bartlett et al., 1992). Average permafrost temperatures in the Arctic have risen 4 ^{o}C in the last 50 years (Lachenbruch and Marshall, 1986), suggesting that the Arctic may already be warming.

In tropical, temperate, and boreal ecosystems, experiments and observational data have identified temperature, nitrogen fertilization, soil moisture, and land use as potentially significant controls over methane production and consumption by soils (e.g., Steudler et al., 1989; Keller et al., 1990; Whalen and Reeburgh, 1990b; Mosier et al., 1991; Witherbee, 1991; Whalen et al., 1991). Although several studies have documented geographic and seasonal patterns of methane flux in arctic and boreal tundra and have described correlations of methane flux with environmental factors (Harriss et al., 1992; Whalen and Reeburgh, 1988, 1990a), there have been no previously published experimental studies that examine environmental controls over methane flux in the Arctic. This study was undertaken to address that gap using field manipulations of nutrient availability, standing biomass, and photosynthetic rate. In addition, methane flux was measured across a natural gradient in soil moisture and vegetation. Use of field manipulations enabled us to examine the relative impact of several factors that are often confounded in correlations developed solely from seasonal or geographic patterns.

Site Description

Research was conducted in tussock tundra and wet meadow tundra at Toolik Lake Field Station (68°38' N 149°34'W, 760m elevation), on the north slope of the Brooks Range in Arctic Alaska. Methane measurements were made from July 15 to July 24, 1991. Weather during the measurements ranged from warm and sunny to cold, windy, and rainy. Thaw depths ranged from 15 to 25 cm in tussock tundra and 20 to 35 cm in wet meadow tundra. The tussock tundra community (e.g., Chapin and Shaver, 1985), also termed moist upland tundra (e.g., Whalen and Reeburgh, 1990a), is dominated by *Eriophorum vaginatum* and is similar to tussock tundra throughout Alaska, Canada, and Russia. The wet-meadow tundra site is dominated by *E. angustifolium* and *Carex aquatilis* with small amounts of *E. Scheuzcheri* and is typical of circumpolar vegetation of the Arctic Coastal Plain. Toolik Lake and environs sit on a lateral moraine of the Itkillik I glaciation (mid-Wisconsin) that became ice-free about 22,000 years ago and has developed an organic mat up to 20 cm thick (Hamilton, 1986).

Measurements were made along a topographic gradient associated with decreasing soil moisture and more mesic vegetation as distance from the lake increased, with wet-meadow tundra representing the wettest site and tussock tundra the most mesic.

Methods

Methane flux was measured using a clear, Plexiglass chamber placed over a stainless steel base (26 cm diameter). A water-filled channel on top of the base gave a gas-tight seal between base and chamber (Whalen and Reeburgh, 1988). Samples were collected in duplicate, in glass syringes, for 10-min intervals in wet-meadow tundra and 15-min intervals in tussock tundra, with fluxes calculated from incubations of 30 minutes and 45 minutes, respectively. Samples were analyzed within 24 h with a Shimadzu GC8A gas chromatograph equipped with a flame ionization detector (FID). Small wooden catwalks were used to minimize disturbance in wet meadow tundra. Analytical precision, determined by repeated analyses of ambient air samples, was greater than 3%.

We measured natural methane flux at four sites along a topographic gradient: saturated wet-meadow tundra on a lake margin with the water table near the soil surface (n=19), wet-meadow tundra with water table about 15 cm beneath the soil surface (n=2), wet tussock tundra at the base of a slope (n=8) and moist tussock tundra on a hill top (n=3). Measurements were made in late July, at time of maximum aboveground biomass and prior to autumn senescence (Shaver and Chapin, 1991).

Soil moisture of the top 10 cm of soil was determined gravimetrically for three sub-samples per chamber and expressed as percent of dry weight after oven-drying ((wet weight-dry weight)/dry weight)x100%. We refer to saturated soils if soil moisture exceeds field capacity. Air and soil temperatures were measured with a Barnant, "J"-type thermocouple thermometer by holding the shaded probe 30 cm above the ground or by inserting it 8 cm deep in soil, respectively.

The depth profile of methane in soil air of moist tussock tundra was sampled through stainless steel tubes (3 mm diameter) inserted to defined depths and capped with a rubber septum (Born et al., 1990). A 5-ml sample was collected in a glass syringe after flushing the tube with approximately 3 times the tube volume (6 ml). In saturated wet-meadow tundra, methane was extracted from soil water. For soil depths from 10 to 30 cm, lysimeters were installed overnight and methane extracted by shaking water vigorously for two minutes and then sampling headspace air. At 2 cm depth, soil water was collected with a syringe and shaken vigorously with equal part (5 ml) air. Repeated extractions with the same water sample showed that the initial extraction captures over 90% of the dissolved methane. Reported values are calculated assuming one-hundred percent extraction efficiency.

To observe the effect of darkness on methane flux in saturated wet-meadow tundra, chambers were covered with opaque black plastic for 30 minutes prior to and during the dark phase of the experiment. The same plots were used for light and dark phases (n=4) and data were analyzed using a dependent pairwise t-test. Air and soil temperatures were measured inside and outside the chamber after the experiment in three cases, and no chamber effect was detected.

Fertilization plots, established in moist tussock tundra, received annual additions of nitrogen (5 g m^{-2} N, as NH_4NO_3) and phosphorus (5 g m^{-2} P, as P_2O_5) from 1981 to 1991. The control and fertilized plots, arranged in a randomized block design (n=3), showed significant changes in plant community composition (Chapin and Shaver, 1985). In the fertilized plots, biomass of birch (*Betula nana*) and other deciduous shrubs, and cloudberry (*Rubus chamaemorus*) increased relative to growth of evergreen shrubs (e.g., *Vaccinium vitis-idaea), Carex,* and mosses (Chapin and Shaver, unpublished). Methane flux measurements were made in the moss mats of intertussock spaces. Significance was determined with an independent *t* test.

Plant removal in saturated wet-meadow tundra was accomplished by plucking out all aboveground biomass and the associated rhizomes and roots. In wet tussock tundra, only graminoids were removed. Live aboveground shoot material was oven-dried at 65°

and weighed. In wet tussock tundra, flux at five plots was measured and measured again after graminoids were removed. Two of the plucked plots were measured a second time after 24 hours. Two companion plots were measured as controls. No time effects were detected. In saturated wet-meadow tundra, flux at 6 sites was measured. Six plots were de-vegetated and compared with controls using a dependent t test. From each plot (wet-meadow n=6, tussock n=5), dry weight, and tiller number by species were determined.

To investigate the mechanisms by which plants facilitate methane flux in saturated wet-meadow tundra, we inserted 5 stainless steel straws (inner diameter=3 mm) to depths of 30, 20, and 15 cm, in place of natural vegetation, in three of the plant-removal plots. To control for disturbance effects, straws were poked into, and removed from, three de-vegetated control plots.

The potential for the soil or soil water from saturated wet-meadow tundra to oxidize methane was evaluated in the laboratory. Glass canning jars (250 ml) were filled with either saturated soil or soil water that was collected at the site of the saturated wet-meadow tundra experiments, or air (a control; n=3). Headspace methane concentrations were elevated to over 10 ppm with Scotty II 100 ppm methane standard. Headspace methane concentration equilibrated for 45 minutes, and concentration was measured over the next 5 hours. The 3-ml samples were analyzed immediately with a GC14A Shimadzu gas chromatograph with FID. This approach gives an ordinate ranking of oxidation ability, rather than an absolute measure of oxidation. If methane was produced by soil during the incubation oxidation would be underestimated.

Results

Methane flux increased across a topographic gradient in soil moisture, temperature, and vegetation (Figure 1), and was 10-fold higher in saturated wet-meadow tundra than in tussock tundra. The vegetation types surveyed shared homogeneous parent material, climate, slope, aspect, weather, and seed pool. The gradients in vegetation type and methane flux reflect a long-term soil moisture gradient that, in turn, cause changes in soil temperature (Kane et al, 1992), so we expect long-term changes in soil moisture to promote changes in vegetation and methane flux according to the pattern shown in Figure 1. Analysis of covariance, using either sample site or vegetation type as covariate, showed that methane flux responded to moisture and temperature in the same way in all sites (i.e., covariates were not significant). Using flux measurements from all sites, multiple regression showed that soil temperature and moisture together explained 75% of the variance in methane flux across all vegetation types (Equation 1).

$$\text{Flux} = -53 + 10.8\,T + 0.04\,M \qquad (1)$$

where F is flux in mg CH_4 m^{-2}; T=soil temperature (°C); and M=soil moisture (% dry weight). Significance of multiple regression is $p=0.004$. There was much less variation in temperature or moisture within than among study sites, so no significant dependence on soil temperature or moisture was detected.

Fluxes in saturated wet-meadow tundra tended to correlate with aboveground plant biomass ($r^2=0.62$, $n=9$, $p=0.06$ using a multiple regression against *C. aquatilis* and *E. angustifolium*, with *C. aquatilis* accounting for most of the effect) but did not correlate with tiller number of any or all species. Aboveground biomass ranged from 155 to 716 g m^{-2}.

Methane flux from saturated wet-meadow tundra tended to be slightly lower in controls (71.4±6.1 SE mg CH_4 m^{-2} d^{-1}) than in plots that had been darkened (100.5±18.0 SE mg CH_4 m^{-2} d^{-1}, $n=4$, $p=0.12$, paired *t* test). The failure of darkness to reduce methane flux supports earlier assertions that methane transport through plants is passive with respect to photosynthesis (Sebacher et al., 1985; Conrad, 1989). Removal of shoots of vascular plants in saturated wet-meadow tundra caused an immediate 11-fold decrease in methane flux (Figure 2; p=0.001, n=6), demonstrating that plants in wet-meadow tundra provide the dominant pathway for methane transport from the soil to the atmosphere. After a 36-hour equilibration, methane flux from wet-tundra plots with straws inserted to replace plants was higher than that from devegetated control plots but was much lower than from vegetated plots (Figure 2; p=0.03, n=3 for repeated measures analysis). This supports the idea that plant transport bypasses a zone of surface oxidation and suggests that sedges are effective in methane transport not only because they provide a conduit to the soil surface but also because their large root surface area and air-filled aerenchyma (Armstrong and Boatman, 1967; Shaver and Billings, 1975) provide a more effective collection system and a more rapid diffusion path than through water-filled straws. Evidence for oxidation by surface soils is also provided by the methane profile in soil, where concentrations decrease sharply above 20 cm (Figure 3), and by laboratory incubations showing that the surface soil had a greater potential to oxidize methane than did the soil water that seeped into the straws (Figure 4).

In wet tussock tundra, the removal of graminoids (predominantly *Eriophorum vaginatum*) tended to decrease flux in each plot, but the effect was not significant (control mean=1.3±1.1 SE mg CH_4 m^{-2} d^{-1}; treatment mean=0.5±0.3 SE mg CH_4 m^{-2} d^{-1}, p=0.33, paired *t* test).

Long-term fertilization also had no significant impact on methane flux (0.01±0.04 SE mg CH_4 m^{-2} d^{-1}) from moist tussock tundra compared to the control (0.03±0.05 SE mg CH_4 m^{-2} d^{-1}; p=0.88 where null hypothesis was that treatment would have no effect on flux). Fluxes were not significantly greater than zero and in soil profiles in the control plots, methane concentrations decreased with depth to below atmospheric concentrations, indicating that soils were consuming atmospheric methane (Figure 5). Whalen and

Reeburgh (1990b) and Whalen et al. (1991) found no significant effect of fertilization on methane flux from taiga forest soils, which are also a weak sink of atmospheric methane.

Discussion

Our results are consistent with previous work showing that soil moisture and vegetation exert the primary controls over methane flux from tundra and that plant productivity is of secondary importance (Sebacher et al., 1986; Whalen and Reeburgh, 1988, 1990a; Bartlett et al, 1992; Morrissey et al., 1992). Dependence on soil temperature was greater than that found by Whalen and Reeburgh 1990a, but similar to that found by others (e.g., Bartlett et al., 1992).

Our results also show that within saturated wet-meadow tundra, where fluxes are highest, virtually all methane flux occurs passively through plants, just as in rice paddies (Cicerone and Shetter, 1981; Wassman et al., 1992) and temperate wetlands (Sebacher et al., 1985). Wetland plants, including those of tundra (Miller et al., 1976), show relatively weak stomatal closure in the dark, explaining why we and others (Morrissey et al., 1992) observe substantial methane flux, even in the dark. Darkness reduces stomatal conductance more in rapidly growing plants in July than in senescent plants in August (Tieszen, 1978; Morrissey, 1992); methane flux tends to follow the same pattern (Morrissey, 1992). Weak stomatal control and long summer photoperiod cause plants to be an effective avenue of methane transport in wet-meadow tundra. The virtual absence of methane flux from saturated tundra soils in the absence of vascular plants indicates that even in these wet soils, surface oxidation is an effective bio-filter that limits methane release from anaerobic soils (Ehhalt and Schmidt, 1978). Darkened chambers (this study; King, 1990) provide further evidence of the importance of oxidation as a control over net flux even in high-flux ecosystems. The increase in net flux seen in darkened chambers in wetlands (this study; King, 1990) may reflect decreased methane oxidation as photosynthesis and oxygen availability decline in the dark. We suggest that environmental controls over this methane bio-filter and plant transport of methane may be at least as important as methane production rates in determining patterns of methane flux from anaerobic soils.

The lack of fertilization effect on methane flux of a low-flux tundra site (this study) and taiga ecosystems (Whalen et al., 1991) contrasts strikingly with temperate-zone studies. These northern areas are characterized by low nitrifier populations (Gersper et al., 1980) and nitrification rates (Kielland, 1990, Nadelhoffer et al., 1991). In contrast, fertilization inhibits methane consumption in temperate grasslands (Mosier et al., 1991) and in temperate forests (Steudler et al., 1989), where large nitrifier populations oxidize methane under nitrogen-limiting conditions. Our results and those of Whalen et al. (1991) in boreal forest suggest that methane flux in tussock tundra will be less sensitive to regional changes in atmospheric nitrogen deposition or nitrogen cycling than to changes in soil moisture, soil temperature, and vegetation.

Our measurements of methane flux in wet-meadow tundra yielded values (52.0±6.4 SE mg m^{-2} d^{-1}, n=21) comparable to those reported elsewhere for Alaskan wet tundra, tending towards the lower end of published results (e.g., Whalen and Reeburgh, 1988; Bartlett et al., 1992).

The methane flux that we measured in tussock tundra (1.4±0.8 SE mg m^{-2} d^{-1}, n=11) was similar to that measured in some tussock tundra sites (Nadelhoffer et al., unpubl., Schimel et al., unpubl., Gillespie and Reeburgh, unpubl.) but 10- to 30-fold lower than that reported in the literature for other tussock tundra sites (Whalen and Reeburgh, 1988, 1990a). The difference in flux values may result from site differences or even microsite differences; our measurements were evenly distributed among tussock and intertussock spaces, the latter having lower flux. These differences may also result from seasonal or annual variation in methane flux; over a four-year period, average methane from one boreal tussock tundra site varied more than 4-fold (Whalen and Reeburgh, in press). Because of the widespread distribution of tussock tundra (6.8 x 10^6 km^2, Matthews, unpublished), the difference in flux rate between our measurements and those previously reported (i.e., 1.4 mg m^{-2} d^{-1}, this study; 31 mg m^{-2} d^{-1}, Whalen and Reeburgh 1990a) leads to a discrepancy of 20 Tg yr^{-1}, a value equivalent to 17% of net methane production attributed to global wetlands by Cicerone and Oremland (1988) and equivalent to half the methane flux they attribute to landfills or termites. These differences in measured fluxes in the Arctic underscore the need for better information on geographic variation and environmental controls over methane flux from tundra, as well as for better matching of measurement sites with mapped vegetation categories.

Global warming is expected to be most pronounced at high latitudes, with the Arctic warmed by as much as 3°C more than temperate or tropical latitudes in the next century (Maxwell, 1992). Although this warming is expected to cause complex, interacting changes in many environmental and biotic parameters affecting methane flux (Figure 6), we suggest that long-term changes in soil moisture will exert the strongest effect on future methane flux by determining vegetation type, litter quality, microbial community composition, rates of decomposition, location of decomposition within the soil, and the dominant decomposition pathways. For example, if realized, the declines in soil moisture predicted due to deeper soil thaw and increased potential evapotranspiration (Kane et al., 1992) would reduce the area of saturated ecosystems characterized by high methane fluxes, as modeled by Chappellaz et al. (1992) for the last glacial maximum. Widespread decreases in soil moisture would also likely result in a larger area of methane-consuming soils, acting as a negative feedback on the atmospheric methane budget (Whalen and Reeburgh, 1990b). In contrast, the expected increases in soil temperature may increase the rate of methane flux from saturated soils and thus create a positive feedback (Harriss et al., 1992). The overall effect of climatic change on methane flux from the Arctic will be a combination of changes in the area of methane producing and consuming soils, increases in methane flux from saturated soils, and a longer thaw season.

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Figure Captions

Figure 1. Methane flux, soil moisture, and soil temperature along a vegetation gradient. Data are means ± SE. Sample sizes for methane flux are: moist tussock tundra, n=3, wet tussock tundra, n=8, wet-meadow tundra, n=2, saturated wet-meadow tundra, n=19. Sample sizes for soil moisture are: moist tussock tundra, n=3, wet tussock tundra, n=7, wet-meadow tundra, n=2, saturated wet-meadow tundra, n=4. Sample sizes for soil temperature are: moist tussock tundra, n=3, wet tussock tundra, n=8, wet-meadow tundra, n=2, saturated wet-meadow tundra, n=8.

Figure 2. Comparison of methane flux from saturated wet-meadow tundra with natural vegetation (n=6), with all plants removed (n=6), and with no plants plus straws (n=3). Data are means ± SE.

Figure 3. Methane concentration in soil water in saturated wet-meadow tundra. Methane extracted by shaking sample with equal volume air to release dissolved methane. Sample sizes are in parentheses.

Figure 4. Methane consumption in headspace of jars incubated over soil or water from saturated wet-meadow tundra for 5 hours (n=3). Change in mean of control (air) was subtracted from treatment means.

Figure 5. Methane concentration in soil air in moist tussock tundra. Sample sizes are in parentheses.

Figure 6. Some of the ecological links between climatic change and methane production and consumption in natural ecosystems. A dashed box indicates the many factors influencing vegetation.

