DISSERTATION

TRACE GAS BIOGEOCHEMISTRY IN RESPONSE TO WILDFIRE AND FOREST MANAGEMENT IN PONDEROSA PINE ECOSYSTEMS OF COLORADO

Submitted by
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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY MARK A. GATHANY ENTITLED TRACE GAS BIOGEOCHEMISTRY IN RESPONSE TO WILDFIRE AND FOREST MANAGEMENT IN PONDEROSA PINE ECOSYSTEMS OF COLORADO BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

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ABSTRACT OF DISSERTATION

TRACE GAS BIOGEOCHEMISTRY IN RESPONSE TO WILDFIRE AND FOREST MANAGEMENT IN PONDEROSA PINE ECOSYSTEMS OF COLORADO

Fire exclusion practices during the last century increased fuel and fire hazard in the western U.S., where conditions have also become drier and warmer in recent decades. As a result, fire frequency and extent have increased significantly. Wildfires and forest management alter soil carbon and nitrogen availability and the physical environment. These factors are primary controls on greenhouse gas (carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O)) flux rates. The two-way interaction between forest wildfires/management and flux rates may be significant considering the positive feedback loop that could lead to further climate warming. I explored these relationships in a series of field studies in which I measured soil trace gas exchange rates in ponderosa pine forests of the Colorado Front Range that had recently experienced a wildfire or forest thinning. I also used the ecological simulation model, Daycent, to simulate the effects of long term climate variability, varied fire frequency and fire suppression in order to estimate the changes in CH_4, N_2O, NO (nitric oxide) fluxes and gross nitrification rates at four sites in the Colorado Front Range.

My findings suggest that soil CO_2 fluxes increase in the years after a wildfire, and that local scale variables such as soil moisture, temperature, and fire severity are important controlling factors for these trace gas fluxes. Forest thinning practices increased substrate availability in some cases such that CO_2 and N_2O fluxes increased, but only when soil moisture was high, during the sampling season. Using Daycent, I found CH_4 uptake was consistent among sites with different landscape characteristics, and showed minimal changes in response to fire. Daycent simulations estimate a 13 – 37

% decrease in N_2O and NO fluxes, and gross nitrification rates during the fire suppression era relative to before the suppression era.

Overall, my research revealed that wildfire and forest management do alter the exchange rates of CO_2 and N_2O primarily by increasing substrate availability and environmental variability. Therefore, as wildfire activity and forest management are anticipated to increase in both frequency and extent, my research suggests that CO_2 and N_2O source strength may increase from Colorado ponderosa pine ecosystems.

Keywords: carbon dioxide, methane, nitrous oxide, trace gas, greenhouse gases, fire, soil, ponderosa pine, Colorado Front Range, wildfire, Daycent, forest management

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Chapter 1

INTRODUCTION

During the four fire seasons that have coincided with the four years that I have pursued my doctorate, approximately 40 million acres (Figure 1) have burned in the United States (Center 2007). Most forested ecosystems of the western United States were shaped by fire (Romme 1982; Shinneman and Baker 1997; Brown *et al.* 1999; Baker and Ehle 2001). Where fire occurs with any regularity, it acts as a selective force leading to plant adaptations such as serotiny, self-pruning, and thick bark, enabling many pines to survive and reproduce (Schwilk and Ackerly 2001). Biogeochemically, fire not only affects vegetation, but also soils (Covington and Sackett 1986; Certini 2005) and microorganisms (Choromanska and DeLuca 2002; Hamman 2006). As a result, fire is a vital component that maintains forest ecosystem structure and function over time (Moore *et al.* 1999; Hall *et al.* 2006) and over large regions (Schoennagel *et al.* 2004).

In the American West, we are fortunate to have some of the most extensive knowledge of fire histories and regimes (Swetnam *et al.* 1999) in the United States. However, we have many unanswered questions regarding these ecosystems as fire exclusion practices have been in place during much of the scientifically observed period (Fule *et al.* 1997; Keane *et al.* 2002; Foster *et al.* 2003). While much remains unknown regarding plant community response to fire, we have substantially greater knowledge regarding this relative to our understanding of fire's biogeochemical consequences. My research seeks to advance our scientific understanding of wildfire and biogeochemical cycling, and to describe the influence of wildfire and forest management on the exchange of trace gases to the atmosphere.