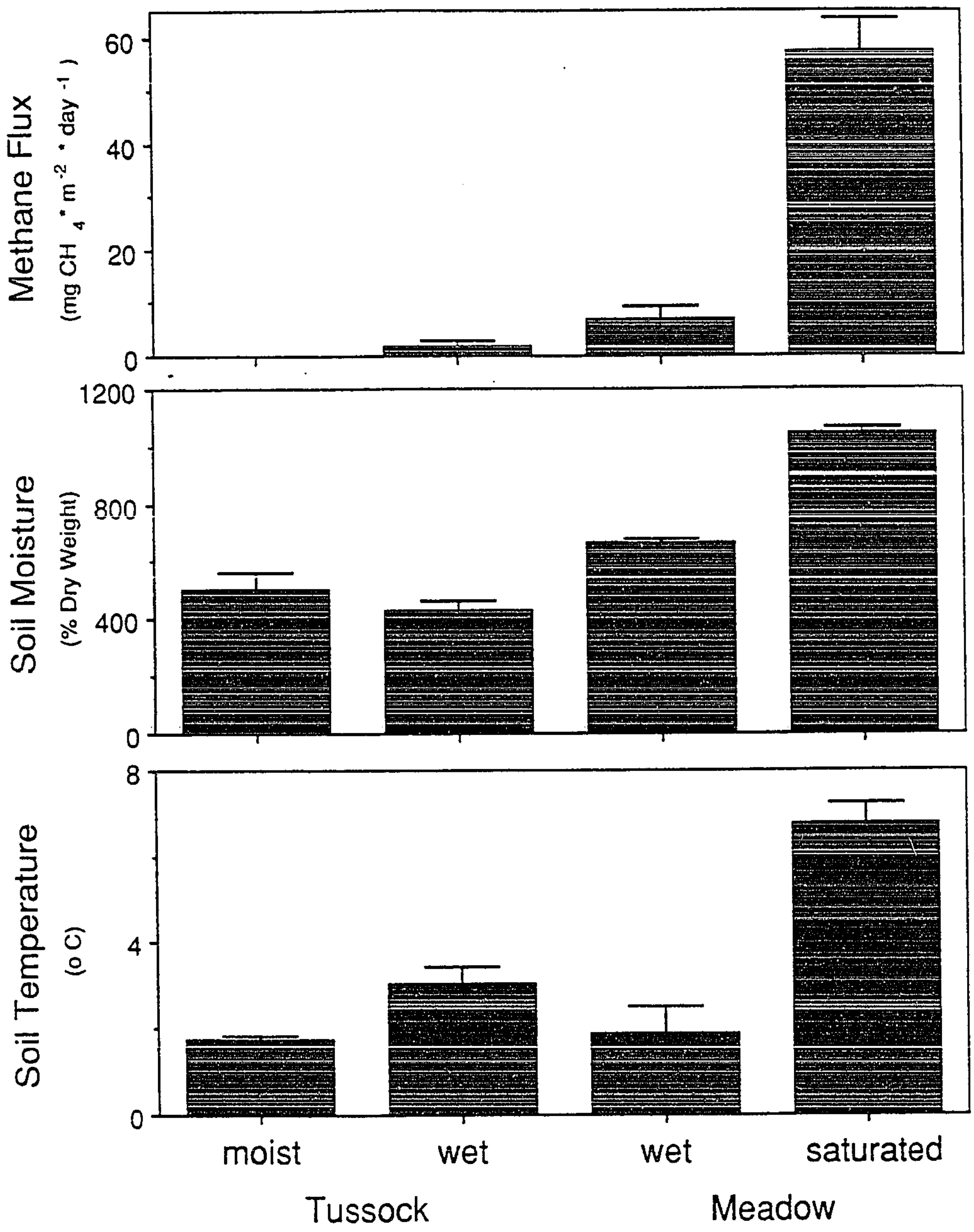
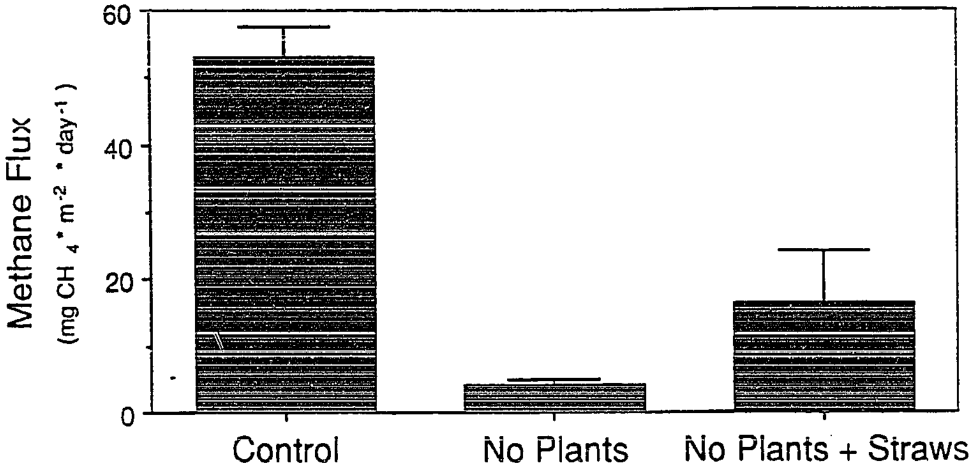

Methane Flux
(mg CH 4 • m -2 • day -1)
60
40
20
0
Soil Moisture
(% Dry Weight)
1200
800
400
0
Soil Temperature
(o C)
8
4
0
moist
wet
wet
saturated
Tussock
Meadow

Figure 1



60
40
20
0
Methane Flux
(mg CH 4 * m-2 * day-1)
Control
No Plants
No Plants + Straws

Figure 2

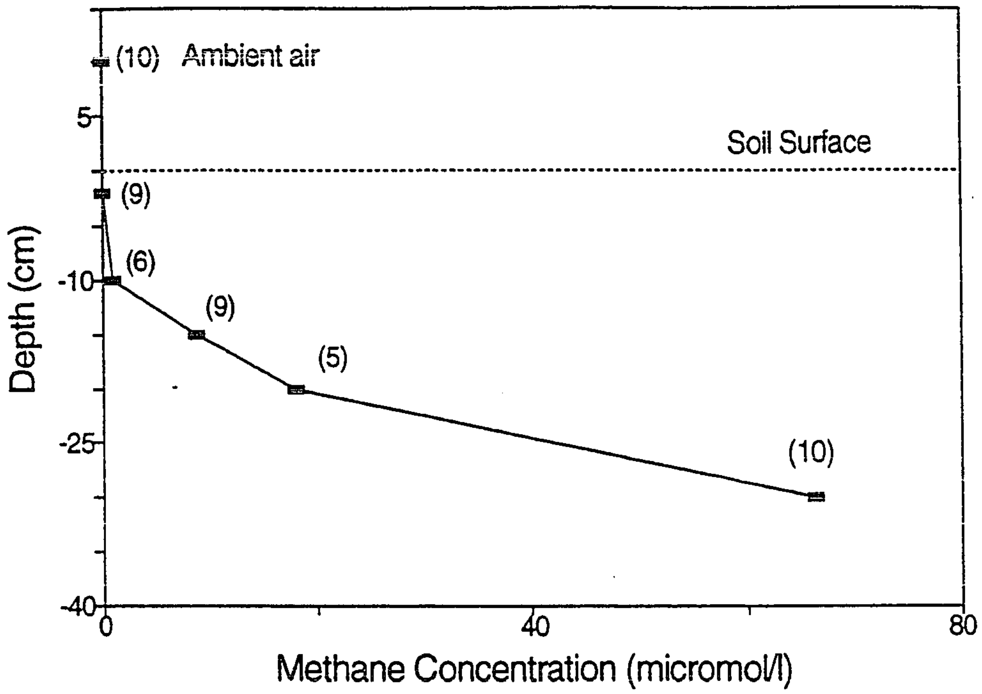

(10) Ambient air
Soil Surface
(9)
(6)
(9)
(5)
(10)
Depth (cm)
5
-10
-25
-40
0
40
80
Methane Concentration (micromol/l)

Figure 3

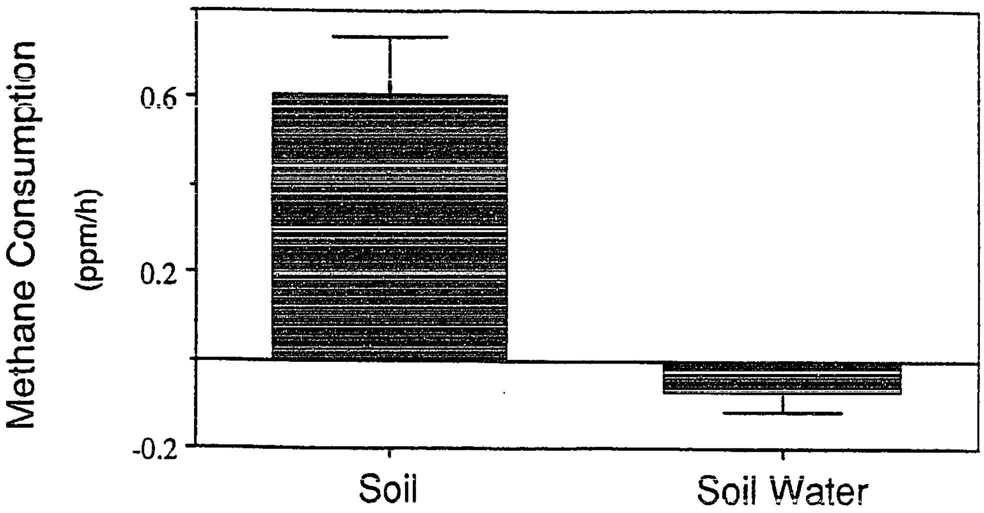


Figure 4

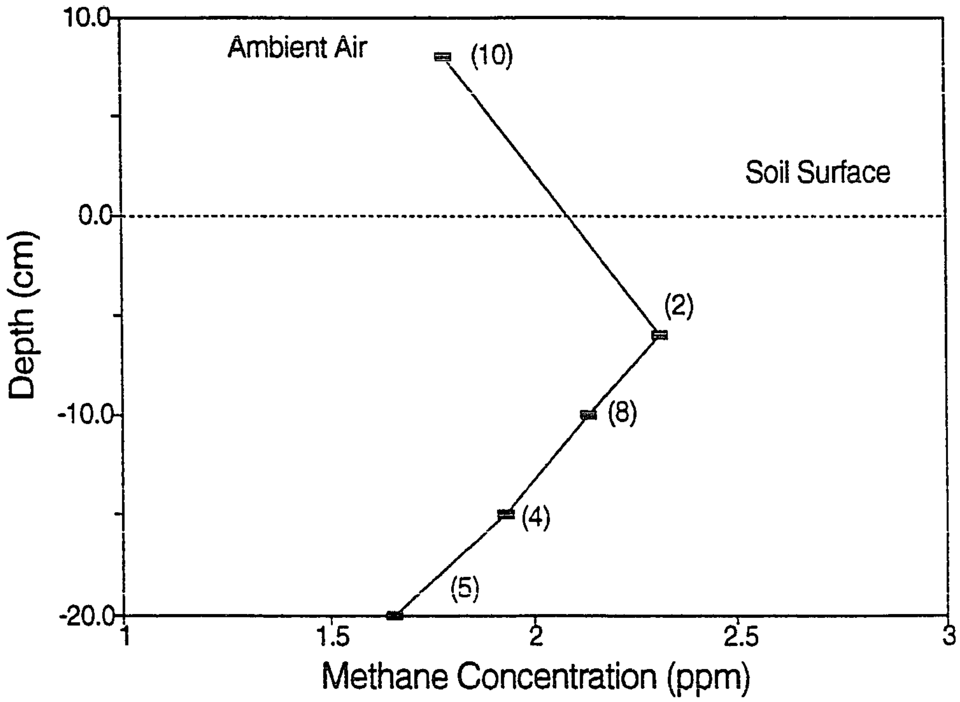

10.0
0.0
-10.0
-20.0
Depth (cm)
Ambient Air
(10)
Soil Surface
(2)
(8)
(4)
(5)
1
1.5
2
2.5
3
Methane Concentration (ppm)

Figure 5

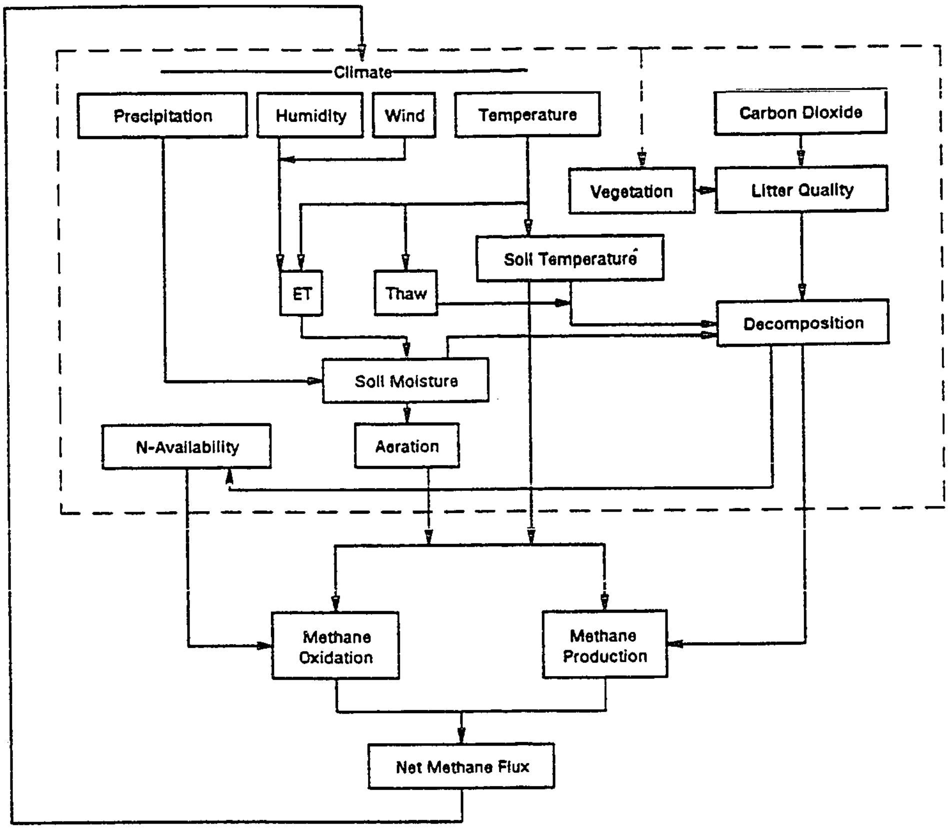

Climate
Precipitation
Humidity
Wind
Temperature
Carbon Dioxide
Vegetation
Litter Quality
Soil Temperature
ET
Thaw
Decomposition
Soil Moisture
N-Availability
Aeration
Methane Oxidation
Methane Production
Net Methane Flux

Figure 6

CHAPTER 3

METHANE CONSUMPTION BY MONTANE SOILS: *IN SITU* EVIDENCE FOR POSITIVE AND NEGATIVE FEEDBACKS WITH CLIMATIC CHANGE

Abstract and Introduction

Ice core data suggest positive feedback between net methane flux to the atmosphere and climatic change (Blunier, et al., 1993; Chappellaz, et al., 1990; Stauffer, et al., 1985). Climatic controls over soil-methane oxidation, the second-most important sink of atmospheric methane (Cicerone and Oremland, 1988; Houghton, et al., 1990), are poorly understood, but negative feedback to global warming has been predicted because soil drying should increase diffusion rates (Jury, et al., 1991; Torn and Chapin, 1993). We report here three years of field observations of methane uptake, averaging - 1.2 mg CH_4 m^{-2} d^{-1} by montane meadow soils[1]. Under ambient climatic variability, soil moisture was a better predictor of methane flux than was soil temperature. Specifically, methane uptake was linearly related to 5-cm moisture and had a quasi-parabolic relationship at 25 cm moisture. This pattern suggests that soil methane oxidation peaks below the surface soil horizon, and that the 5 cm moisture influences diffusion while the deeper soil moisture influences both diffusion and microbial activity. The uptake rate was maximum at an intermediate soil moisture of about 30% by weight (60% WHC). These results provide the first *in situ* characterization of microclimate showing that extreme soil drying

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[1] This chapter is adapted from a paper co-authored by Professor John Harte. The statement of permission to use co-authored material is reproduced in Appendix A.

may diminish the soil sink strength for methane. They indicate that soil methane consumption may generate either negative or a positive feedback with climatic change, depending on initial microclimatic conditions.

Methods, Results, and Conclusions

Our research site is a montane meadow on the western slope of the Rocky Mountains, Gunnison County, Colorado, USA. Each of 10 (3 m x 10 m) experimental plots spans a gradient of elevation, microclimate, and vegetation, extending from a dry ridge with sagebrush scrub down to a moist meadow swale, referred to as dry zone and moist zone, respectively (Table 1). Habitat physiognomy is similar to another subalpine meadow where methane uptake was observed (Mosier et al. 1993), but soils are sometimes drier than in that study or most other methane studies (Adamsen and King, 1993; Castro, et al., 1993; Keller, et al., 1990; Steudler, et al., 1989; Torn and Chapin, 1993; Whalen and Reeburgh, 1990a; Whalen and Reeburgh, 1990b; Whalen, et al., 1992).

We measured methane fluxes in the dry and moist zones of each plot in the spring and summer of 1991, 1992, and 1993 using static chambers (Whalen and Reeburgh, 1990b) accessed from elevated boards. The round, plexiglass chambers (26 cm diameter) were placed on stainless steel collars that were inserted 2-4 cm into the soil 30-60 minutes before sampling. Height of the collar plus chamber averaged 24 cm. A water-filled moat at the rim of each collar provided a gas-tight seal between the collar and chamber. Headspace gas, collected with duplicate 10-ml glass syringes, was sampled 4 times during incubations of 21 to 45 minutes. Gas samples were analyzed within 12 hours using a flame ionization detector on a Carle gas chromatograph with helium carrier gas. Methane uptake was calculated from changes in headspace concentration by a linear regression on all four points. In fewer than 10% of the incubations, methane depletion decreased uptake rates and the R^2 was improved by more than 0.1 units by dropping the last data point. In these cases, the last data point was dropped. Because the saturation effect was slight, non-linear saturation methods were not needed (Hutchinson and Livingston, 1993).

We measured methane flux in each zone on 11 sampling days distributed over three snowfree seasons, always between 1100h and 1400h (MST). Flux measurements were made on all 10 plots; each day's plot value is the average of 1 or 4 (1991) or 2 (1992-93) chambers per plot. In 1993 we also measured methane fluxes every four hours over two diurnal cycles in each zone, with one chamber per plot.

We recorded soil temperature and soil moisture every two hours year round with thermocouples and gypsum blocks (Campbell Scientific CR10 datalogger), respectively, located within one meter of each static chamber at depths of 5, 12, and 25 cm. We calibrated the gypsum-block voltages to gravimetric moisture content. The water-holding capacity (WHC) of the soil is 42% and 52% for the dry and moist zones, respectively. Soil moisture expressed as a percent of WHC (%WHC) approximates that fraction of the soil pore space that is filled with water. This is only a relative measure of the diffusivity of the soil, since changes in air-filled pore space may not be related linearly to changes in diffusivity (Hillel, 1980; Jury, et al., 1991).

The experimental site is part of an intensive investigation of physical, biogeochemical, and vegetation responses to meadow warming. The warming is achieved with infrared heaters suspended 2.6 m above every other plot, radiating approximately 18 W m^{-2} downward to the soil surface. Although the heaters altered the snowfree-season averaged soil temperature and moisture and advanced the date of snowmelt (Harte, et al., 1994), they had a negligible effect on soil temperature or moisture during the specific hours when methane flux was measured (Table 1).

Methane uptake in the meadow averaged -1.2 mg CH_4 m^{-2} d^{-1} (range 0 - -3.4 mg CH_4 m^{-2} d^{-1}). Uptake was significantly greater in the dry zone (-1.5 mg CH_4 m^{-2} d^{-1}) than in the moist zone (-1.0 mg CH_4 m^{-2} d^{-1}) by t-test or ANCOVA with soil moisture ($p<0.001$). Uptake rates are expressed as negative flux throughout this chapter. These rates are higher (more negative) than or comparable to those reported for most terrestrial ecosystems (Keller, et al., 1990; Keller, et al., 1993; Mosier, et al., 1991; Striegl, et al., 1992; Whalen and Reeburgh, 1990a; Whalen, et al., 1992; Whalen, et al., 1991), including another sub-alpine meadow (Mosier, et al., 1993), but lower than those reported for temperate hardwood forests (Castro, et al., 1993; Steudler, et al., 1989). Methane concentration in the soil atmosphere, sampled on three days via stainless steel tubes inserted 10-, 20-, and 30-cm deep, never exceeded ambient atmospheric levels, indicating that there were no near-surface sources of methane.

In none of the diurnal measurement cycles was a significant effect of hour detected by ANCOVA with soil temperature and moisture as covariates and plot as categorical variable (i.e., repeated measured design; $p>0.112$). Moreover, no significant effect of the heaters on methane flux was detected in any year or zone. All subsequent analyses in this paper will use only the midday data, from both heated and control plots.

Soil moisture had more influence over uptake rates than did soil temperature and in multiple regression with both variables only soil moisture was significant. Averaging all 10 plots on each midday sampling date (11 sampling dates per zone), the single-factor linear regressions gave a coefficient of determination and p-value of $R^2=0.425$, $p<0.001$ for moisture and $R^2=0.278$, $p<0.01$ for temperature at 5 cm. Soil moisture at 12 cm gave results similar to those at 5 cm, but with lower significance levels, and will not be discussed further.

Differences in soil moisture only partially explained the difference in flux rates between the dry and moist zones. Accounting for zonal differences in soil diffusivity by expressing moisture as %WHC exacerbated the difference between zones because the dry zone's WHC was smaller than the moist zone's. There was no significant interaction between zone and moisture in linear analysis, indicating that the response of flux to moisture was similar in each zone.

In addition to moisture and zone, flux rates differed by year, with the annually-averaged rate declining over the three years of study. Overall, the most explanatory and parsimonius model for characterizing flux at this site is:

Methane Uptake = Constant + Zone + Year + Moisture at 5 cm

For this model, $p<0.01$ for all factors, $R^2=0.746$, and $n=22$. Within each zone, soil moisture and year were significant (ANCOVA $p<0.005$ for both variables in either zone).

To discern any effect of climate above the noise of spatial heterogeneity, we analyzed each plot mean from each sampling date separately (each plot value is the average of 1-4 chambers/plot; n~100 plot-measurements per zone). The influence of soil moisture on flux was significant over the natural variability in the 10 plots, two treatments, two moisture zones and three snow-free seasons ($p<0.001$ for a linear regression with moisture at 5 cm or a non-linear fit with 5 and 25 cm, discussed below; $n=197$). Lacking an *a priori* model of the functional form of the dependence of methane consumption on soil moisture, we compared the fit of quadratic and linear functions to a single linear regression of flux on moisture. In both comparisons, described below, the non-monotonic fit was better than the simple linear fit.

While the linear fit of the disaggregated data with 5-cm moisture alone explains only 11% of the variance in flux, adding a quadratic 25-cm moisture term, representing a parabolic response function, explains 25% of the variance for both zones combined (Figure 1). The improvement in fit is more dramatic for the dry zone alone (Figure 2;

quadratic fit). No other combination of linear or quadratic moisture terms improved the fit of the linear 5-cm model (Figure 1).

In a second test of non-monotonicity, we divided all of the flux data into two moisture classes, those above 35% moisture and those below. We repeated the analysis with moisture classes below 30%, 25% and 20% moisture. For the 35% division, the best-fit linear regressions for the two data classes form a "V" shape with maximum consumption in the center, which for this division was at 35% moisture (Figure 1; linear fit). The slope below 35% moisture is significantly less than zero for the entire data set and for the dry zone alone. The moist zone data alone give a nearly significant negative slope; there are few "dry" data points, however, from this zone. The slopes were even more negative for the data below 25% and 20% soil moisture, for either zone or zones combined, but these slopes were not significant.

The negative slopes on the left half of Figure 2a-2c (linear and quadratic fits) indicate that soil drying (e.g., from climatic warming) under already-dry conditions could reduce methane consumption. In contrast, the positive slope, seen above 25-35% soil moisture in Figure 2 corroborates earlier reports that drying of moist soil could increase methane consumption.

These results are consistent with, and may point to mechanisms that help explain, observations that desert and rangeland soils show maximum methane uptake after rainfall (Mosier, et al., 1991 ; Striegl, et al., 1992).

The pattern in methane flux we observed--a linear relationship with 5-cm moisture and a non-monotonic relationship at 25 cm--can be explained by considering that the soil methanotrophs are less active near the soil surface than they are lower in the soil. A below-surface maximum in methane oxidation, either below the organic soil horizon or below 10-15 cm depth, has been observed in aerobic soils of temperate and boreal ecosystems (Adamsen and King, 1993; Koschorreck and Conrad, 1993; Steudler, 1994;

Valentine, et al., 1993; Whalen, et al., 1990). With this relatively deep distribution of methanotroph activity, surface soil moisture would influence diffusion and the lower-depth moisture would influence both diffusion and methylotrophy. The influence of soil moisture on the diffusion component of consumption is always negative and monotonic. The influence of soil moisture on methanotroph activity is more complex. Our data suggest that the influence of soil moisture *in situ* is to decrease oxidation rates at very low moisture levels. The decrease in consumption on dry days suggests that methanotroph activity may be moisture-limited under ambient levels of soil drying. This is consistent with several laboratory studies that have demonstrated a non-monotonic response curve of methane oxidation to soil moisture (Reeburgh and Whalen, 1993; Schimel, et al., 1993; Valentine, et al., 1993; Whalen, et al., 1990).

Although methane uptake is generally thought to be diffusion-limited (Bartlett and Harriss, 1993; Dorr, et al., 1993; Striegl, 1993), the factors limiting methane uptake at this site can be summarized as: under very dry conditions, methane consumption is microbially limited; under mesic moisture conditions, consumption is substrate-transport limited; and under wet conditions, methane oxidation is limited by the transport of methane and direct toxicity from anaerobiosis. The retardation of microbial methane-oxidation by low soil moisture could be an important rate-limiting step in other soils and ecosystem types, although the soil-moisture level at which consumption begins to be inhibited may differ spatially and temporally.

Soil drying due to climatic warming could reduce methane consumption in soils with low moisture content, generating positive feedback to climatic warming. A climate feedback with methane consumption could affect two important aspects of the methane budget. First, soil consumption of atmospheric methane is roughly equal to the magnitude of the current imbalance between methane sources and sinks that is giving rise to a 1% per year increase in atmospheric methane (Houghton, et al., 1990). Second, methane consumption on land is an important filter to terrestrial emissions, oxidizing almost half of all soil-produced methane (Reeburgh, et al., 1992). Some insight into this difficult to observe 'filter'-consumption process may be gained by understanding the mechanisms influencing soil uptake of atmospheric methane *in situ*. Although methanotrophic communities that filter soil-produced methane are found in moist soils, drying-induced reductions in methylotrophy should be investigated as a possible explanation for observed methane-emission pulses from drying wetlands (Moore and Roulet, 1993).

The low coefficient of determination for the regression of flux on moisture with disaggregated data (R^2=0.120, linear; R^2=0.258, quadratic) indicates that other biotic and abiotic factors are also important in fluctuations in methane flux over time and space (the spatial factors being the primary difference between the aggregated (n=22) and disaggregated (n=197) regressions). We did not measure several spatial factors that are likely to affect methylotrophy, including the distribution of rocks, gopher tunnels, roots, and nitrifier activity. Nevertheless, these results bear on climate change analyses because many potentially important factors, such as soil texture (Dorr, et al., 1993), are unlikely to change rapidly or in a spatially-coherent fashion in response to climatic change or other environmental trends.

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Table 1. Site Characteristics. Soil microclimate data are averages of two-hourly readings over depth (5, 12, 25 cm) and year (1991-93) from the end of snowmelt to late August. Soil moisture is expressed as gravimetric percent (g H_2O /100 g soil). Zonal-averaged soil temperatures and gravimetric moistures 13.6°C, 26%, 12.6°C, 32%, and 13.6°C, 23% for 1991, 1992, and 1993, respectively.

Property	Value	
Location	lat 38°53'N, long 107°02'W	
Elevation	2920 m	
Average Annual Precipitation	700 mm, 80% as snow	
Average Summer Air Temperature	10°C	
Snow-free season	Typically May 20-November 1	
Average Summer Soil Temperature and Soil Moisture		
moist zone	14.0 °C, 22 %	
dry zone	12.5 °C, 33 %	
Range of Soil Temperature and Moisture During Methane Flux Measurements		
soil temperature	7 - 31 °C	
soil moisture	6 - 56 %	
Mean Effect of Heaters During Methane Flux Measurements		
On Soil Temperature		
moist zone	- 0.3 °C	
dry zone	+ 0.8 °C	
On Soil Moisture		
moist zone	- 0.2 (g H_2O/100 g soil)	
dry zone	- 2.3 (g H_2O/100 g soil)	
Soil Properties	Cryoboroll (rocky glacial till), pH ~ 6.3	
Organic matter		
dry zone	12 % to 75 cm depth	(zone difference is not significant)
moist zone	11 % to 75 cm depth	
Dominant Vegetation		
dry zone, sagebrush steppe	*Artemisia tridentata, Mertensia fusiformis, Vicia americana, Lathyrus leucanthus, Festuca thurberi*	
moist zone, montane meadow	*Pentaphylloides floribunda, Claytonia lanceolata, Erythrocoma integrifolia, Melica spectabilis*	

Figure 1. Evidence for non-monotonic fit of methane consumption to soil moisture at 25-cm depth. The linear regression of methane flux on 5-cm moisture is significantly improved by the addition of a 25-cm moisture quadratic term. There is no significant improvement from adding the square of 5-cm soil moisture or a linear 25-cm term. M25 =moisture at 25-cm depth; M5=moisture at 5-cm depth; a=constant. Includes every midday plot value where both $M25>0$ and $M5>0$ ($n=185$). For each regression, $p<0.001$.

	Flux = Constant + M5	$R^2 = 0.111$
	Flux = Constant + M5 + M25	$R^2 = 0.118$
	Flux = Constant + M25 + $(M25\text{-}a)^2$	$R^2 = 0.153$
	Flux = Constant + M5 + $(M5cm\text{-}a)^2$	$R^2 = 0.169$
-->	Flux = Constant + M5 + $(M25\text{-}a)^2$	$R^2 = 0.253$

Figure 2. The non-monotonic fit of methane uptake to soil moisture at 25 cm shown three ways: binned data clusters, best quadratic fit and linear fit of two moisture classes. Figures show (a) dry zone , (b) moist zone, and (c) both zones combined. The binned data clusters are averages (± SE) of clusters generated by dividing the moisture axis at 8% (8 g H_2O/100 g soil) intervals. The average flux and moisture for each interval are graphed. Both the quadratic equations and the linear regressions were generated from all the midday data (n=102 for dry zone, n=96 for moist zone, n=198 for both zones combined), not from the clusters.

Quadratic Fit: The quadratic curves show the significant non-linear fit for the dry zone and both zones combined, with maximum consumption around 25% moisture. The moist-zone quadratic fit is not signficantly better than the linear fit (SYSTAT 6.0 NonLin; Wilkinson, 1990). M25=soil moisture at 25-cm depth.

(a) Dry zone: $\text{methane flux} = -0.4072 - 0.1104*\text{M25} + 0.0022*(\text{M25})^2$
(b) Moist zone: $\text{methane flux} = -0.4026 - 0.0505*\text{M25} + 0.0008*(\text{M25})^2$
(c) All Data: $\text{methane flux} = -0.8900 - 0.0508*\text{M25} + 0.0010*(\text{M25})^2$

Linear Fit: The straight lines show linear regressions of flux on 25-cm soil moisture, for soil moisture < 35% and soil moisture > 35%.
Regression model: Flux = constant + m* moisture at 25 cm

	Slope (m) for line Soil moisture < 35%	p slope less than zero	n
(a) Dry zone:	- 0.026	0.033	54
(b) Moist zone:	- 0.027	0.057	25
(c) All Data:	- 0.019	0.040	79

Figure 2 is continued on the next page

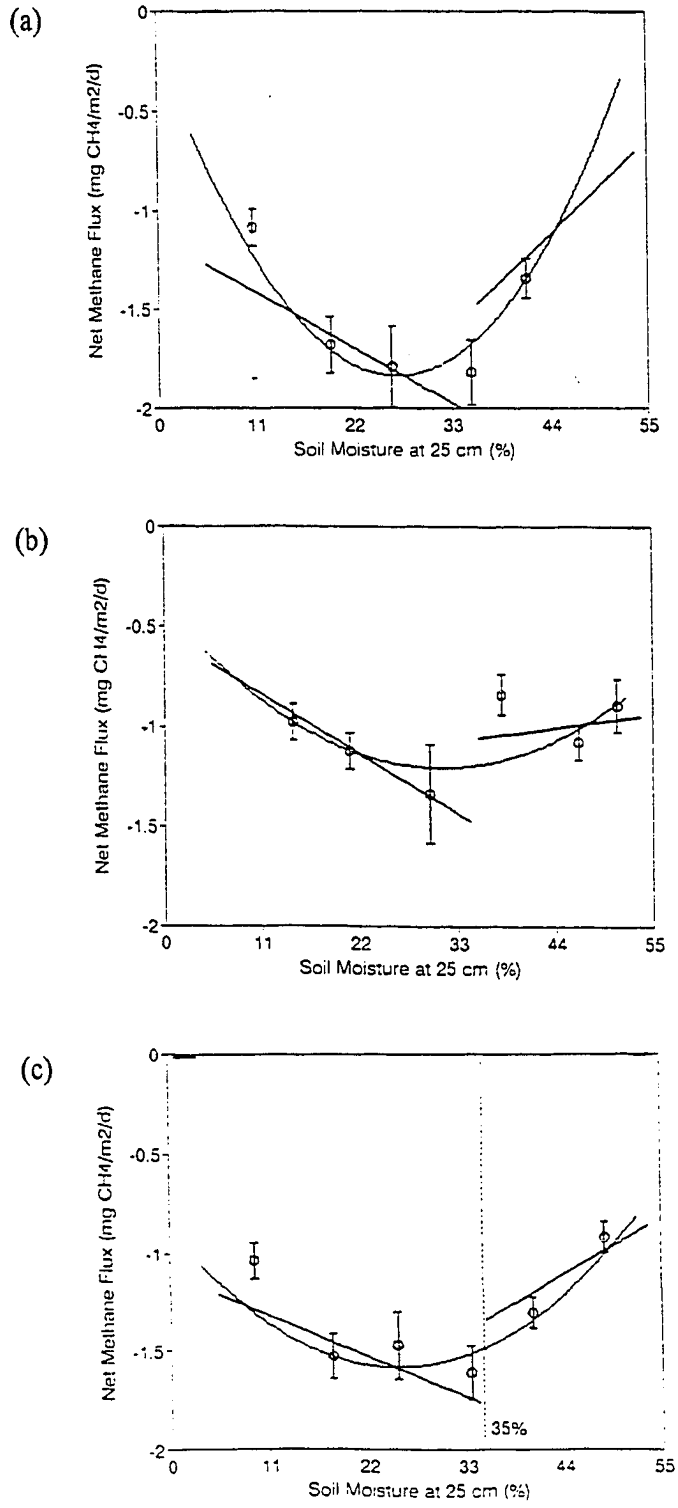
(a)
Net Methane Flux (mg CH4/m2/d)
0
-0.5
-1
-1.5
-2
0
11
22
33
44
55
Soil Moisture at 25 cm (%)
(b)
Net Methane Flux (mg CH4/m2/d)
0
-0.5
-1
-1.5
-2
0
11
22
33
44
55
Soil Moisture at 25 cm (%)
(c)
Net Methane Flux (mg CH4/m2/d)
0
-0.5
-1
-1.5
-2
35%
0
11
22
33
44
55
Soil Moisture at 25 cm (%)

Figure 2

CHAPTER 4

METHANE EMISSION AND RELEASE IN A POND-GRASSLAND ECOSYSTEM IN CALIFORNIA

Abstract

The annual cycle of methane emission and uptake was studied in an annual grassland and the seasonally-inundated soils near a small pond in California from 1991 to 1993. Static chamber and depth-profile measurements of methane were used to determine whether production and consumption differed in their response to seasonal variations in temperature and moisture. The pond surface consistently emitted methane (0-229 mg CH_4 m^{-2} d^{-1}). The grasslands consumed atmospheric methane at an average rate of -0.7 mg CH_4 m^{-2} d^{-1}, until heavy rains raised the pond level over the soil. The newly-flooded area emitted methane. Similarly, pond soils exposed at the end of the dry season showed net methane consumption. The response of flux to changes in the water table was rapid and direct, rather than occurring via moisture-induced changes in vegetation. Methane production and consumption responded differently to changes in temperature and moisture. Methane emissions were positively correlated with soil temperature, whereas methane uptake was not significantly related to temperature. The effective temperature response (e.g., Q_{10}) for emissions from sites with both production and consumption is much larger than the Q_{10} for production alone. As seen in other ecosystems, moisture saturation increased methane emissions and reduced methane uptake. Methane uptake in the grassland sites was highly and positively correlated (R^2=0.97) with soil carbon and nitrogen content, with no effect of grazing by sheep.

Introduction

The global flux of methane from natural ecosystems is the balance between methane release and uptake (Reeburgh, et al., 1992). Moreover, methane flux in a given site is often the balance between microbial production and consumption of methane. Globally, approximately 65% of all biogenically produced methane is oxidized before it reaches the atmosphere (Reeburgh, et al., 1992). The balance is controlled by vertically layered anaerobic and aerobic conditions (Knowles, 1993; Oremland and Culbertson, 1992a; Oremland and Culbertson, 1992b; Schimel, et al., 1993) or by seasonally alternating periods of wet and dry soils (Bartlett, et al., 1988; Delmas, et al., 1992; Harriss, et al., 1982; Tathy, et al., 1992).

Production and consumption involve two different microbial pathways and may have different responses to the same environmental change (Yavitt, et al., 1990b). Thus, soils or regions that currently have very low net fluxes but high gross fluxes could experience a dramatic change in net flux due to climatic change.

There are several studies documenting the balance between methane production and consumption in rice paddies (Delwiche and Cicerone, 1993; Holzapfel-Pschorn, et al., 1985; Masscheleyn, et al., 1993; Wassmann, et al., 1993) and in laboratory soil incubations (Dunfield, et al., 1993; Valentine, et al., 1993), but few direct measurements in natural ecosystems (Harriss, et al., 1982; Yavitt, et al., 1990a). There is even less research reported on how environmental factors affect the ecosystem balance of methane production and consumption (King, 1990). Studies of flux at the soil/air interface in tropical, temperate, and boreal ecosystems have shown that saturated, methane-emitting soils may shift to consuming atmospheric methane if the soil dries (Bartlett, et al., 1988; Delmas, et al., 1992; Harriss, et al., 1982; Roulet, et al., 1992; Tathy, et al., 1992). In other words, methane production responds negatively to a step-wise decrease in moisture, and net methane consumption responds positively to the same trend--a biogeochemically critical example of a differential response. Laboratory experiments with soil cores confirm this differential response to moisture (Moore and Roulet, 1993; Valentine, et al., 1993).

Field and laboratory measurements of methane flux from soils of different biomes suggest that there may also be a differential response to changes in temperature. Methane emission from soil cores and *in situ* appears to respond positively to increasing temperature (Bartlett, et al., 1989; Bartlett, et al., 1988; Bartlett and Harriss, 1993; Dunfield, et al., 1993; King and Adamsen, 1992; Valentine, et al., 1994; Westerman, 1993). In contrast, most studies do not find a significant influence of temperature on methane uptake (Chapter 3; Dorr, et al., 1993; Schimel, et al., 1993; Tate and Striegl, 1993 ; Valentine, et al., 1993). As a microbially-mediated process, soil-methane oxidation might be expected to respond exponentially to temperature, but reported Q_{10} values (King and Adamsen, 1992) are close to 1, probably because methane uptake in most soils is diffusion-limited (Bartlett and Harriss, 1993; Striegl, 1993). Although these results suggest a differential response, no research has been done on the influence of temperature on methane production and consumption while holding site variables constant, e.g., within a single site. The study presented here investigates this differential response in methane production and consumption using observations from a pond and the seasonally-flooded annual grassland surrounding it.

Grasslands are generally thought to be net sinks of atmospheric methane (e.g., Mosier, et al., 1991). The ridgetop grasslands sampled at this site will add data on methane uptake in temperate annual grasslands to the existing data on perennial grasslands. Grasslands in the Guyana Shield of Venezuela release methane during the dry season (Hao, et al., 1988; Scharffe, et al., 1990), however, suggesting that grasslands may be a good site to look for a gradient of methane producing and consuming sites.