I chose to study three greenhouse gases: carbon dioxide (CO_2), methane (CH_4) and nitrous oxide (N_2O). Once in the upper atmosphere, each of these three trace gases acts as a greenhouse gas. Volumetrically, CO_2 accounts for 379 parts per million (ppm) of the atmosphere as of 2005 (IPCC 2007). Methane and nitrous oxide exist in the atmosphere at low concentrations (1774 and 320 parts per billion, ppb) relative to CO_2. However, on a molecule-to-molecule basis CH_4 and N_2O are stronger greenhouse gases than carbon dioxide. The common convention for expressing the impact of methane and nitrous oxide is to use CO_2 equivalents global warming potentials (GWPs), such that 1 g CH_4 is equivalent to 23 g CO_2 and 1 g N_2O is equivalent to 296 g CO_2. These GWPs incorporates a molecule's atmospheric lifetime and radiative activity (Robertson *et al.* 2000). In ecosystems the production and consumption of these three greenhouse, or trace, gases is biologically mediated (Conrad 1995; Conrad 1996), but also strongly controlled by chemical (Mosier *et al.* 2002) and physical (von Fischer and Hedin 2007) factors.

The interactions among climate, fire, and land-use are often studied independently, though each is related and dynamically changing, such that we need a new, dynamic understanding of the relationships. The potential for climate to influence fire extent, season, and severity has already been observed in the American West (Westerling *et al.* 2006). Randerson *et al.* (2006) investigated the potential for a feedback mechanism(s) between the radiative forcing of wildfire and global climate in the boreal forest and found that the net effect of a fire (including changes in albedo, CO_2 and CH_4 fluxes) had a negative feedback to climate warming.

In the Colorado Front Range, there have been many studies addressing the relationships between climate variability and wildfire activity, and how together these forces have shaped the forested landscape (Veblen *et al.* 2000; Keane *et al.* 2002; Hicke *et al.* 2004; Veblen and Donnegan 2005; Platt *et al.* 2006). The following three chapters ask how trace gas fluxes respond to wildfires over short time periods (Chapter 2), their response to forest management and changes in nutrient availability (Chapter 3), and their response to variability in climate and fire regime (frequency and severity) over longer time spans using a modeling approach (Chapter 4).

Wildfires are known to affect Rocky Mountain ecosystems across a wide range of spatial and temporal scales. Many of the ensuing changes are greatest for environmental factors, such as substrate and microclimate, which are known to control exchanges of greenhouse gases (GHGs) between the soil and atmosphere. My second chapter investigates this link and develops an understanding of fire's influence on the cycling of these greenhouse gases for ponderosa pine forests. Of particular interest, is the influence of time and topography on soil trace gas flux rates and identifying variables that can be used to best predict flux rates in these post-fire forest ecosystems.

The population density of the Front Range has continued to increase, so too has land use (exurbanization) and land management. While a reduction in fire risk and hazard is readily achieved by forest thinning practices, these are often conducted without a full knowledge of their ecological consequences. I measured trace gas fluxes from the soils of a ponderosa pine forest in Boulder County, Colorado to determine how these are influenced by forest management practices and nutrient amendments. At the stand level I examined the effect of two methods of forest thinning, thinning-only and broadcast-chipping. I also analyzed environmental factors (soil temperature, soil moisture, and soil nutrients) that influence trace gas production. Lastly, I evaluated the role of nutrient limitation to these flux rates using a 2x3x3 randomized complete block design where C, N, and P availability are experimentally manipulated.

Chapter 4 continues the investigation of trace gas flux rates, but diverges from the field based studies (as in Chapters 2 and 3) to a modeling approach. I use a simulation approach to investigate trace gas exchanges between the soil and atmosphere in ponderosa pine forests of Colorado, with three objectives: 1) to test the Daycent model's (Parton *et al.* 1998; Del Grosso *et al.* 2000; Parton *et al.* 2001) ability to simulate this ecosystem, 2) to examine how fire may change trace gas flux rates over the short-term and 3) to determine the potential effects of fire exclusion over the long-term.