In addition to soil temperature and moisture, fertilization and soil carbon and nitrogen have been identified as controls over methane uptake by aerobic soils. Whether carbon and nitrogen availability inhibit or promote uptake, however, is not resolved. Nitrogen fertilization inhibited uptake in pine and mixed hardwoods (Steudler, et al., 1989), Colorado pasture (Mosier, et al., 1991), and boreal birch forest (Kielland and Schimel, 1991; Schimel, et al., 1993) but had little effect on uptake or oxidation by taiga communities (Whalen, et al., 1991), tundra soils (Kielland and Schimel, 1991; Torn and Chapin, 1993) or temperate hardwood-coniferous forest soils (Adamsen and King, 1993). This inconsistency also pertains to observations across natural fertility gradients; Mosier et al. (1991) reported a negative correlation with inorganic nitrogen in Colorado prairie swales but Melillo (1994) found that methane uptake increased along a natural gradient of soil nitrogen in temperate forests. To see how organic matter and nitrogen are related to methane uptake by annual grasslands, as well as to compare the effects of natural vs. artificial (e.g., altered by fertilization) carbon and nitrogen content, I measured methane uptake in grasslands across a natural gradient of organic matter and a combination of long-term fertilization and sheep-grazing manipulations.

Methods and Site Description

Research was conducted in a temperate oak savanna at the U.C. Hopland Research and Extension Center, Hopland, California. The climate is Mediterranean with hot, dry summers and cool, wet winters (Figure 1). The research sites spanned a gradient in elevation and moisture from a small pond up to a ridge between watersheds (Figure 2). Vegetation and soil characteristics of the sites are described in Table 1.

At the margin of the pond, three sampling sites were established: pond, transition, and pond grassland (from lowest to highest elevation). At each site, methane flux was measured in four replicate chambers located approximately 2-4 meters apart at a constant elevation. Chamber locations were permanent at the pond grassland site, which had vegetation typical of annual grassland in California. The location of chambers at the transition site, which included annual grassland species as well as mint (*Mentha pullegium*) and other hydrophyllous species, shifted seasonally to maintain sites on non-saturated surface soils a distance of 1.5-2 meters from the pond margin. The location of the pond-site chambers shifted seasonally to maintain a water depth of 2 - 11 cm standing water, except at the end of each rainy season when the water was too deep to sample. Emergent aquatic sedges and tule plants (*Carex sp.* and *Typha sp.*) below 10 cm height were occasionally covered by a chamber at the pond margin.

The transition site was flooded during the rainy seasons of '91-'92 and '92-'93. The pond grassland site was unsaturated until heavy rains ended a 6-year drought and raised the pond level sufficiently to flood the site from January to April, 1993 (rainfall measured with a Belfort 5-780 recording rain gauge at the Hopland headquarters building). Before flooding, the pond grassland vegetation was similar to that of the ridgetop. Flooding resulted in the establishment of mint (*Mentha pullegium*) and other transition-site species, which have persisted through April 1994.

Permanent sampling sites on the ridgetop were established on north- and south-facing slopes (R-I and R-II, respectively) of a ridge above the pond. These sites have vegetation characteristic of California annual grasslands with scattered oak trees. Sampling sites were also established in a fertilized grassland (airplane dispersal of phosphorus and seeds of nitrogen-fixing plants) bordering a madrone forest (R-III). Each ridge site consisted of sheep-grazed and ungrazed treatments that have been maintained by Hopland since 1958. Sheep density in the fertilized treatment was about 2.5 sheep ha^{-1} y^{-1} and was half that in the two unfertilized sites (R-IG and R-IIG). Grazing by native Columbian black-tailed deer was not controlled. Dominant vegetation is listed in Table 1. The fertilized, ungrazed site (R-IIIF) had several plant species in abundance that were not found at the unfertilized grassland sites, including *Phalaris aquatica* and *Abina sp*. The grazed, fertilized treatment site (R-IIIFG) appeared degraded. It had low-statured vegetation characteristic of disturbance (Table 1), little bromus or other annual monocots, and scattered patches of bare soil. At each ridge site, methane flux was measured with three chambers per treatment.

Methane flux, methane in soil air, soil moisture and soil temperature were measured at regular intervals between October 1991 and April 1993, with 7 sampling days at the pond area and 6 sampling days at the ridge sites. Sampling dates are shown in Table 2 and Figure 1.

I measured methane flux at the soil/air interface using round, Plexiglass chambers placed on stainless steel collars (26 cm diameter) that were inserted 2-4 cm into the soil 1 hour before sampling (Whalen and Reeburgh, 1990). Height of the collar-plus-chamber averaged 24 cm. A water-filled channel on the collar made a gas-tight seal between collar and chamber. Headspace gas, collected with duplicate 10-ml glass syringes, was sampled 4 times during incubations of 21 to 45 minutes. Gas samples were analyzed within 24 hours using a flame ionization detector on a Shimadzu GC14A gas chromatograph. Methane flux was calculated by a linear regression on all four points except, where moderate saturation was evident, the last data point was dropped.

The concentration of methane in the soil atmosphere or water was measured with three to six replicates per soil depth of 5, 10, 15, 20, and 30 cm in soil and 2-5 cm and 10 cm in water. The stainless steel sampling tubes (3-mm diameter; Born, et al., 1990; Whalen, et al., 1992) were located within 20 cm of chambers. To extract methane from water, samples were shaken vigorously with equal parts air for 2 minutes (Torn and Chapin, 1993).

Soil or water temperature was measured with a Barnant, "J"-type thermocouple thermometer at 10-cm depth on two sides of each chamber and the averaged value recorded. Moisture content of the top 10 cm of soil, excluding litter, was determined gravimetrically and expressed as percent of dry weight after oven-drying. Water-holding capacity was estimated to be the water content of flooded soil after excess water was allowed to drain (average = 116 g / 100g, n=11, SE = 8).

Carbon and nitrogen content of the soil was analyzed by elemental analysis (Carlo Erba C/N autoanalyzer). Soil samples for carbon and nitrogen analysis were collected in October 1992, except ridge III samples were collected in April 1994. Bulk density of soil was estimated from the volume of water displaced by intact soil cores (Blake, 1965). Three ~60 cm^3 soil samples from each site were measured.

I used methyl fluoride (CH_3F) to inhibit methane oxidation in the soil at the transition site on May 4-5, 1992. Methyl fluoride was injected into the soil through 4 stainless steel tubes (4 mm diameter) at 10-30 cm depth. Soil-atmosphere concentrations of methyl fluoride were elevated to over 1%, the concentration necessary to inhibit oxidation (Oremland and Culbertson, 1992a; Oremland and Culbertson, 1992b)

Results

Methane fluxes differed among sites by more than an order of magnitude at each sample date, as well as among sample dates at each of the three pond-area sites (Figure 3). These seasonal and spatial patterns in flux were largely determined by patterns in soil moisture. At the consistently saturated sites, annual average fluxes were high and positive. The annually-averaged methane emission rate from the pond surface was 38.2 mg CH_4 m^{-2} d^{-1} (± 16.8 SE, n = 18). At the consistently unsaturated sites, methane was consumed year round. The annually-averaged methane uptake rate in the control annual grassland sites was -0.7 mg CH_4 m^{-2} d^{-1} (± 0.1 SE) with 42 measurements in three different watersheds (Table 2), excluding measurements in February 1993 when the pond grassland was flooded.

The sheep-grazed pastures tended to have slightly higher methane uptake, soil nitrogen , and soil carbon than the control grasslands (Figure 4), but for uptake this difference was not significant. Specifically, for soil nitrogen and carbon, respectively, $p \leq 0.017$ and $p < 0.05$ for analysis of variance with location as a cofactor and n=18. For methane uptake, $p < 0.9$ for analysis of variance with location and day as cateogrical factors, n = 84; $p<0.26$ for repeated meaures analysis of variance by location.

The average rate of methane uptake in the grassland sites was highly correlated with soil organic content as measured by soil carbon and nitrogen content. For unfertilized grasslands, the correlation coefficient (R^2) was at least 0.97 with or without the grazed sites (Figure 5, Table 3). Uptake rates at the fertilized, ungrazed site were higher than predicted by a regression based on the unfertilized sites, but the overall correlation with all grasslands is still fairly high, $R^2=0.73$, n=7 sites.

Due to seasonal flooding, the transition site is not dominated by annual grass species and it has high carbon and nitrogen content. During the dry season, when the transition site consumes atmospheric methane, the uptake rate was lower than would be predicted by the regression line (Figure 5).

Over the annual cycle and over the elevation gradient, soil moisture was an important controller of methane emissions ($p<0.001$ for linear regression; Figure 6). Methane emissions were observed from all sites with saturated soils, whether those sites were always flooded or were only temporarily inundated after heavy rains. Likewise, methane uptake was observed from all sites with dry soils (e.g., below 55% moisture; with one exception discussed below) whether those soils were aerobic year-round or only exposed during the end of the dry season. Clearly, the shifts from source to sink or vice-versa were direct consequences of changes in soil moisture, rather than depending on indirect effects of moisture on vegetation, detritus, or microbial communities that might take several growing seasons to be observed.

Comparing the locations showing methane emissions with locations showing uptake reveals different responses to soil moisture and temperature. Increasing moisture from unsaturated to saturated conditions caused increased methane release. Once moisture is sufficient to saturate soils, however, increases in soil moisture or inundation did not increase emissions ($p < 0.245$). In the grasslands, uptake rates were highest in summer and fall when soils were driest, and lowest in winter and spring when soils were moist (data not shown), and a linear regression of uptake on moisture was significant ($p < 0.045$, n=35, based on all measurements in ungrazed grasslands in which flux was negative). In Colorado (Chapter 3), I found that under extremely dry conditions further drying leads to a decrease in uptake--implying that in some cases uptake and emissions both respond negatively to drying. I did not find a non-monotonic relationship with moisture at Hopland, but this may have been because at Hopland I measured moisture at 0-10 cm depth whereas in Colorado I found the non-monotonicity only with moisture deeper than 12 cm (at 25 cm).

Considering only the locations showing methane release, emission rates increased with soil temperature (Figure 7). The best fit was exponential ($R^2=0.373$), rather than linear ($R^2=0.172$). Both regressions are shown in Table 4. The $Q_{10} = 2.75$ for emissions at Hopland from 10°C to 20°C (where Q_{10} is a measure of the increase in flux caused by a 10°C warming and is calculated as the ratio (flux at T):(flux at T-10)) for the natural-log fit. The range of soil temperatures included in the regression was 6-29°C.

In contrast with the methane-emitting sites, a regression of flux on temperature for locations showing methane uptake showed no significant relationship with temperature (Figure 7 and Table 4), i.e., the Q_{10} for uptake was essentially 1.

The exception to having net consumption from all soils with soil moisture less than 55% was on a warm day in May 1992, when all the chambers of the transition site emitted methane (Figure 8). Three types of observations indicate that both production and consumption were occurring in the soil profile on this day, and that net emissions were the balance between production and consumption in the soil profile. First, the soil profile of methane showed greater than ambient concentrations at depth, indicating that there was a source of methane under the surface (Figure 9). Second, the moisture content of the surface soil at the transition site was roughly 40%, indicating that conditions at the surface were favorable for methane oxidation (Figure 6). Third, the dramatic increase in net flux after application of an oxidation-inhibitor gives strong evidence that there was oxidation at the surface and methane production below (Figure 8). The three adjacent control (no methyl fluoride application) chambers had lower, but positive, flux rates and a soil profile indicating methane production.

On other days as well, measurements of methane in soil air showed microsites of methane production below 10 cm when the surface soil showed net uptake of methane (Figure 9). In total, fifteen percent of the profile measurements under the 35 pond-area chamber measurements with net consumption showed greater than ambient methane concentration (Table 5), and most profiles were consistent with the direction of flux at the surface (Figure 9). Microsites of production in forest soils have been documented with isotope analysis of methane profiles (Steudler, 1994).

Overall, the annual flux from this landscape was the balance of seasonally-shifting areas of net methane production and net consumption. Moreover, at certain sites, net flux was the balance of production in the saturated soil at depth and methane consumption in the overlying, aerobic surface soil, as evidenced by soil methane profiles and *in situ* application of an oxidation inhibitor.

Discussion

The annual grassland sites have fairly consistent rates of methane uptake year round, even though plant growth and climate are highly seasonal. Rates of uptake (-0.7 mg CH_4

m^{-2} d^{-1}) were comparable to rates measured in other grassland ecosystems, such as tropical grasslands and savannas (-0.51 mg CH_4 m^{-2} d^{-1}; Delmas, et al., 1991), and perennial grasslands and prairie (-0.44 mg CH_4 m^{-2} d^{-1}; Tate and Striegl, 1993; -0.61 mg CH_4 m^{-2} d^{-1}; Mosier, et al., 1991; -0.82 mg CH_4 m^{-2} d^{-1}; Ojima, et al., 1993).

Methane uptake in the grasslands was highly correlated with soil carbon and nitrogen content regardless of whether the sites were grazed or not. For example, fertility explains 98% of the variance in average uptake among the 5 unfertilized grassland sites.

These results are inconclusive in comparing the influence of natural vs artificial level of organic carbon and nitrogen on methane uptake. The fertilized site had a higher uptake rate than predicted by carbon and nitrogen content alone, while the grazed, fertilized site overlaps closely with an ungrazed, unfertilized site (R-I) in Figure 5.

The transition site shows much lower uptake rates than predicted by an extrapolation of the regression to the high carbon and nitrogen content of that site. Possibly the linear extrapolation is not appropriate because uptake does not continue to increase with carbon and nitrogen due to secondary limitation, e.g., by diffusion rates. In addition, it is possible that the periodic flooding at the transition site reduces its populations of aerobic methanotrophs and changes soil texture.

The positive association between uptake and natural carbon and nitrogen content may be due to the maintenance of a larger population of facultative methanotrophs in soils with more nitrogen (Melillo, 1994). Pinpointing the influence of carbon and nitrogen content is confounded in this study by the correlation of carbon and nitrogen with soil bulk density ($R = -0.76$, $n=4$; Table 1), which influences fluxes by affecting diffusion rates. Similarly, the Colorado swale site studied by Mosier et al. (1991), which had higher fertility and lower flux than their other sites, also had a finer texture than their other study sites.

Over the annual cycle, there was a positive influence of soil moisture and temperature on rates of methane flux. This pattern was mainly due to the large change in flux rates between unsaturated and saturated soil, and the temperature responsiveness of methane emissions. Soil moisture had less effect on uptake than seen in some other studies (e.g., (Mosier, et al., 1991; Torn, 1994).

Modeling changes in methane fluxes in response to seasonal or long-term trends in moisture requires making assumptions about the time lags between the creation of inundated areas and the onset of emissions. Emissions may be low until the build up of suitable substrate (organic matter and decomposer communities) or the establishment of emergent aquatic vegetation for methane transport. In this research, methane emissions occurred within a few weeks of inundation and the presence of emergent plants was not necessary for methane emissions. I could not distinguish between methane produced in the newly-inundated area or methane that migrated from the permanently-flooded center of the pond. Nevertheless, total-pond emissions probably increased following the increase in pond surface-area. These results suggest that the transition in a site from methane sink to methane source can be rapid, and can respond directly to changes in moisture conditions.

There was a strongly differential effect of temperature on methane emissions and methane uptake at Hopland. The Q_{10} for emissions was 2.75 and Q_{10} for uptake was 1 (no temperature response). This Q_{10} for emissions is lower than the value of 3-4 reported for field conditions by Conrad (1989); or by Morrissey et al. (1993) who reported an 9-fold increase in emissions in wet-meadow tundra corresponding to a 6^{o}C warming (from 3.3 to 9.3 ^{o}C), and is similar to that graphed by Harriss (1993) and Bartlett and Harriss (1993) in reviews of global wetland emissions. The observed temperature effect in all these studies (including the present one) may be confounded, however, since the largest changes in temperatures were due to the seasonal progression and topographic moisture gradients (Bartlett, et al., 1989). In laboratory studies with soil from northern wetlands, Valentine et al.(1994) found Q_{10} of methane production of 1.7-4.7. In slurries of peat soil, Schimel (1993) found Q_{10} of 3-4.

The lack of a temperature response for uptake has been reported by many other studies (e.g., Dorr, et al., 1993; Keller, et al., 1983; Schimel, et al., 1993; Steudler, et al., 1989; Striegl, et al., 1992; Torn, 1994; Valentine, et al., 1993). A few laboratory studies, however, report Q_{10} for consumption in the range of 1.4-1.9 for a temperature range 0-25 ^{o}C (Dunfield, et al., 1993; Whalen, et al., 1990).

The differential response of methane production and consumption to temperature has implications for the seasonal cycle of methane and how the annual cycle of methane flux is modeled or extrapolated from a limited set of field measurements. This research suggests that the differential response may result in changes in fluxes that are more rapid and larger than expected, particularly in ecosystems with seasonally-shifting areas of production and consumption and/or vertically layered production and consumption.

The differential response is also important for modeling the impacts of global warming on the methane budget. Currently, oxidation in sediments is the single largest sink of methane, accounting for 50% more oxidation than atmospheric OH^- (Reeburgh, et al., 1992). Approximately 70% of the methane produced in soils is oxidized before it reaches the atmosphere. The current net flux of 255 Tg/yr from ecosystems (wetlands, rice paddies, and landfills) is the difference between 879 Tg/yr of methane produced in soils and 624 Tg/yr consumed in soils (Reeburgh, et al., 1992). If warming increases methane production more than it increases soil-methane oxidation, as these results suggest, warming may cause a large change in the net flux of methane from soil to atmosphere.

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Whalen, S.C., Reeburgh, W.S., and Sandbeck, K.A. (1990). Rapid methane consumption in a landfill cover soil. Applied and Environmental Microbiology, 56(11), 3405-3411.

Yavitt, J.B., Downey, D.M., Lang, G.E., and Sextone, A.J. (1990a). Methane consumption in two temperate forest soils. Biogeochemistry, 9, 39-52.

Yavitt, J.B., Lang, G.E., and Sextone, A.J. (1990b). Methane fluxes in wetland and forest soils, beaver ponds, and low-order streams of a temperate forest ecosystem. Journal of Geophysical Research, 95D(13), 22,463-22,474.

Table 1. U.C. Hopland Research and Extension Center (39°00' N, 123°04' W). Ridge I is mapped to Yorkville series (Pachic Argixerolls) soils and glaucophane schist and related metamorphic rock parent materials. Ridge II and Ridge III are mapped to Josephine series (Typic Haploxerults) soils and hard sandstone and shale parent materials. The three pond-area sites are mapped to Sutherlin series (Ultic Haploxeralfs) soils and hard sandstone and shale parent materials[1].

Site	**Dominant Vegetation** [2]	**Elevation Relative to Pond Surface**[3]	**Soil Carbon Content**	**Soil Nitrogen Content**	**Soil Bulk Density 0-12 cm (g/cm^3)**
Pond margin	*Typha sp.*, *Juncus sp.*, and *Carex spp.*	0 m	6.4 %	0.72 %	na
Transition	*Mentha pullegium*, *Juncus sp.*, and *Cradium sp.*	0.6 m	6.4 %	0.65 %	1.22
Pond grassland	*Bromus rigidus*, *Viscia sp*, and *Mentha pullegium*	1.5 m	3.9 %	0.37%	1.34
Ridge I grassland	*Bromus spp.*, *Poa scabrella*, *Stipa pulchra*, and *Aegilops triuncialis*	80 m	2.5 %	0.25 %	1.44
Ridge II grassland	*Bromus spp.*, *Poa scabrella*, *Viscia sp.*	60 m	1.2 %	0.13 %	na
Ridge III grassland fertilized	*Bromus spp.*, *Phalaris aquatica*, and *Abina sp.*	260 m	2.0 %	0.17 %	na
Ridge I grassland grazed	*Bromus mollis*, *Aira caryophyllea*, *Brodea sp.*, *Lasthenia sp.* and *Plantego sp.*	80 m	3.0 %	0.30 %	1.42
Ridge II grassland grazed	*Bromus spp.*, *Poa scabrella*, and *Viscia sp.*	60 m	1.6 %	0.16 %	na
Ridge III grassland fertilized and grazed	*Hordeum vulgare*, *Cerastium viscosum*, *Erodium botrys*, and *Trifollium subterraneum*	260 m	2.5 %	0.21 %	na

[1] Soil types from personal communication from Chuck Vaughn, U.C. Hopland Research and Extension Center.