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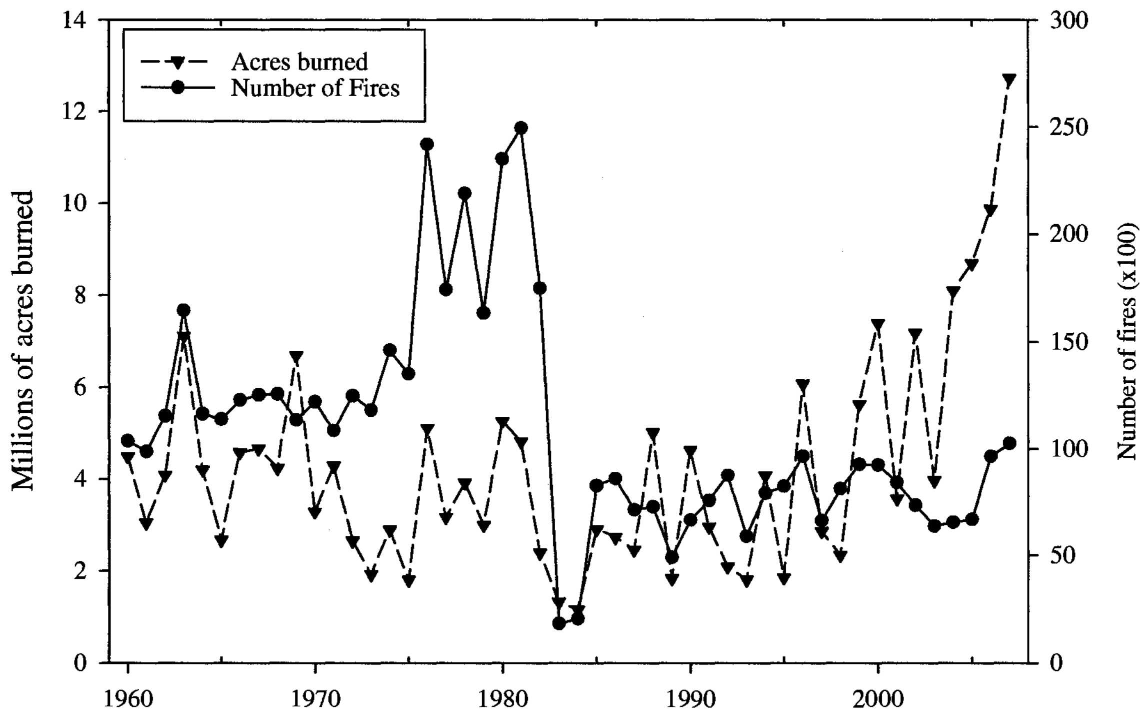

Figure 1. This figure depicts the number of fires and acres burned (in millions) in the United States between 1960 and 2007. Data were obtained from the National Interagency Fire Center (www.nifc.gov).

Chapter 2

POST-FIRE SOIL FLUXES OF CO_2, CH_4, AND N_2O ALONG THE COLORADO FRONT RANGE

Abstract

Wildfires are known to affect Rocky Mountain ecosystems across a wide range of spatial and temporal scales. Many of the resulting changes are greatest for environmental factors, such as substrate and microclimate, which are known to control exchanges of greenhouse gases (GHGs) between the soil and atmosphere. My research investigated this link and developed the understanding of how fire influences the cycling of these greenhouse gases for ponderosa pine forests. I measured and compared trace gas flux rates between recently burned sites and topographical aspects. I also calculated the ability of five factors (soil temperature, soil moisture, fire severity, aspect, and time since fire) to describe the variability in the flux rates measured from these forest ecosystems. The first part of my study revealed that CO_2 fluxes were significantly different between sites, while aspect was not found to be significant. Methane uptake was not different between sites or aspect. Nitrous oxide fluxes had a significant interaction between site and aspect with the greatest N_2O release occurring on north facing aspect at one year post-fire. Using a likelihood approach, I determined the strength of support in the data for model combinations of five environmental variables. Of these, the single variable models, soil moisture, time since fire, and severity best described the CO_2 CH_4, and N_2O flux data, respectively. My data show that following a forest fire in the Colorado Front Range, > 98% of the global warming potential of the measured soil-atmosphere fluxes is contributed by the soil CO_2 flux.

Introduction

The increasing concentrations of carbon dioxide (CO_2), methane (CH_4) and nitrous oxide (N_2O) in the atmosphere continue to be of concern in light of their potential influence on global climate. Together these three greenhouse gases (GHG) contribute approximately 70% of the total atmospheric warming potential (Sommerfeld *et al.* 1993). Increases over the past fifty years are primarily attributed to the combustion of fossil fuels, and secondarily to changes in land use (Crowley 2007). According to the Intergovernmental Panel on Climate Change (Denman *et al.* 2007) the scientific knowledge remains incomplete regarding these increases and their source-sink relationships. The IPCC further suggest the need to better understand the effects of rapid, large-scale disturbances (such as fire) on the atmospheric balance of these trace gases.