[2] Grassland sites also include unidentified annual grass species.

[3] Base elevation of pond = 980 m. Elevations from USGS topographic map.

Table 2. Net Methane Flux by Elevation Level. Mean flux rate is averaged over one annual cycle (October 1991 - October 1992) except where it is noted that 1993 data are included.

Site	**Mean Net Flux (± SE)** **mg CH_4 m^{-2} d^{-1}**	**Range**	**n**	**Implied Annual Flux** **g m^{-2} y^{-1}**
Pond	38.2 (± 16.8)	-0.1 - 229.8	18	13.9
Transition	6.0 (± 2.3)	-1.8 - 43.5	22	2.2
Pond grassland	-0.7 (± 0.1)	-2.2 - 0.2	24	- 0.26
Ridge grassland	-0.6 (± 0.2)	-2.3 - 0.3	18	- 0.23
Pond and ridge grassland	-0.7 (± 0.1)	-2.3 - 0.3	42	- 0.25
Pond grassland (including when flooded in 1993)	2.3 (± 1.5)	-2.2 - 25.8	28	
Ridge grassland including 1993	-0.4 (± 0.1)	-2.3 - 0.8	30	
Flooded soil (pond surface measurements when the surface was at pond, transition or grassland elevation)	30.8 (± 11.1)	0 - 229.8	27	

Table 3. Correlation Between Methane Uptake and Soil Carbon or Nitrogen Content. Methane uptake is the average of all measurements at each site except the Transition site, which includes only measurements with downwards flux (uptake). (pond grassland n= 6 days (24 chambers); R-I n= 6 days (18 chambers per treatment); R-II and R-III n= 4 days (12 chambers per treatment); transition n =3 days (11 chambers).

Land Use	**Sites**	**Pearson R^2 Carbon**	**Pearson R^2 Nitrogen**	**n**
natural grasslands	pond grassland, R-I, R-II	0.980	0.989	3
grazed and ungrazed grasslands	pond grassland, R-I, R-II, R-IG, R-IIG	0.973	0.990	5
All grasslands	pond grassland, R-I, R-II, R-IG, R-IIG, R-IIIF, R-IIIFG	0.541	0.419	7
All sites except fertilized	pond grassland, R-I, R-II, R-IG, R-IIG, transition site	0.677	0.646	6
All sites	(all sites except pond)	0..389	0.324	8

Table 4. Regressions of Methane Flux on Soil or Water Temperature. Positive flux refers to mass flow from soil to atmosphere. Regressions do not include data collected in February 1993, because disturbance of mud may have artificially increased flux rates. Dropping the two high flux measurements from July 1992 does not significantly change the log(flux) regression. The methane uptake sites do not include grazed or fertilized pastures. Temperature is soil or water temperature at 10 cm below the surface. For logarithmic equation, temperature is Kelvin (°C+273.15).

Model	**Constant**	**Slope (m)**	**R^2**	**p, m<>0**	**n**
Methane-emission sites					
Flux = Constant + m*Temperature	-42.534	3.908	0.172	<0.025	29
Ln(Flux) = Constant + m*Temperature	-26.64363	.101157	0.373	<0.001	29
Methane-uptake sites					
Flux = Constant + m*Temperature	-0.880	0.012	0.014	<0.372	58

Table 5. Methane Concentrations in Soil Where There is Methane Uptake at the Surface. Greater than ambient ($[CH_4] > 2.0$ ppm) concentrations may indicate microsites of methane production in the soil. Data from the pond area (pond, transition, and pond grassland sites). Columns C and D refer to profile measurements under chambers showing methane uptake at the soil-atmosphere boundary (Column A).

Date of observation	A. Number of chambers showing methane uptake at surface	B. Total number of soil-atmosphere concentration measurements under chambers in Column A	C. Number of soil-atmosphere concentration measurements with $[CH_4] > 2.0$ ppm	D. % of soil-atmosphere concentration measurements with $[CH_4] > 2.0$ ppm
Jan 21,'92	8	45	5	11 %
Feb 3, '93	0	--	--	--
Mar 4, '92	4	29	4	14
May 5, '92	4	38	18	47
Jul 8, '92	4	28	1	4
Oct 10,'92	8	61	2	3
Oct 31,'91	7	12	2	17
TOTAL	**35**	**213**	**32**	**15 %**

Figure Captions

Figure 1. Monthly mean air temperatures (average of daily maximum and of daily minimum) and rainfall at U.C. Hopland Research and Extension Center, Hopland, California (39°00' N, 123°04' W). Sampling dates for the pond and/or ridgetop are indicated by empty circles along the x-axis. Temperature was measured with National Bureau of Standards calibrated mercury thermometer. Rainfall was measured with a Belfort 5-780 recording rain gauge. The empty circles on the horizontal axis shows dates of sampling.

Figure 2. Schematic of the relative elevation of the sampling sites during (a) the dry season and (b) with the grassland site flooded in winter 1993.

Figure 3. (a) Methane flux (positive flux is emission, negative flux is uptake), (b) soil moisture , and (c) soil temperature at the pond, transition, and pond grassland sites over 17 months.

Figure 4. Comparison of grazed and ungrazed grasslands: (a) methane uptake, (b) soil carbon content, and (c) soil nitrogen content.

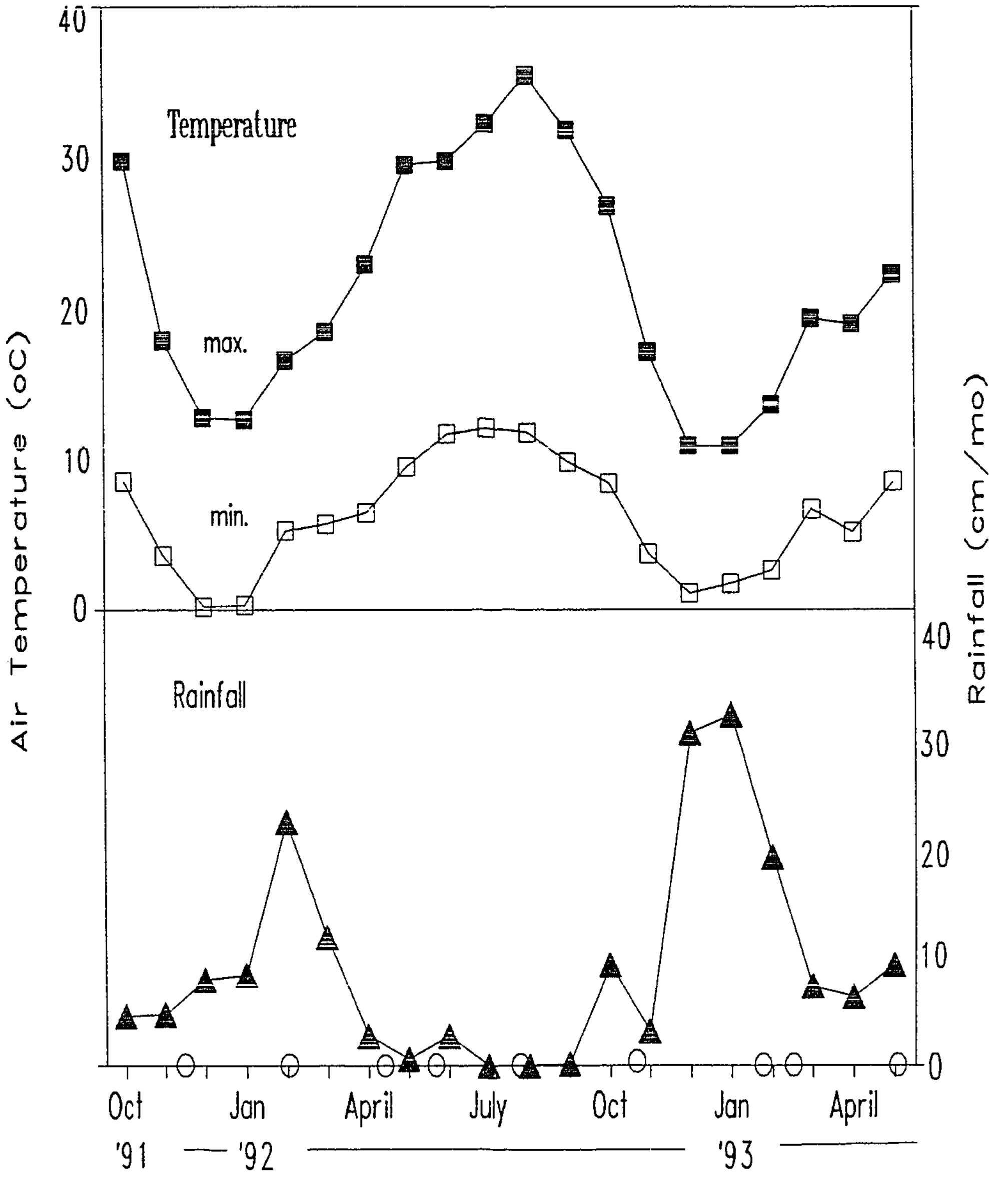
Figure 5. Methane uptake vs (a) soil nitrogen content and (b) soil carbon content for each of the grassland sites and the transition site. The transition-site flux value is the average of the measurements at that site with methane uptake (n=11). The regression line was generated from the 5 unfertilized grassland sites.

Figure 6. Net methane flux vs. soil moisture with data from all ungrazed, unfertilized sites (n=68). On vertical axis, positive flux is emission and negative flux is uptake.

Figure 7. Net methane flux vs. temperature for (a) sites of methane emission and uptake and (b) only for sites of uptake. On vertical axis, positive flux is emission and negative flux is uptake.

Figure 8. Net methane flux and soil moisture in May 1992. (a) Methane flux in control chambers. (b) Soil moisture. Data are means and + 1 standard error. At the pond site, n= 2 chambers, at the transition site control n= 3 and methyl-fluoride n=1, and at the grassland site n=4. On vertical axis, positive flux is emission and negative flux is uptake..

Figure 9. Depth profiles of methane in soil atmosphere in spring (May) and fall (October) of 1992. The numbers on the right border of the May, grassland graph give the concentration of methane in soil atmosphere for single measurements at the indicated depths . These individual points indicate microsites of methane production. Each data point is the mean of 4-8 samples collected near the chambers. The standard errors for mean concentrations in May were: Pond Grassland: SE = 0.17, 0.16, 0.77, 0.47, and 0.37 ppm for 10, 15, 20, 30, and 50 cm depth, respectively, not including the two data points shown separately on right-hand side of graph. Transition: control chambers: SE = 112 and 67 ppm for 10 and 15 cm depth, respectively. Transition, inhibitor-added chamber: SE = 182 and 39 ppm for 10 and 15 cm depth, respectively. The standard errors for mean concentrations in October were: Pond Grassland: SE = 0.04, 0.07, 0.08, and 0.06 ppm for 10, 15, 20, and 30 cm depth, respectively. Transition: SE = 0.21, 0.03, 0.09, and 0.04 ppm for 10, 15, 20, and 30 cm depth, respectively.



40
30
20
10
0
Air Temperature (oC)
Temperature
max.
min.
Rainfall
Rainfall (cm/mo)
40
30
20
10
0
Oct
Jan
April
July
Oct
Jan
April
'91
'92
'93

Figure 1

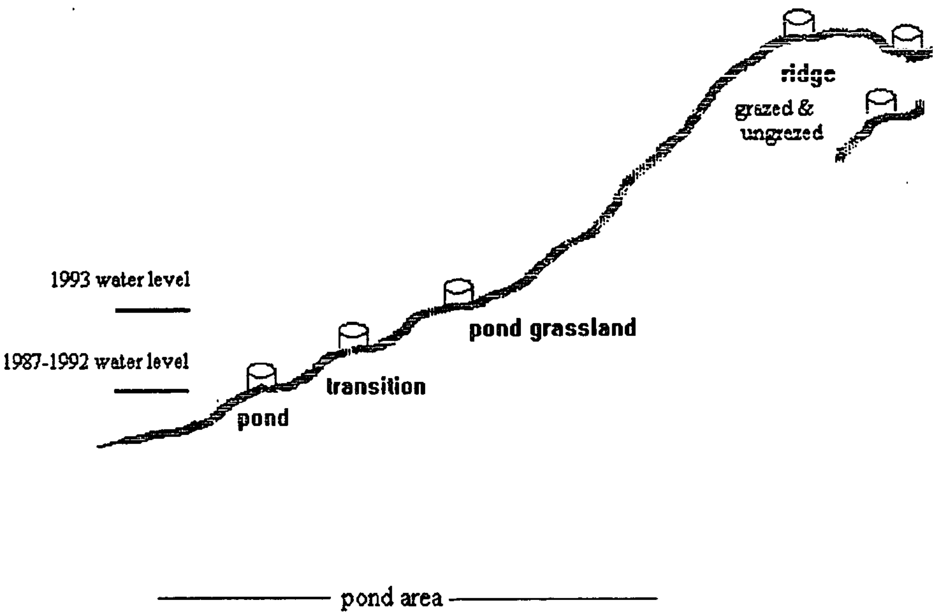

1993 water level
1987-1992 water level
pond
transition
pond grassland
ridge
grazed &
ungrazed
pond area

Figure 2

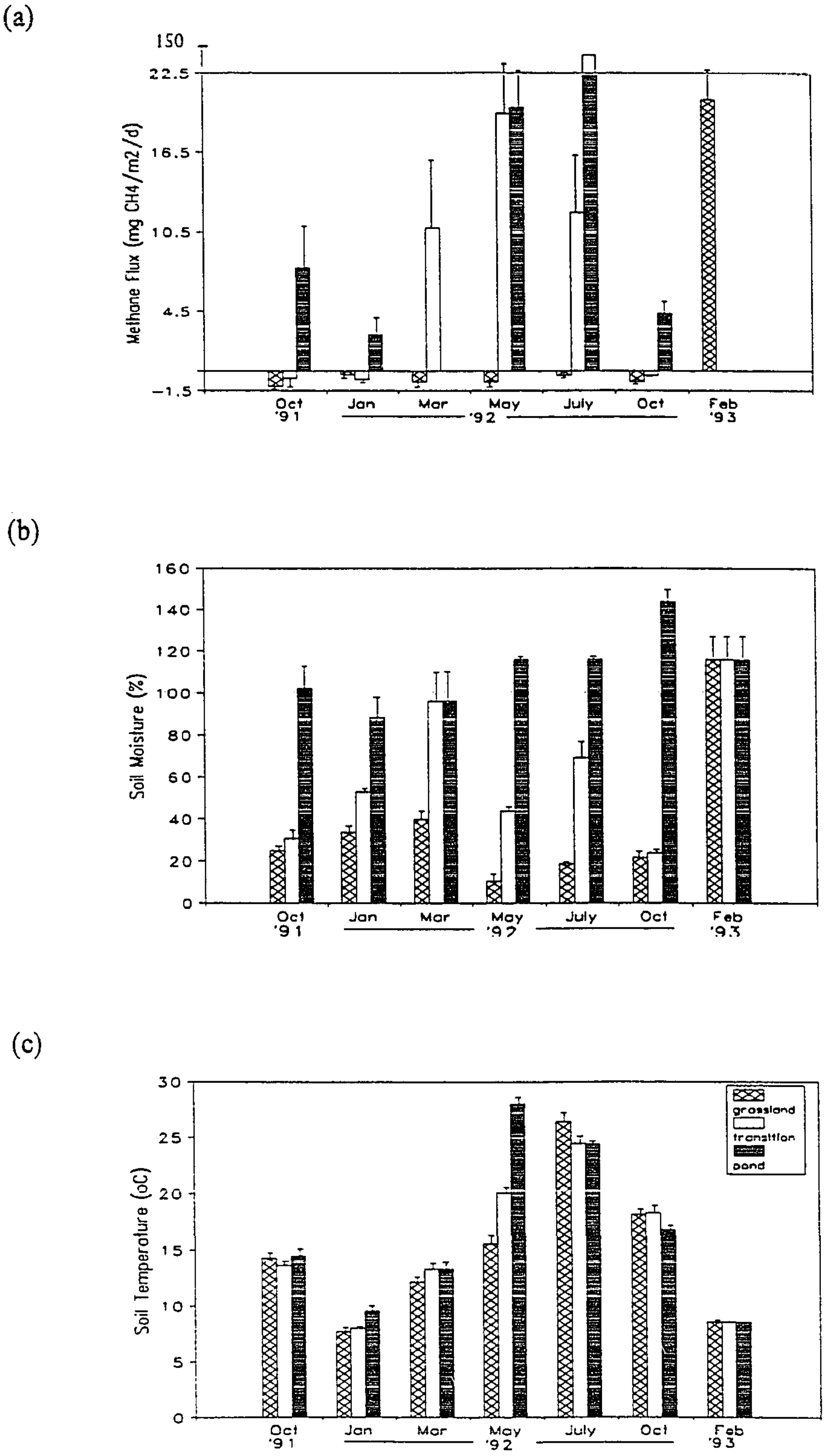

(a)
150
22.5
16.5
10.5
4.5
-1.5
Methane Flux (mg CH4/m2/d)
Oct '91
Jan
Mar
May '92
July
Oct
Feb '93
(b)
160
140
120
100
80
60
40
20
0
Soil Moisture (%)
Oct '91
Jan
Mar
May '92
July
Oct
Feb '93
(c)
30
25
20
15
10
5
0
Soil Temperature (oC)
grassland
transition
pond
Oct '91
Jan
Mar
May '92
July
Oct
Feb '93

Figure 3

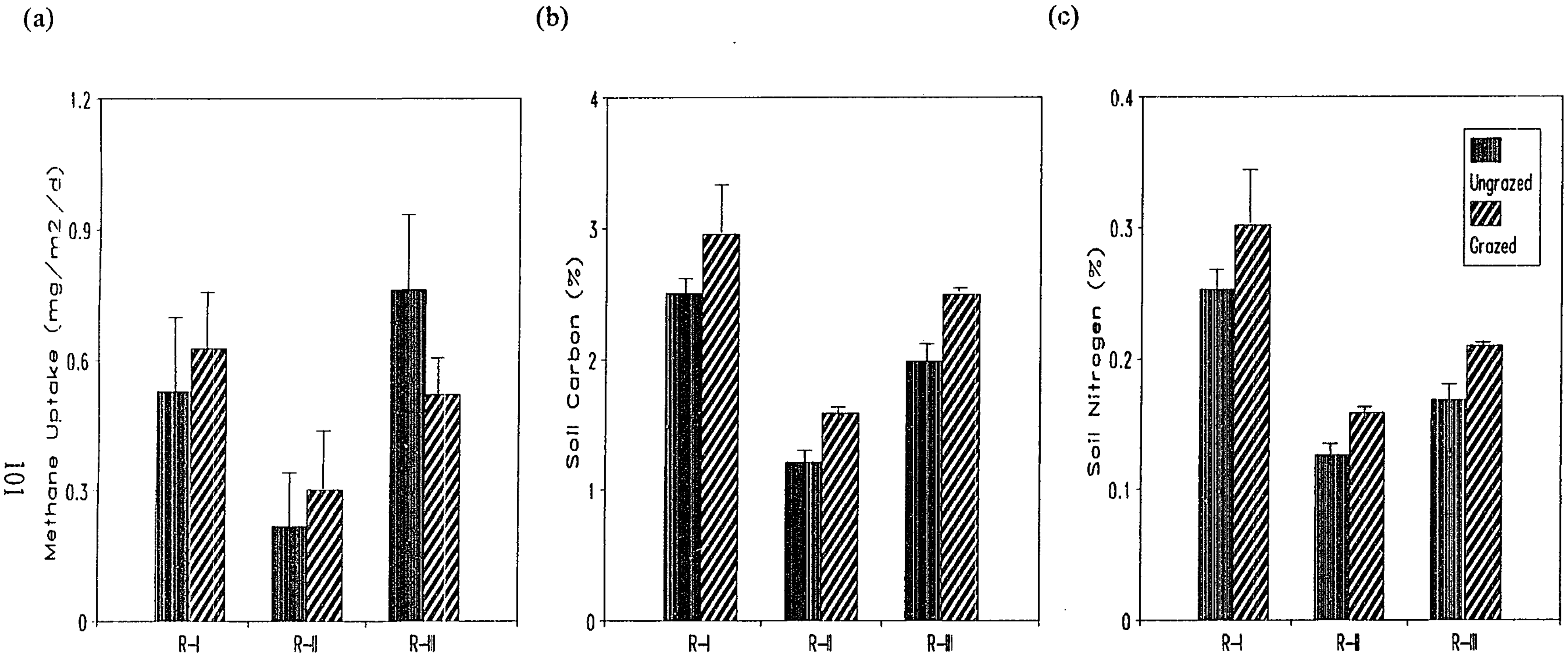

(a)
(b)
(c)
Methane Uptake (mg/m2/d)
1.2
0.9
0.6
0.3
0
R-I
R-II
R-III
Soil Carbon (%)
4
3
2
1
0
R-I
R-II
R-III
Soil Nitrogen (%)
0.4
0.3
0.2
0.1
0
R-I
R-II
R-III
Ungrazed
Grazed