Recent wildfire activity in the Rocky Mountain West and the Colorado Front Range has sparked a great deal of interest. In a recent study, Westerling *et al.* (2006) found dramatic increases in fire frequency and extent, since the mid-1980s as compared to fifteen years prior (since 1970). They attributed this pattern to global climate change and the drought conditions that have characterized the climate of the western United States during the past three decades. Observations of past climate and projection models predict a continuation of this drying and warming trend in the West (McCabe *et al.* 2004; Seager *et al.* 2007), suggesting a strong potential for continued increases in fire frequency and extent (Flannigan *et al.* 2000).

Following fire, ecosystem structure and function can vary greatly across the matrix of burn severities. Often correlated with the burn severity and altered fire regime, researchers observe post-fire changes in plant (Mast *et al.* 1998; Veblen *et al.* 2000) and soil microbial communities (Hamman 2006; Hamman *et al.* 2007), available substrate, and environmental conditions (Grady and Hart 2006) within the wildfire's perimeter.

While wildfires have been shown to dramatically alter ecosystem structure and function, limited information exists regarding the effect(s) of wildland fires on soil gaseous fluxes. The two primary limiting factors to both CO_2 and N_2O fluxes are substrate availability and soil moisture, particularly in semiarid regions. Johnson and Curtis (2001) found in their meta analysis that fires increased soil carbon and nitrogen, and that these changes persisted for several years. Neary *et al.* (1999) suggest that soil carbon and nitrogen availability is also a function of the fire severity, where ecosystems experiencing light to moderate severity fires retain more carbon and nitrogen just following fire, relative to high severity fires. Wildfire severity is correlated with fire intensity, which is determined by the available fuel, topography (slope and aspect), and weather at any particular location at the time of the fire. Following a wildfire soil moisture and temperature regimes show increasing variability as tree mortality increases (Neary *et al.* 1999). These changes and changes in the soil's physical (bulk density) and chemical characteristics such as pH, CEC, and nutrient availability have been found to affect biotic activity (Hamman 2006; Hamman *et al.* 2007).

In contrast to CO_2 and N_2O fluxes, consumption of methane by methanotrophs is primarily constrained by two parameters; biological activity and physical soil environment (von Fischer and Hedin 2007). Del Grosso *et al.* (2000) suggests that maximum CH_4 uptake (~ 0.05 mg C m^{-2} h^{-1}) in coarse soil occurs at 7.5 % WFPS (water filled pore space). In the Colorado Front Range, Hamman *et al.* (2007) measured a 55 %

increase in soil moisture in forest stands that experienced high severity fires relative to unburned controls as plant transpiration greatly decreased (Kaye *et al.* 1999).

The goal of this chapter was to investigate how soil flux rates vary with time since fire and topography along the Colorado Front Range, and to evaluate what environmental factors are important to flux rates that can be affected by wildfire, and may be useful in predicting post-fire fluxes from this ecosystem. An improved understanding of the controls on trace gas fluxes in temperate forests is important for predicting and scaling up estimates of soil trace gas flux rates, particularly when viewed in light of the dynamic fire regime that characterizes much of this region. My a priori expectation was that fire results in increases in heterotrophic activity (hence CO_2 and N_2O fluxes), due to increases in detrital pools following fire, and that this effect varies with soil moisture and topographic location, and that soil physical responses (particularly change in soil moisture availability) to fire would affect methane consumption in these dry forest soils. I had two objectives: 1) to describe the spatial and temporal variability in post-fire flux rates and 2) to evaluate the relationships among environmental variables and soil trace gas flux rates.

Materials and methods

Study sites

I sampled locations along the Front Range that have experienced a wildfire in the past five years. Sampling occurred during the summer of 2005. The four sites (and year burned) include Picnic Rock (2004), Hewlett Gulch (2002), Hayman (2002), and Bobcat Gulch (2000). These were located between 1600 and 2200 m in the ponderosa pine zone of the Colorado Front Range. The climate of this region is controlled by its interior continental location (Peet 1981; Veblen and Donnegan 2005). During the winter, weather patterns are dominated by cold, high-pressure maritime polar and arctic air masses. These bring cold, dry air to the eastern slope of the Rocky Mountains. Spring and summer weather patterns are dominated by maritime tropical air masses that originate in the Gulf of Mexico. This resulting shift in predominant wind direction is often referred to as the summer monsoon. This creates upslope conditions that draw Gulf moisture to the region during late summer and early autumn and generate conditions leading to high lightning frequency. At approximately the center of my site's latitude range and within the altitude range, Veblen *et al.* (2000) found mean annual temperature to range between 10.9 and 4.7°C, with mean annual precipitation values of 482 mm and 536 mm at 1646 and 2450 m elevation, respectively.