Figure 4

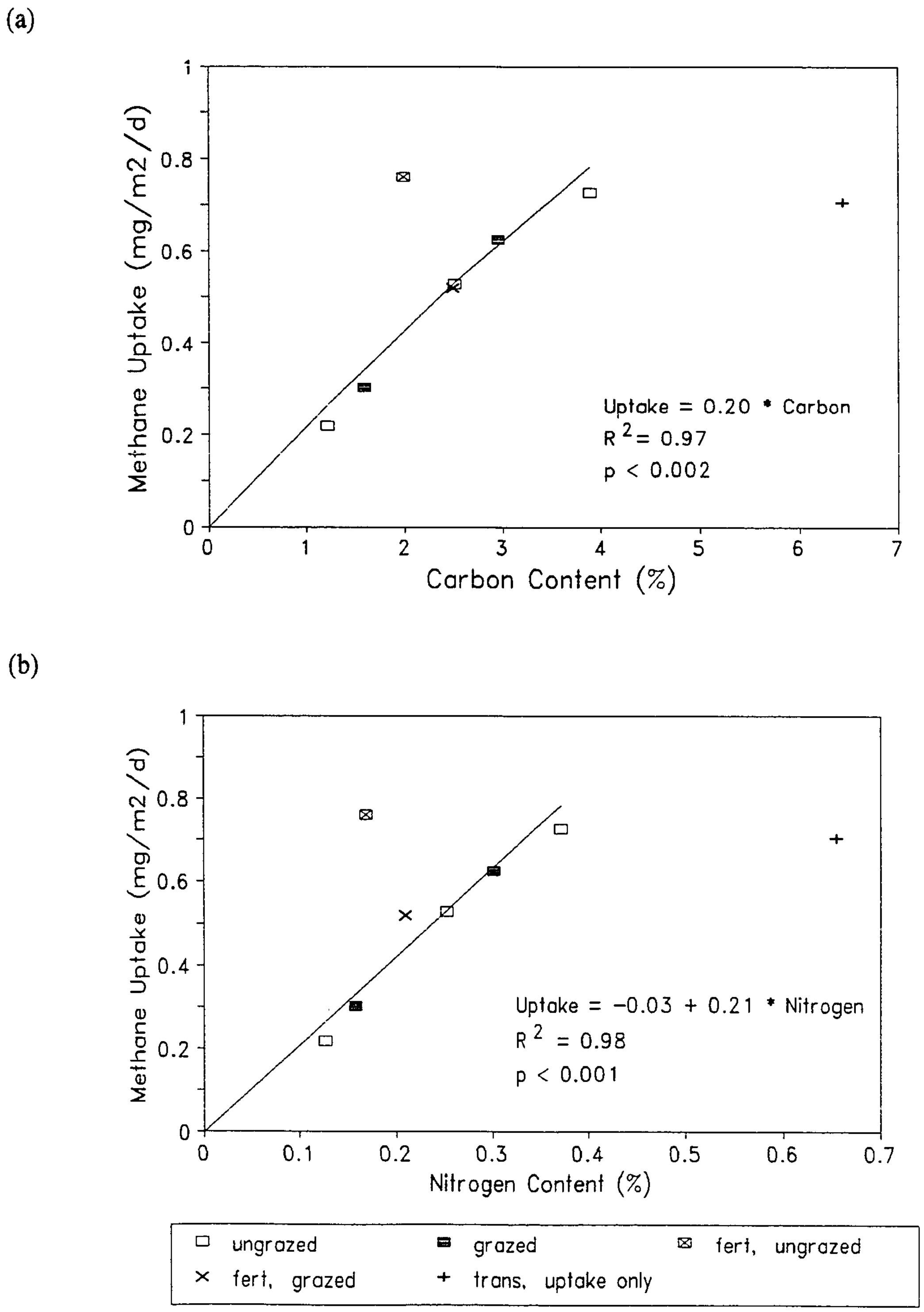
(a)
Methane Uptake (mg/m2/d)
0
0.2
0.4
0.6
0.8
1
0
1
2
3
4
5
6
7
Carbon Content (%)
Uptake = 0.20 * Carbon
R 2= 0.97
p < 0.002
(b)
Methane Uptake (mg/m2/d)
0
0.2
0.4
0.6
0.8
1
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
Nitrogen Content (%)
Uptake = -0.03 + 0.21 * Nitrogen
R 2 = 0.98
p < 0.001
□ ungrazed
▬ grazed
☒ fert, ungrazed
× fert, grazed
+ trans, uptake only

Figure 5

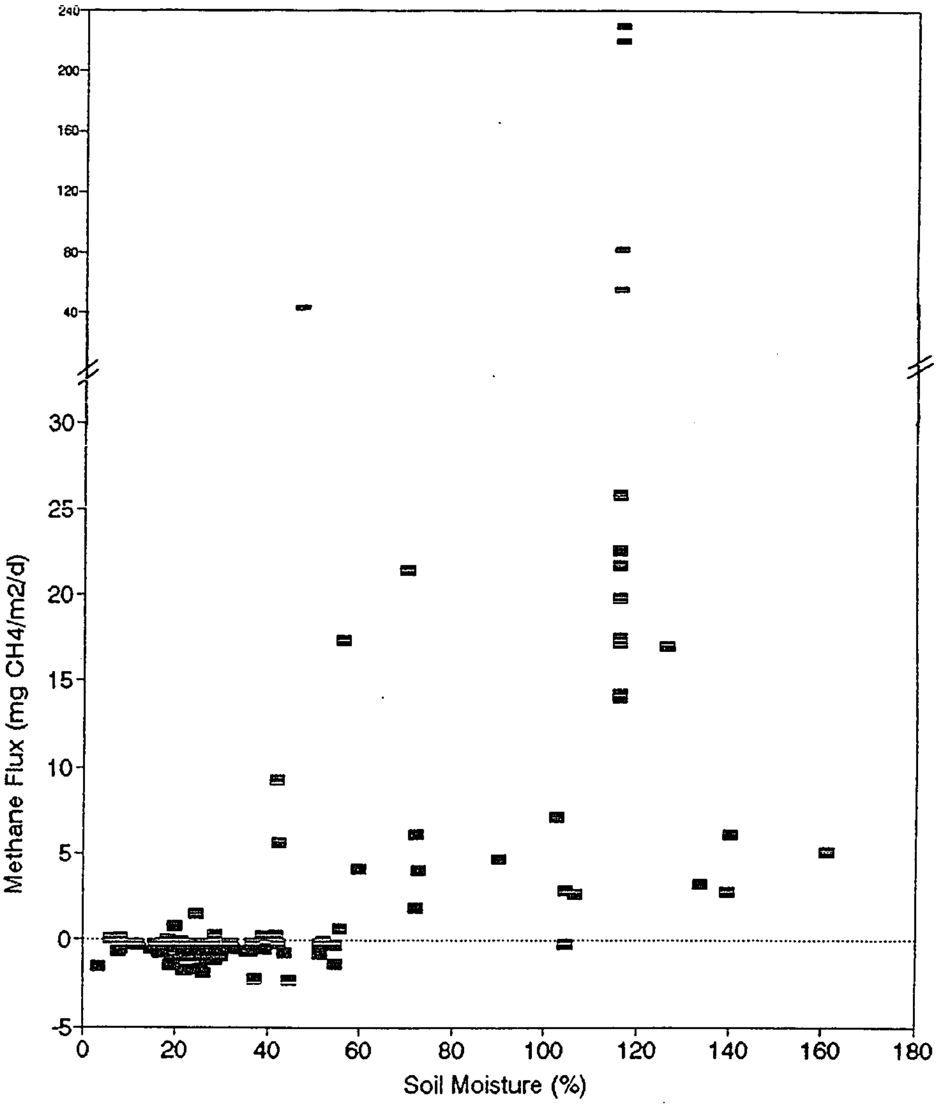
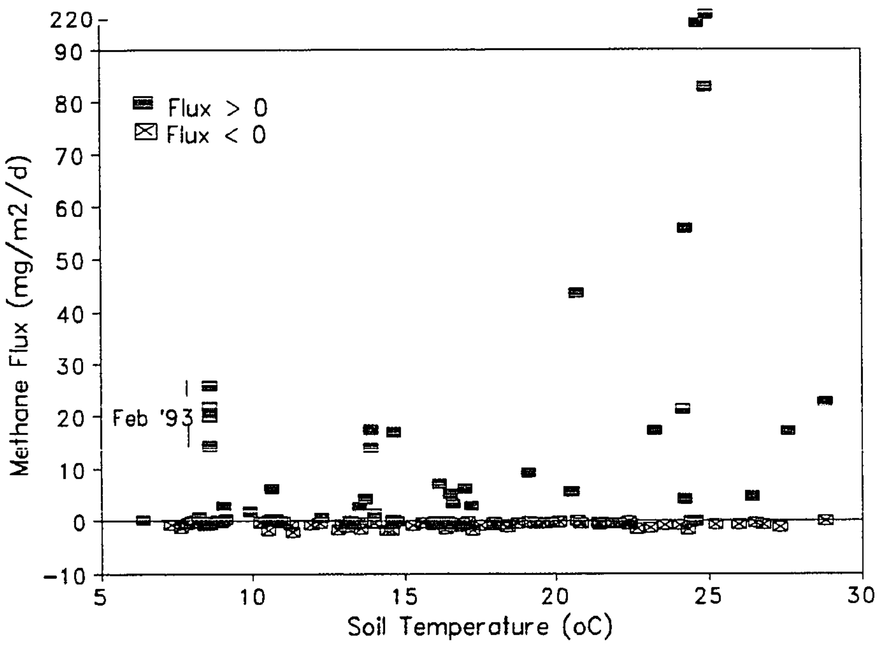

240
200
160
120
80
40
30
25
20
15
10
5
0
-5
Methane Flux (mg CH4/m2/d)
0
20
40
60
80
100
120
140
160
180
Soil Moisture (%)

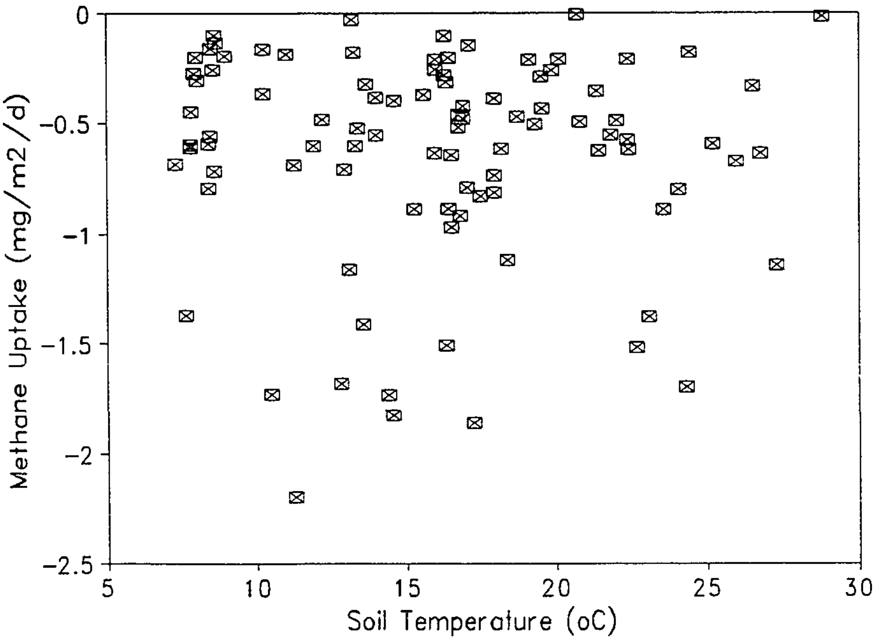
Figure 6

(a)



220
90
80
70
60
50
40
30
20
10
0
−10
Methane Flux (mg/m2/d)
Flux > 0
Flux < 0
Feb '93
5
10
15
20
25
30
Soil Temperature (oC)

(b)



0
−0.5
−1
−1.5
−2
−2.5
Methane Uptake (mg/m2/d)
5
10
15
20
25
30
Soil Temperature (oC)

Figure 7

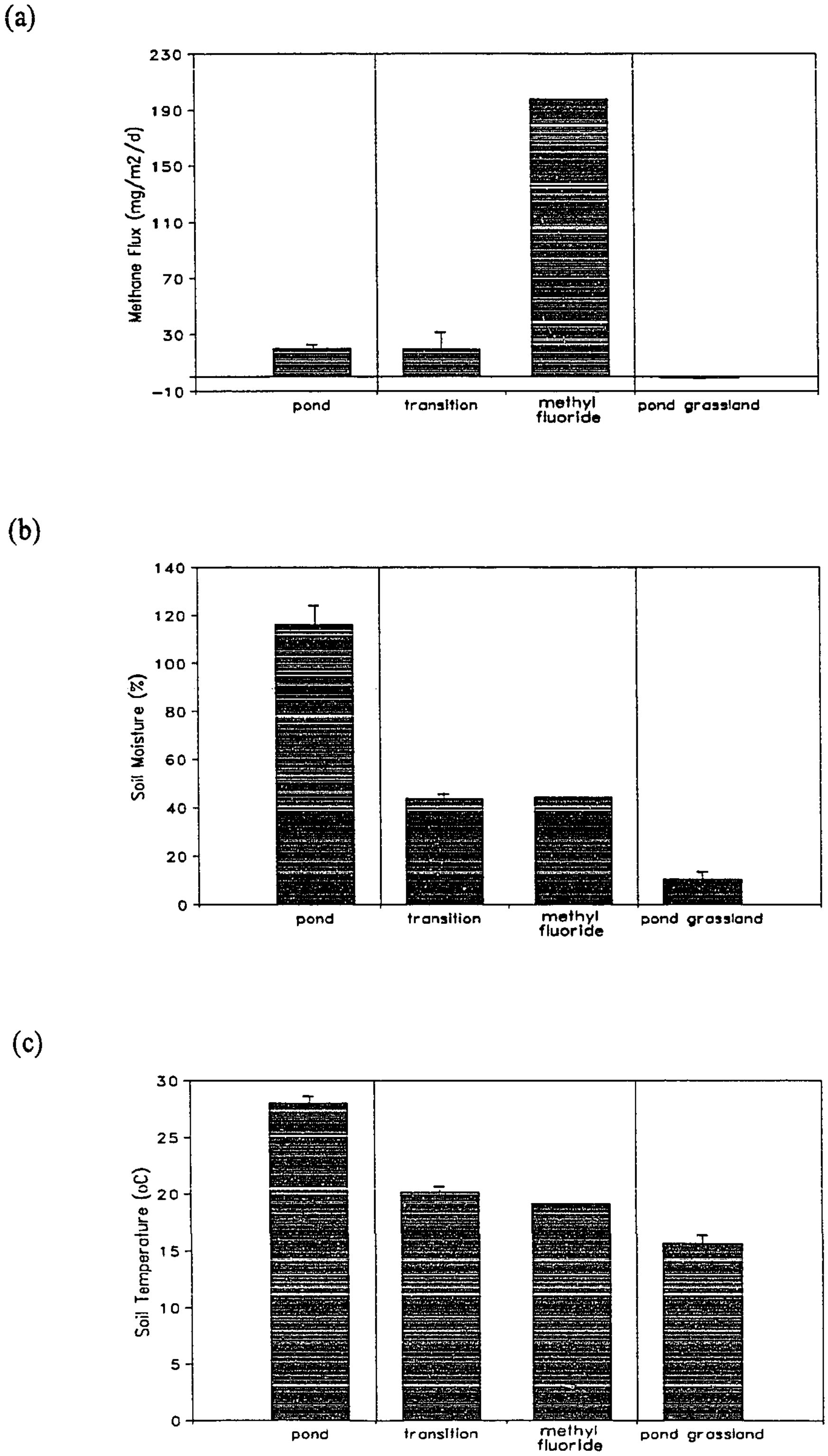

(a)
230
190
150
110
70
30
−10
Methane Flux (mg/m2/d)
pond
transition
methyl fluoride
pond grassland
(b)
140
120
100
80
60
40
20
0
Soil Moisture (%)
pond
transition
methyl fluoride
pond grassland
(c)
30
25
20
15
10
5
0
Soil Temperature (oC)
pond
transition
methyl fluoride
pond grassland

Figure 8

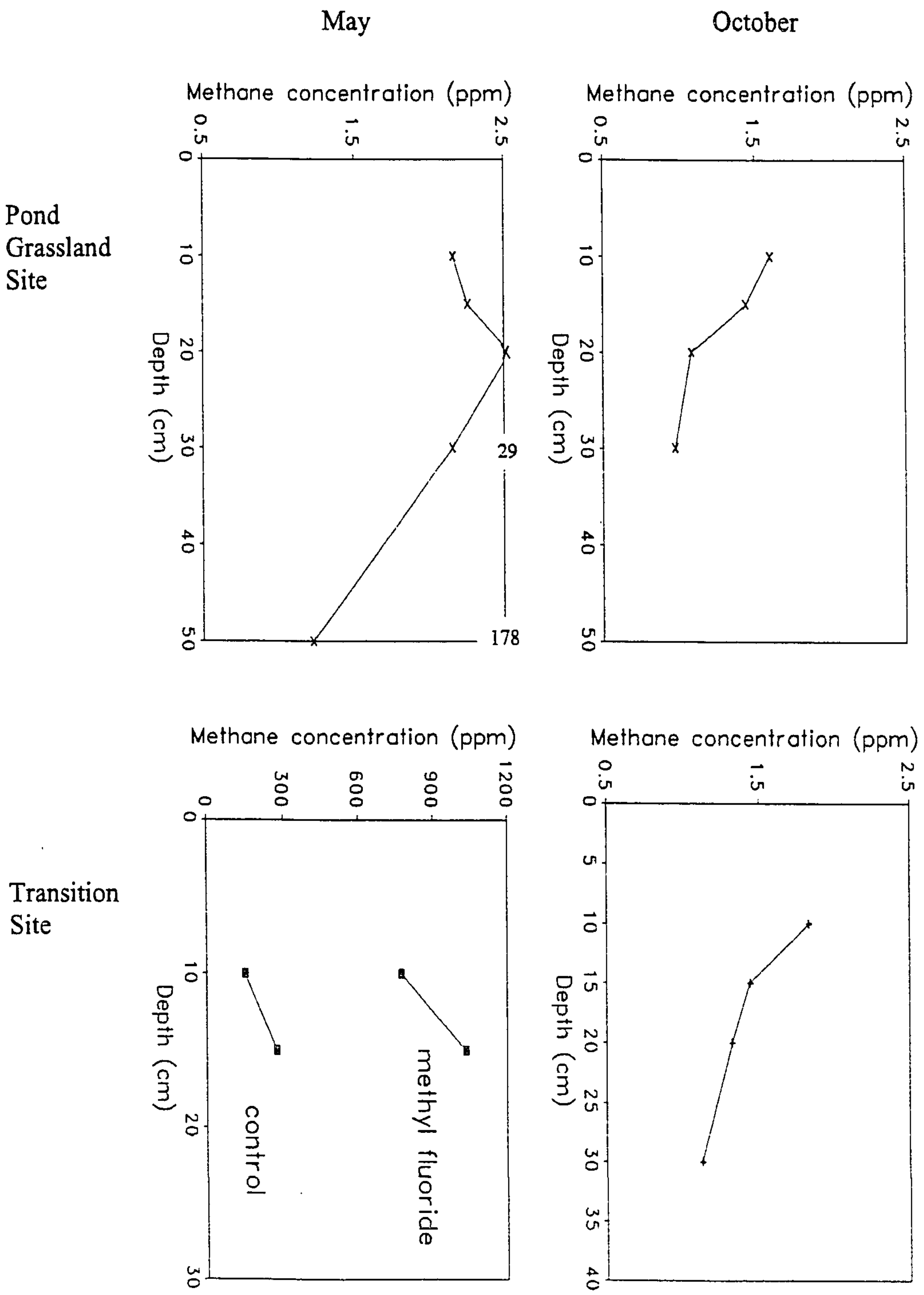

May
October
Pond Grassland Site
Transition Site
Methane concentration (ppm)
0.5
1.5
2.5
Depth (cm)
0
10
20
30
40
50
29
178
Methane concentration (ppm)
0
300
600
900
1200
Depth (cm)
0
10
20
30
methyl fluoride
control
Methane concentration (ppm)
0.5
1.5
2.5
Depth (cm)
0
5
10
15
20
25
30
35
40

Figure 9

CHAPTER 5

CONCLUSION

My dissertation research investigated the environmental factors that influence methane release and uptake (production and consumption) by ecosystems. The goals of my research were (1) to characterize methane flux from previously unstudied ecosystems, (2) to compare the response of production and consumption to environmental change, and (3) to consider the potential for anthropogenic influences on ecosystems to alter global methane fluxes and thereby change the greenhouse performance of the atmosphere.

To address these goals I conducted field experiments at three sites in the western United States: arctic tundra in Alaska, montane meadow in Colorado, and annual grassland in California. These sites spanned a range of temperature and moisture regimes, vegetation communities, and experimental conditions. At each site I measured methane fluxes from soil to the atmosphere by the static chamber method, as well as measuring a suite of climatic and ecological factors.

The central hypothesis of my dissertation is that because methane flux between ecosystems and the atmosphere is the balance of two larger fluxes (methane production and methane consumption within ecosystems), and, because methane production and consumption respond differently to the same environmental change, it follows that ecosystems or regions that currently have low net fluxes but high gross fluxes could experience a dramatic change in net flux due to climatic change.

The results of my research bear this hypothesis out. Due to the influence of temperature on ecosystem-methane fluxes, there is potential for positive feedback between climate and ecosystem-methane release. Moreover, the potential strength of this feedback is greater than would be predicted if one analyzed only methane production. Specifically, the potential strength of this feedback is greater because ecosystem-methane flux is the balance between production and consumption, and these two processes respond differently to temperature change. My second major finding regarding feedback is that the direction and strength of feedback with climatic change may depend on initial climatic conditions rather than being always linear with change in climatic variables.

In this concluding chapter I summarize three sets of empirical results. First, I present average flux rates for each ecosystem in which I worked. Second, I discuss the influence of two climatic factors, temperature and moisture, on methane release and uptake. This discussion is the centerpiece of the chapter, where I make my arguments supporting the hypothesis described above. Third, I summarize my observations about the influence of several non-climatic environmental factors on methane flux, including the linkages between anthropogenic activities and methane release and uptake. Finally, I conclude with a brief discussion of the implications of my research for research and public policy. More detailed analysis behind the conclusions about Alaskan tundra is found in Chapter 2; about Colorado montane meadow in Chapter 3; and about California grasslands and pond in Chapter 4.

Methane Fluxes

The ecosystems of the western United States that I studied have methane fluxes comparable to those of similar ecosystems in other parts of the world. Methane emissions at both wetland and pond ecosystems were as high as 230 mg CH_4 m^{-2} d^{-1}.

The average emission rate for the temperate pond site was 38 mg CH_4 m^{-2} d^{-1} and the average for the Alaskan wet tundra (wetland) site was 52 mg CH_4 m^{-2} d^{-1}. These emission rates are slightly lower than those reported by other researchers for tundra (Bartlett and Harriss, 1993; Harriss, et al., 1993) or ponds in the eastern U.S. (Yavitt, et al., 1990). Methane uptake at the drier sites ranged as high as -3.4 mg CH_4 m^{-2} d^{-1}, with average uptake of -1.2 mg CH_4 m^{-2} d^{-1} in the montane meadow and -0.7 mg CH_4 m^{-2} d^{-1} in the annual grassland. Since these were the first measurements published for uptake in montane meadow or annual grassland ecosystems, direct comparisons are not possible. Uptake rates at these sites were higher, however, than in prairie (Ojima, et al., 1993; Tate and Striegl, 1993), sagebrush-grasslands (Mosier, et al., 1991), or sub-alpine meadow (Mosier, et al., 1993) ecosystems.

The values given above are for measurements made at midday in the summer (for the northern or high altitude systems) and year 'round in California. To extrapolate these measurements to an estimate of annual methane flux rate requires making assumptions about the diurnal and annual cycles of fluxes. Investigating the diurnal and annual cycles in flux is also a way to study the influence of change in temperature and moisture on flux. In this section I present the temporal patterns of flux. The next section addresses explicitly the influence of temperature and moisture on flux.

My research suggests that there is not a strong diurnal cycle in methane flux. In Colorado, where I measured 4 diurnal cycles of uptake, I did not see a significant diurnal cycle (i.e., effect of hour in an analysis of variance). Furthermore, I am not aware of any published studies that have found a pronounced diurnal cycle in uptake. It appears that variation in temperature and moisture over a time scale of hours does not affect uptake rates. For methane emissions, there is an additional avenue for diurnal variation, because plants that transport methane may close their stomatal openings in the dark and thus decrease emissions at night. However, at the methane-emitting sites of Alaska, I found that the plant transport of methane was not reduced in experimentally darkened sites relative to sites with full light (Chapter 2).

The annual cycle of methane flux reflects changes in soil conditions (including inundation and freezing/thawing), snowpack, and plant biomass. According to my research, the influence of vegetation is important for methane emissions but not for methane uptake (Chapters 2, 4). Regarding uptake, then, the magnitude of the annual cycle is greatest where climate is most severe (Alaska) and flattest where climate is mildest (California). Methane consumption is near zero during the winter in the tundra and boreal systems (Whalen and Reeburgh, 1992). Uptake may persist under snowpack in some regions, however, such as the midwest U.S. (Mosier, et al., 1993; Sommerfeld, et al., 1993). I saw almost no intra-annual variation in uptake by grasslands except where inundation was a factor. In those cases, seasonal changes in inundation changed flux by an order of magnitude (Chapter 4). The estimated annual flux rate from each ecosystem is given in Table 1, both with and without the inclusion of seasonally saturated sites for the grassland average. I use snow-free days as an estimate for microbially-active days.

The Balance of Methane Production and Consumption

The net flux from each ecosystem I studied was the balance of seasonally-shifting areas of net methane production and net consumption. In California the most important element of this shift was change in the water level of the pond; the grassland at the pond margin shifted from methane uptake to methane release when covered with water. In Colorado, just below the meadow sites there was a willow bog that emitted methane in the spring and early summer (data not shown). In Alaska, the topographic moisture gradient from wetlands to tussock tundra is associated with a gradient in flux from high emissions to very weak uptake; presumably, different areas of the landscape become microbially-active (i.e., release or take up methane) at different times as the soil thaws out in late spring and early summer.

At certain sites, net flux was the balance of production in the saturated soil at depth and methane consumption in the overlying, aerobic surface soil. In California, I demonstrated that both processes were occurring using a combination of soil methane profiles, a soil moisture curve, and *in situ* applications of an oxidation inhibitor. In Alaska, the same processes were documented using plant removal, plant replacement (with straws[1]), and laboratory incubations. At the California and Alaska sites, I concluded that surface oxidation was an effective bio-filter limiting methane release from anaerobic soils.

The Influence of Soil Temperature and Moisture on Methane Flux

Over the annual cycle and across landscape gradients at a given time, I saw a positive influence of soil moisture and temperature on methane fluxes at all three sites, with moisture being the dominant factor. This pattern was mainly due to (a) the large change in methane flux rates between unsaturated and saturated soil and (b) the temperature responsiveness of methane emissions. Specifically, unsaturated soils were generally sites of methane uptake (small negative fluxes) while saturated soils were sites of methane emissions (large positive fluxes) that increased as temperature increased. Methane uptake also increased as temperature increased in montane meadow, but not in annual grassland[2].

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[1] Straws were either plastic "party" straws (~4 mm diameter) from the Toolik dining hall or stainless steel tubes (3 mm diameter).

[2] I had insufficient data to analyze tundra response.

Potential for Feedback with Climate Change

The ecosystems of the western United States (that I studied) have methane fluxes that are highly responsive to variation in climate. All my observations support the potential for feedback between climate change and ecosystem-methane flux. The ecosystem responses vary, however, generating both positive and negative feedback with climate change. The feedback loop I am considering consists of atmospheric greenhouse-gas concentrations, climate factors, and methane emissions/uptake. For example, a negative feedback means that climatic changes caused by an increase in atmospheric methane influence ecosystems such that less methane is emitted and/or more is taken up.

The effect of moisture on methane fluxes was not linear for either emissions or uptake. As shown in Figure 1, emissions do not continue to steeply increase with increases in soil moisture or water depth once soils are inundated; a decrease in moisture does not continue to increase uptake rates once moisture content gets very low. Specifically, at the pond margin, fluxes increased sharply with an increase of moisture when moistures bracketed saturation; but once soils were inundated by more than a few cm of water, the depth of water or the water content of sediment was not significantly correlated with emissions rates. In the montane meadow, where soil moistures ranged from saturated to only 10% gravimetric moisture, the relationship between methane uptake and moisture followed the non-monotonic shape shown in Figure 1. Decreases in soil moisture when the soil was moist were correlated with increased uptake; but with dry soil (e.g., <25% gravimetric water content), further drying was associated with decreased uptake. I did not see a parallel response in the annual grassland, possibly because I measured soil moisture at the surface whereas in the montane meadow this result was detected with soil moisture at 25 cm depth (the depth of greater methanotrophic activity).

For feedback with respect to climatic change (where, for the sake of an example, climatic change means soil drying), the implications for response at a given site are four-fold: (1) if the water table stays above the soil surface, inundated ecosystems may generate no feedback or weak negative feedback; (2) if the water table is at, or falls below, the soil surface, inundated ecosystems may generate strong negative feedback; (3) under moist to mesic conditions, uptake may generate negative feedback; and (4) under dry conditions, uptake may generate positive feedback. These feedbacks are given for the case where global warming reduces soil moisture; for the opposite case, the sign of feedback is reversed.

Regarding changes in temperature (independent of effects on moisture), the feedbacks are easier to characterize. Assuming that global warming increases soil temperatures, methane emissions will generate positive feedback with warming. Methane uptake may generate no feedback or a weak negative feedback with warming.

What do these site-specific feedback-responses tells us about climate change and global methane fluxes? Climatic change in the next centuries is predicted to be spatially variable as well as proceeding at different rates in different parts of the world (Hansen, et al., 1988a; Hansen, et al., 1988b; Harte, et al., 1992; Houghton, et al., 1990; Schneider, et al., 1992). Moreover, The linkages between regional climatic change and microclimatic change are complex. For example, extrapolating changes in air temperature and infra-red radiation to changes in soil temperature depends on plant canopy cover, soil texture, and soil moisture. In a similar vein, translating a change in rainfall, runoff, or evapotranspiration into changes in inundation or soil moisture requires site-specific information about topography, vegetation, soil texture, and land use. Even with the same change in local climatic conditions, two places may respond differently depending on their initial conditions. The timing of response may also be site-specific. For example the creation of new emission sites may depend on the establishment of vegetation. In conclusion, I would not expect to see a coherent or simultaneous response to climate change.

Yet, in the past there must have been large-scale trends in biogenic methane fluxes (as opposed to only changes in the OH sink rate and/or release of clathrates) if ecosystems played any role in the paleontological correlation between atmospheric methane concentration and temperature (Blunier, et al., 1993; Chappellaz, et al., 1990). In the next section, I assume that there would be a large-scale trend in global emissions in response to global warming, for the purpose of evaluating different models of this response to warming.

Differential Response To Moisture and Temperature

Methane emissions and uptake responded differently to the same environmental change: there was a differential response to both moisture and temperature. Despite the non-linearities in moisture response, a fair generalization is that methane emissions and methane uptake had the opposite response to changes in soil moisture. Specifically, an increase in moisture increased emissions/production and decreased uptake/consumption. The differing effect of temperature on methane emission and uptake was less dramatic but quantitatively important. Emissions increased approximately exponentially with temperature increases[3]. Methane uptake showed no response to temperature in grasslands or tussock tundra, and a weak, linear, positive response in montane meadow[4].

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[3] Reviews of emissions from wetlands found the same relationship (Bartlett and Harriss, 1993; Harriss, et al., 1993). Reported Q_{10} are in the range of 3-4 for field studies (Conrad, 1989) and 1.7-4.7 in lab studies (Schimel, et al., 1993; Valentine, et al., 1994).

[4] The lack of a temperature response for uptake has been reported by many other studies e.g.,(Dorr, et al., 1993; Keller, et al., 1983; Schimel, et al., 1993; Steudler, et al., 1989; Striegl, et al., 1992; Valentine, et al., 1993). A few laboratory studies, however, report Q_{10} for consumption in the range of 1.4-1.9 for a temperature range 0-25 oC (Dunfield, et al., 1993; Whalen, et al., 1990).

The differential response is important for modeling the impacts of global warming on the methane budget, e.g. for quantifying the feedbacks described above. One of the main conclusions of my dissertation is that the predicted effect of warming on methane flux is very different depending on whether or not one accounts for (1) the differential response of methane production and consumption and (2) the fact that net emissions are the balance of two gross fluxes. Thus far, global budgets and models have not synthesized these two properties of the methane cycle.

Currently, oxidation in soils is the single largest sink of methane, accounting for 50% more oxidation than atmospheric OH (Reeburgh, et al., 1992). Approximately 70% of the methane produced in soils is oxidized before it reaches the atmosphere (Reeburgh, et al., 1992). If warming increases methane production more than it increases soil-methane oxidation, as these results suggest, warming may cause a large increase the net flux of methane from soil to atmosphere.

To estimate the possible magnitude of this effect, I compare the predicted change in global methane flux (from soil to the atmosphere) calculated with and without taking into account the differential effect and the gross fluxes. These calculations are based on Q_{10} values for methane production and methane consumption. A Q_{10} is a measure of the increase in flux caused by a 10°C warming and is calculated as the ratio (flux at T):(flux at T-10). A Q_{10} of 2 means that methane emissions would double in response to a 10°C warming.

I use temperature-response factors (Q_{10}) from my research and from the literature. In California, the Q_{10} for emissions was 2.75 and Q_{10} for uptake was 1 (no temperature response), based on temperatures at 10-cm depth. Using these as estimates of the Q_{10} for production and consumption, respectively, may exaggerate the differential effect (as explained below). For a conservative estimate of the importance of the differential response, I repeated the calculations with a Q_{10} of production (2.0) and consumption

(1.5), which represent the low and high end, respectively, of published values for these indices[5].

For global methane production and consumption in ecosystems, Reeburgh et al. (1992) estimate that the current net flux of 255 Tg y^{-1} from soils (wetlands, rice paddies, and landfills) is the difference of 879 Tg y^{-1} of methane produced in soils minus 624 Tg y^{-1} consumed in soils (Table 2). For data on gross fluxes from a specific site, I use measurements made in a rice paddy near the end of the growing season (Schütz, et al., 1989) in which consumption and production are nearly equal.

I compare three approaches to calculating a change in global emissions: (1) Single-variable Model 1, which assumes that methane emissions represent all the methane produced in soil (i.e., no consumption filter), (2) Single-variable Model 2, which assumes that methane consumption responds to temperature in the same fashion as does production ($Q_{10,\text{Production}} = Q_{10,\text{Consumption}}$) and (3) Two-variable Model , which assumes that net emissions are the difference of two gross fluxes, each with a different response to temperature. The proportional increases in flux for these models are calculated as:

(1) No Gross Fluxes (Single-variable Model 1) $= (P\text{-}C) * Q_{10,P}) / (P\text{-}C)$

(2) Gross Fluxes, No Diff. Response (Single-variable Model 2) $= (P * Q_{10,P} - C * Q_{10,P}) / (P\text{-}C)$

(3) Gross Fluxes, Differential Response (Two-variable Model) $= (P * Q_{10,P} - C * Q_{10,C}) / (P\text{-}C)$

Where:
P = current production in soil
C = current consumption in soil
$Q_{10,P}$ = temperature response of production
$Q_{10,C}$ = temperature response of consumption
$P\text{-}C$ = net emissions to the atmosphere

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[5] See the two previous footnotes.

Considering the global methane budget, both single- and two-factor models predict large changes in response to warming. There are, however, large differences between these models' predictions. Warmer temperatures cause a much bigger increase in methane emissions based on a model that includes the gross fluxes and differential response to temperature than they do based on models that do not include these features of the methane cycle (Table 2). For a 10^{o}C warming, the single-factor models predict that global methane emissions from rice paddies, wetlands, and landfills increase from 255 Tg y^{-1} to 510-701 Tg y^{-1}, for the conservative literature and California results, respectively. For the same warming, the two-factor model predicts increases to 821-1793 Tg y^{-1}, for the conservative literature and California results, respectively. The two-factor model predicts 1.5 to 3 times more increase in global emissions in response to warming than do the single-factor models. The difference is even more dramatic when consumption and production are roughly equal so that net emissions are near zero, such as in rice paddies. For the example of a single rice paddy, the two-factor model predicts 3-7 times more temperature response than does the single-factor model.

While demonstrating that ignoring the gross/net flux dynamic and the differential response leads to a serious underestimate of change in methane response to warming, I do not represent these calculations as definitive estimates of the response of methane-emissions to global warming. My approach does not include the indirect effects of temperature increases on other environmental factors. For example, in this global estimate I assume that all other factors, such as soil moisture and area of inundation, stay constant under the warming scenario. Furthermore, I have not established a causal linkage between soil temperature and emission rates in my own data set. Although laboratory findings support my results, it is possible that the temperature response I observed was due to plant senescence or other unmeasured environmental parameters that might become less-coupled with temperature with climatic change. Even with a relationship between temperature and flux, the Q_{10} is an imperfect description of temperature response since microbial responses are not linear or independent of initial temperature (Howard and Howard, 1993). In addition, the California and Colorado Q_{10} may tend to exaggerate the differential effect for two reasons. First, the Q_{10} for net emissions is, of course, for the balance of production and consumption at the chamber sites. Therefore this Q_{10} may be an overestimate of the Q_{10} for production alone. Nevertheless, it is in the range of values for Q_{10} found by a variety of laboratory slurry experiments and field studies. Second, the California and Colorado Q_{10} 's for uptake, based on aerobic sites, may underestimate the temperature response of methanotrophs found in saturated systems (Valentine, et al., 1993).

Environment and Methane Flux

Variations in soil microclimate are important in explaining differences in flux rates among ecosystem types and also in explaining temporal variation in flux at a specific location. Within landscape units (e.g., vegetation types), however, there is a large component of spatial heterogeneity that microclimate could not explain. My research identified factors that explained much of this heterogeneity in the grasslands and the arctic wetlands, but not in the montane meadow or other study sites. In arctic wetlands, where plants provide the dominant pathway for methane transport from the soil to the atmosphere, aboveground biomass of aerenchytomous[6] plants explained over 60% of variation in emissions. Plant biomass did not appear to affect emissions by upland tundra, however.

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[6] Aerenchyma are straw-like structures inside plants for transporting oxygen to roots.