Soils at my sites are dominated by ustolls being most common at low elevation, dry sites while cryoboralfs can be found at more mesic sites at higher elevations (Veblen and Donnegan 2005). Generally, soils of the northern Front Range are coarse textured and rocky, derived from schist, granite and gneiss. Vegetation patterns are strongly related to the climate and soils, which vary with elevation and aspect (Peet 1981; Veblen and Donnegan 2005). Within the elevation range where my sites were located, ponderosa pine (*Pinus ponderosa*) dominates the canopy composition. Douglas-fir (*Pseudotsuga menziesii*) comprises a small portion of the canopy, though it is important to the subcanopy, which is very important to fire behavior in these systems (Kaufmann *et al.* 2000). Stand age and structure are heterogeneous across the landscape (Kaufmann *et al.* 2005) with the greatest tree densities on the more mesic, north-facing slopes (Peet 1981; Hall *et al.* 2006).

Study design

At each of the four sites, I identified forested stands on both north- and south-facing slopes that had experienced a wildfire. Beginning in June 2005, I sampled trace gas fluxes along transects on north- and south-facing aspects at each site. When possible, I sampled one aspect per day on consecutive days (eight days per sampling cycle). I completed a total of 3 sampling cycles (2 aspects at each of four sites) between June and September 2005. On each sampling day, I established a 20 m transect and inserted chambers at least 5 cm into the soil. Five trace gas flux measurement chambers were placed on each transect, equidistantly spaced, perpendicular to the slope. Each chamber had two parts made of PVC, the base and cover (Hutchinson and Mosier 1981). To constrain diurnal variability, I conducted all sampling between 9.30am and noon.

Field sampling and lab analyses

To address the spatial and temporal variability in trace gas fluxes following fire I collected air samples from the headspace of each chamber at 0, 10, 20, and 30 minutes after placing the cover on the base, following methods of Hutchinson and Mosier (1981). On each chamber I attached a 5 cm length of plastic tubing that was fitted with two-way leur-lock valve. The valves were only opened at sampling times when 30 mL nylon syringes were fitted to valve and a 25 mL air sample was collected. I transferred air samples to pre-evacuated (200 millitorr) serum vials (with rubber septa) by fitting each syringe with a hypodermic needle and injecting the sample to the vial. Samples were stored in vials until analysis, generally within two weeks of sampling (and never more than four weeks). I collected standards in the field to control for storage effects, but found no change in concentrations. I measured trace gas concentrations of the samples using a Shimadzu GC 14A that was fitted with an electron capture detector (ECD for

N_2O) and flame ionization detector (FID for CH_4 and CO_2). Atmospheric nitrogen (N_2) was used as the carrier gas. Oven and column temperatures were set at 280°C and 60°C, respectively. I utilized a linear, 3-point calibration curve for each of the three gases of interest and regularly compared with field standards. I used linear regression to derive flux rates as the change in concentration over time (Robertson *et al.* 1999).

I also sought to understand the importance of readily measured environmental variables in predicting post-fire trace gas flux rates. To achieve this, I collected data on soil temperature, soil moisture, fire severity, aspect, and time since fire. I measured soil temperature at a 5 cm depth (at time 0 and 30) at each chamber and used these data to calculate transect means. I also recorded aspect (degrees), latitude/longitude, and fire severity (0 = unburned, 4 = stand canopy burned) based on stand damage (Omi and Kalabokidis 1991). While other metrics of fire severity are available, I selected this metric as it provided a reliable estimate of fire intensity even though the fire may have burned several years prior. Following chamber headspace sampling, I collected soil cores from each chamber's center and subdivided them as 0 – 5 cm and 5 – 15 cm segments. Soil cores were dried to a constant weight at 55°C and weighed to determine bulk density and gravimetric water content. I calculated % water-filled pore space (%WFPS) assuming a particle density of 2.65 g cm^{-3}.

I used the trace gas flux data to calculate global warming potentials (GWPs) from these flux rates (Robertson *et al.* 2000). This provides information as to the relative importance of each measured flux rate with respect to the others (e.g. CO_2 versus CH_4) so as to focus future research efforts.

Statistical analyses

To address the spatial and temporal variability of flux rates, I used a two-way analysis of variance with nested sub-sampling for topographic (aspect) and site differences. I considered site (n = 4) and aspect (n = 2) to be fixed effects, while transect (3 per aspect per site, n = 24) was considered a random effect. I used LSD pairwise comparisons to identify significant differences within factors when significant effects were observed.