Prevailing hypotheses in the literature are that methane uptake *in situ* is diffusion-limited and that soil texture (diffusivity) can be used to estimate uptake in different regions. In the annual grasslands, soil carbon and nitrogen explained 97% of the spatial variation in uptake rates (I did not examine carbon and nitrogen in the other sites). Soil carbon and nitrogen may be used as measures of soil organic content, which is correlated with soil texture. In the montane meadow, my data contradicted the first clause, in that I found microbial activity to be limiting under very dry conditions. Texture may help explain why the uphill zone of the montane meadow had higher flux rates than the downhill zone. These two sites did not differ in bulk density; I did not, however, quantify the difference in rockiness of these two very rocky soils.

Human Impacts on Methane Flux from Natural Ecosystems

Observations that atmospheric methane concentrations began to increase in the early 1800's, before fossil fuel use was widespread, tell us that other human activities are at least partly responsible for the rising concentrations. Sources of methane that have been increasing for the past two centuries are flooded rice cultivation, the number of cattle and other domestic ruminants, and biomass burning (Lelieveld, et al., 1993). In addition, methane fluxes from ecosystems are sensitive to many kinds of perturbations. Methane uptake by soils is reduced when forests are converted to pastures (Keller, et al., 1990), forests or grasslands are cultivated (Bronson and Mosier, 1993; Keller, et al., 1990; Mosier, et al., 1991), or when rangeland, grasslands, or forests are fertilized (Mosier, et al., 1991; Steudler, et al., 1989). Methane uptake may be increased after fires (Tate and Striegl, 1993). Chronic acidic deposition is linked to low emission rates from peat soils (Yavitt, et al., 1993).

My research results stand in contrast to the studies cited above. In my experiments, methane uptake was not sensitive to perturbation by fertilization, grazing by sheep, or artificial warming. I found no effect of fertilization on methane uptake in either tussock tundra or in annual grassland. Grazing by sheep increased uptake slightly relative to controls in annual grassland, but the difference was not statistically significant. Also grazing did not appear to increase soil compaction, since there was no effect on bulk density. Although both temperature and moisture were correlated with methane uptake in Colorado, the warming treatment *per se* did not have an effect on methane uptake. The warming treatment altered season-averaged soil temperature and moisture, and advanced the date of snowmelt (Harte, et al., 1994), but they had a negligible effect on soil temperature or moisture during the specific hours when methane flux was measured. I conclude from these results that not all ecosystems are sensitive to all kinds of perturbation, but do not think they cast doubt on any previous study showing ecosystem-methane sensitivity to perturbations.

Methane production and consumption probably respond differently not only to climate, but also to anthropogenic impacts on the environment, because of the different metabolic pathways and bio-chemical requirements of methanogenic and methanotrophic bacteria. The literature is not systematic in the types of impacts or ecosystems researched. I present here a framework for considering this differential effect, for facilitating research of it as much as for evaluating it. In Table 3 I outline in a generic sense how different human activities affect ecosystems, how these ecosystem impacts alter the soil micro-environment, and how these micro-environment impacts affect methane production and consumption.

Future Research

In my dissertation research I have found, in certain ecosystems, evidence for feedback between climatic change and ecosystem-methane fluxes, and evidence that this feedback may be stronger than is predicted by current models. My research also delineated factors behind spatial patterns in methane flux, such as the strong correlations of soil carbon and nitrogen with methane uptake. To generalize these results to the global methane cycle, research is needed to test my findings in other ecosystems and to identify the mechanisms behind the results presented. I identify here a few research projects that would be logical extensions of my dissertation research. I have emphasized empirical research, but clearly one of the main goals of further research, and particularly items 1 and 2 below, must be to synthesize a more mechanistic and detailed model of the methane cycle for use in spatial extrapolation as well as in understanding and predicting changes in methane fluxes.

1. Methane-climate feedback. One negative feedback to climate change that would be fairly simple to model is the effect of sea-level rise on methane emissions from tidal wetlands. Salinity inhibits methanogenesis (DeLaune, et al., 1983). Tidal wetlands (e.g., of the southeast United States) are major sources of methane (Bartlett, et al., 1987). Sea level rise would increase salt water intrusion into estuarine and coastal wetlands (Williams, 1985) and thus decrease emissions.

Experimental field manipulations of temperature and moisture are needed so that the influence of these two factors can be assessed independent of each other as well as independent of seasonal and geographic patterns. This should be done with wetlands and rice paddies in different regions, as well as with a few representative types of terrestrial ecosystems.

In my conclusions, I extrapolate my findings from the aerobic soils of montane meadow and annual grassland to rice paddies and wetlands, sites of methane consumption in which the microbes are found in saturated conditions. Research is needed to compare the temperature and moistures responses of methane-consuming communities found in these two environments. Because it is technically easier to monitor consumption rates in soils that do not also have methane production occurring, it would be useful to know what kinds of results on uptake from aerobic systems can rigorously be applied to wetlands and rice paddies. A good place to start on this question would be laboratory manipulations to generate temperature and moisture response curves for microbial cultures (or soil samples, or both) from aerobic and anaerobic ecosystems in conjunction with identification of the methane-oxidizing bacteria in each sample.

A smaller, related experiment would be laboratory manipulations or intensive field research to elucidate if and why emissions rise when water table is first lowered. The rise in emissions was found by Moore and Roulet (1993). If the increase in emissions can be documented, the next step would be to determine what proportion of the increase was due to (a) increased methane production, (b) increased release of stored methane, and (c) decreased methane consumption.

2. Methane-climate feedback and differential controls hypothesis. To extrapolate my findings on the differential effect of temperature, both wetlands and rice paddies should be investigated, with explicit study of methanotrophic communities that live in these saturated environments.

In addition, the differential effect hypothesis for temperature could be tested or investigated with a time-series of oxidation-inhibition experiments along the pond margin at California.

3. California's historical and current methane budgets. In the last 150 years, California has undergone extensive changes in land uses that removed natural sources of methane while adding anthropogenic sources. The state's upland, methane-consuming ecosystems have also been impacted in ways that might change their sink strength. For example, historically, California had over 4 million acres of freshwater 1.6 million ha of freshwater wetlands, which my research in California suggests may have been large sources of methane. Over 94% of these wetlands have been converted to land uses that probably do not emit methane (e.g., residential and commercial development,

agriculture) (Jensen, et al., 1993). At the same time new sources have created in seasonally-flooded rice and alfalfa fields, and landfills. Methane emissions from rice paddies in California have been measured (Cicerone and Shetter, 1981; Cicerone, et al., 1983); but no research at all has been done on methane flux from alfalfa fields. About 30% of California's land is grazed by cattle at some time in the year, but there is little data on the effect of cattle grazing on methane uptake. Survey data of California's different land uses could be combined with maps of historical and current land use to compare the magnitude and seasonality of methane fluxes from California two hundred years ago with those at present.

4. Methane uptake and soil fertility There are many emerging questions related to uptake and soil fertility, including those about the correlation between methane uptake and soil carbon and nitrogen, the impact of nitrogen fertilization, and the interaction between bacteria type (e.g., genus, metabolic traits) and soil nutrients on uptake. Fruitful research could be undertaken using long-term manipulations of soil fertility in conjunction with measures of soil nitrogen cycling and activity of soil nitrifying bacteria and methanotrophic bacteria.

Results with Potential Policy Implications

1. Climate factors influence methane production and consumption in ways that suggest the potential for significant and rapid feedback with climatic change. Considering the direct effects of temperature alone, there is potential for a large positive feedback. One of the most important implications of a positive climate-methane feedback is that warming would occur more quickly and more severely than is currently forecast by GCMs. In other words, the warming commitment of a given anthropogenic emissions scenario (e.g., draconian, business-as-usual, etc) would be greater than predicted and will occur more quickly. The warming commitment would be larger because every degree of

warming currently predicted would be accompanied by an additional, currently unpredicted input of greenhouse gases by ecosystems. The expected warming would occur more quickly because the atmospheric forcing would be enhanced (atmospheric concentrations of methane would increase more rapidly; Figure 2).

It is commonly recognized that positive feedbacks can create unstable, or runaway conditions. Although methane is a potent greenhouse gas, it is unlikely that positive feedback with natural-ecosystem methane-fluxes would lead to runaway warming for three reasons. First, the positive feedback associated with the direct effects of temperature will likely be accompanied by negative feedbacks generated by ecosystems and climatic change. For example, global warming is predicted to lead to a reduction in flooded area which would reduce global methane emissions, generating a strong negative feedback (e.g., Whalen and Reeburgh, 1990). The net, combined feedback generated by ecosystem methane-flux and climate may be negative or positive. Second, the warming potential of methane will decrease as methane concentrations increase, due to saturation of the wavelengths that methane absorbs. Third, ecosystem methane accounts for about 15% of the increase in greenhouse effect each decade. Reductions in anthropogenic greenhouse-gas emissions could practically compensate for increases in ecosystem-methane fluxes. Nevertheless, by adding to the positive feebacks and offseting the negative feedbacks that are generated by ecosystem methane-flux and climatic change, the positive feedback with temperature change would make warming scenarios more severe, and efforts to control atmospheric greenhouse-gas concentrations more difficult, than they would be without such a feedback.

2. The magnitude of climate-methane feedbacks is probably much larger than currently estimated by traditional methane-cycle models, which ignore both the differential response of production and consumption to temperature and moisture and the large gross fluxes of methane. The biosphere could experience much larger changes in

methane flux than is currently predicted--in response to climatic or other ecological perturbations.

3. Methane fluxes are affected by many human activities--including forest conversion, grazing, and air pollution--that are caused by individual or regional actions. These activities tend to affect methane production and consumption differently. Viewed through the lens of my work on differential controls, these activities could very well cause a much bigger change in methane fluxes than would otherwise be expected. These changes in methane flux, though caused by non-climatic impacts, would contribute to feedbacks in the climate-biosphere system.

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Table 1. Mean Daily and Annual Net Methane Flux at Research Sites in Alaska, Colorado, And California. For Alaska and Colorado, annual flux is extrapolated from spring and summer measurements. The years of data collection for the three sites were: Alaska, 1991; Colorado, 1991-93; California, 1991-92.

Research Site	**Ecosystem**	**Mean Net Flux** (mg CH_4 m^{-2} d^{-1})	**n**	**Active Days**	**Implied Annual Flux** (g m^{-2} y^{-1})	**Global Area of Ecosystem Type**[1] (10^{12} m^{-2})
Alaska , Toolik Lake Field Station	Wet-meadow Tundra	52.0	21	100	5.2	1.5 - 3
	Tussock Tundra	1.4	11	100	0.14	6.8
Colorado, Rocky Mountain Biological Laboratory	Montane Meadow and Sagebrush Steppe	-1.2	211	175	-0.21	5 - 10
California, U.C. Hopland Research and Extension Center	Pond	38.2	18	365	13.9	0.12[2]
	Annual Grassland	-0.7	42	365	-0.25	9[3]

[1] Area estimates from Harte (1985), Matthews and Fung (1987), Elaine Matthews (pers. comm.), and Aselmann and Crutzen (1989).

[2] Includes only Europe, Africa, and the Americas

[3] Includes all grassland (perennial and annual) but no savanna.

Table 2. The Increase in Methane Emissions Resulting from a 10°c Warming as Estimated by Two Models: (1) assuming that all methane produced in soil is released to the atmosphere (no gross fluxes or differential effect; i.e. new flux = current emissions*Q_{10} prod) or (2) assuming that net emissions are the balance of methane production and consumption and that temperature effects these two processes differently (i.e., flux =(Current production*$Q_{10,Prod}$ - Current consumption*$Q_{10,Cons}$) / (Current production-Current consumption) . These two models are applied with Q_{10} (1) derived from the current study and (2) representative of literature values. All fluxes in Tg yr^{-1} except in the last row.

Ecosystem or Land Use	Current Global CH_4 Production[1] (Tg yr^{-1})	Current Global CH_4 Consumption[1] (Tg yr^{-1})	Current Net Emissions to Atmosphere (Tg yr^{-1})	**Net emissions with 10°C warming calculated with Q_{10}-based models**			
				(a) Field Data, This Study[3] **Prod. Q_{10} = 2.75** **Cons. Q_{10} = 1.0**		**(b) Conservative Literature Values[4]** **Prod. Q_{10} = 2.0** **Cons. Q_{10} = 1.5**	
				1. No gross fluxes or differential response	**2. With gross fluxes and differential response**	**1. No gross fluxes or differential response**	**2. With gross fluxes and differential response**
Wetlands	170	55	115	230	413	316	258
Rice paddies	629	529	100	200	1200	275	464
Landfills	80	40	40	80	180	110	110
All Three	879	624	255	510	1793	701	821
Rice Paddy[2]	373 ml m^{-2} h^{-1}	340 ml m^{-2} h^{-1}	33 ml m^{-2} h^{-1}	66 ml m^{-2} h^{-1}	686 ml m^{-2} h^{-1}	91 ml m^{-2} h^{-1}	236 ml m^{-2} h^{-1}

[1] Global methane flux estimates are from Reeburgh et al. (1992).

[2] Rice paddy data are from Schütz (1989) for a single rice paddy in 1985 near the end of its growing season.

[3] The temperature response (Q_{10}) of production and consumption were calculated from results of the present study, for warming from 10 to 20 °C.

[4] The temperature response (Q_{10}) of production and consumption represent the conservative range of literature values (for a conservative estimate of the effect of gross fluxes and differential response).

Table 3a. Human Activities Impact Environmental Conditions that are Important for Methane Production and Consumption

Human Impact on Environment	Environmental Factors Altered
Climate change	soil temperature and moisture, soil organic matter, plant productivity, saltwater intrusion
Water diversions, dredging, filling	salt water intrusion, wetland shrinkage
Water pollution	plant productivity
Fertilization	available NH_4^+, NO_3^-, plant productivity
Acidic deposition, air pollution	soil pH, sulfate, nitrate
Ecosystem conversion to pasture or agriculture	soil compaction, available NH_4^+, NO_3^-
Grazing	soil compaction, available NH_4^+, NO_3^-

Table 3b. Relating Macro-Scale Environmental Factors to Micro-Scale Factors that Influence Methane Production or Consumption

Macro-Scale Environmental Factors	**Micro-Scale Environmental Factors**	**Effect of Increase in Macro Factor on:**		**Selected References**
		Production	**Consumption**	
Soil Moisture	methane diffusion oxygen diffusion	increase	decrease	Current Study
Organic Matter, Acetate, H_2, CO_2	substrate for methanogenesis	increase	n.e.	Oremland, 1988
Temperature	microbial activity solubility of methane diffusion	increase	n.e.	Current Study
pH	nitrogen species & mobility organic reactions? microbial toxicity?	decrease	?decrease	Yavitt et al., 1993 Valentine et al., 1994
Compaction	soil diffusivity (see Moisture)	n.e.	decrease	Dorr et al., 1993 Striegl, 1993
Nitrogen turnover and availability	NH_4^+ availability size of active microbial pool	increase (rice)	increase or decrease	Steudler et al., 1989
Wetland Plants	plant-mediated transport, in-sediment oxidation	increase	decrease (as % of prod.)	Torn and Chapin, 1993
Salt water intrusion	SO_4^{2-}, NO_3^-, Fe^{3+}	decrease	decrease, n.e.	DeLaune et al., 1983

n.e. = negligible effect

Figure Captions

Figure 1. Qualitative representation of methane flux vs. soil moisture. Shows that methane uptake (negative flux) decreases at the very dry and moist ends of the moisture spectrum, and that methane emissions (positive flux) increase rapidly with increasing moisture around saturation (100% water-filled pore space). Vertical axis is not drawn to scale.

Figure 2. Qualitative illustration of the effect of positive methane-climate feedback on greenhouse forcing in the atmospheric (through changes in methane concentrations). Shown is radiative forcing over the next one hundred years based on (A) Business-as-usual emissions scenario (Houghton et al., 1990) and (B) Business-as-usual emissions scenario plus the additional methane due to a positive feedback between methane emissions and global warming due to greenhouse gas emissions. These scenarios are intended to illustrate the feedback concept and are not quantitatively accurate.

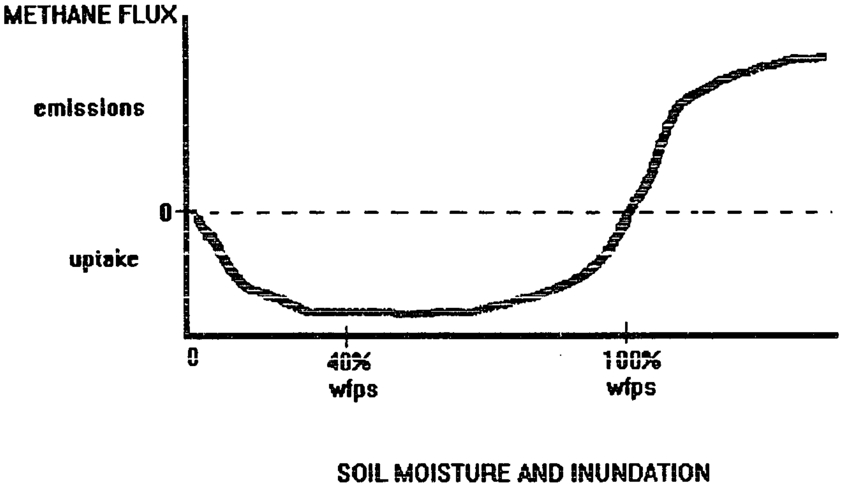
METHANE FLUX
emissions
0
uptake
0
40%
wfps
100%
wfps
SOIL MOISTURE AND INUNDATION

Figure 1

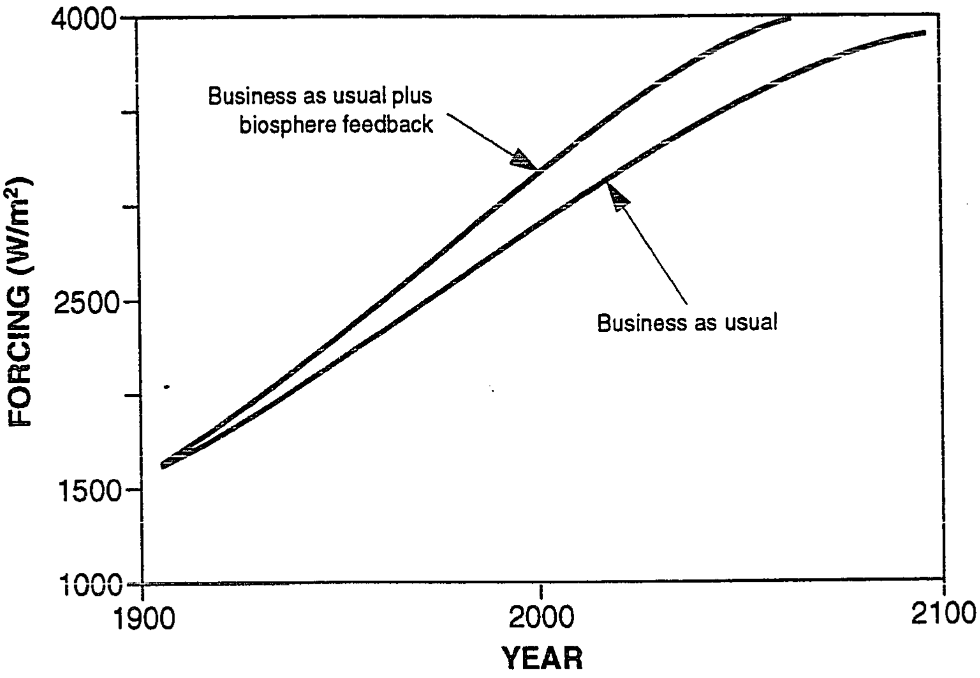
4000
2500
1500
1000
FORCING (W/m^2)
1900
2000
2100
YEAR
Business as usual plus biosphere feedback
Business as usual

Figure 2

APPENDIX A

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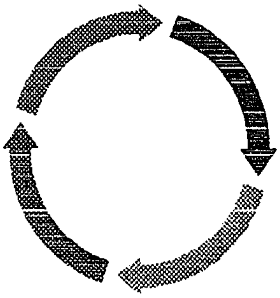

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