In order to determine what variable, or combination, best described the flux data I used a likelihood approach that determines the strength of support in the data for all combinations of my five measured environmental variables (% water filled pore space, soil temperature, fire severity, aspect, time since fire). I used the sum of squares error (SSE) from regression analyses of all thirty-two candidate models (including intercept only) for each of the three trace gases measured. Each model's SSE was then used to calculate the corrected Akaike Information Criterion (AIC_c). I ranked the candidate models and chose *a priori* to report only the top five models for each trace gas. I calculated Akaike weights (w_i) that provide information regarding the ability of each model to describe the observed data (1 is a perfect fit) and provide a means of comparing the relative importance of each model and constituent factors.

I also used a multiple regression approach to calculate partial-r^2s between each trace gas flux rate and measured environmental factors (soil moisture, soil temperature, severity, aspect, and time since fire). Each factor's partial-r^2 describes the proportion of variability in trace gas flux rates by that factor independently of the other factors. Statistical tests and calculations were performed with SPSS Version 14.0 (SPSS-Inc. Chicago, IL).

Results

Site & aspect differences

Carbon dioxide fluxes were significantly different ($p = 0.001$) between my sites, indicating that time since fire (Figure 1) is an important factor controlling soil C dynamics at these sites. CO_2 flux rates were greatest at the oldest post-fire site, Bobcat Gulch (BG, Figure 1). Hayman was the driest of all these sites and at three years post-fire had the lowest CO_2 flux rate at 78 ± 22 mg C m^{-2} h^{-1} (mean ± SE). Picnic Rock (1 year post-fire) and Bobcat Gulch (5 years post-fire) were most different from one another, with Hewlett Gulch intermediate and not significantly different from either endpoint (Figure 1). Carbon dioxide fluxes were not significantly different between aspects ($p = 0.057$). Averaging across aspect and sampling cycle, I found that average CO_2 flux rates increased from 123 mg C m^{-2} h^{-1} at one year post-fire to 203 mg C m^{-2} h^{-1} at five years post-fire.

All of my sites showed net methane uptake by soils, but, I found no significant differences for methane uptake among sites of differing fire history ($p = 0.586$) or between north- and south-facing aspects ($p = 0.733$, Figure 2). At Picnic Rock, 1 year post-fire, the mean uptake (0.16 ± 0.02 mg C m^{-2} h^{-1}) was double the uptake measured at Bobcat Gulch (5 years post-fire, 0.08 ± 0.02 mg C m^{-2} h^{-1}); however, variability was great.

Nitrous oxide (N_2O) fluxes were significantly influenced both by site and by aspect; however, a significant interaction effect ($p < 0.001$) was also found between these main factors. This significant interaction was driven by the greatest fluxes observed on the N-facing, most recently burned transects at Picnic Rock (data not shown). While still a relatively low flux (1.27 ± 0.18 μg N m^{-2} h^{-1}), this mean was six times greater than that at the next greatest site-aspect combination, Hewlett Gulch-South (0.19 ± 0.12μg N m^{-2} h^{-1}). Post-hoc analyses revealed that the most recently burned site (Picnic Rock, 1 year post fire) had significantly greater ($p = 0.041$) N_2O flux rates than Bobcat Gulch, the site with the most time since fire.

Global warming potentials

In order to understand the relative magnitude (and importance for future study) of each soil trace gas flux, I calculated global warming potentials (GWPs). By normalizing methane uptake and nitrous oxide fluxes to CO_2 equivalents, I can see that both contribute little to the total that includes CO_2 GWP (Table 1). My data indicate that greater than 98% of the GWP of the measured soil to atmosphere fluxes is contributed by CO_2 alone.

Likelihood analysis of soil trace gas fluxes

Carbon dioxide

Likelihood analyses revealed that the %WFPS and the %WFPS + time models showed the greatest strength in describing the CO_2 flux data (Table 2). Each of the top five models had a %WFPS factor. This implies that CO_2 flux rates are very strongly constrained by water in these dry, recently burned forests. Soil temperature was the only variable I measured that did not to appear in the top five models. This suggests that CO_2 fluxes are not constrained by soil temperatures in the range that I measured (between 10 and 34°C).

Methane

The likelihood analysis of CH_4 uptake rates revealed an interesting pattern; the top five models each contained only one of the five measured variables (Table 2). Also, no factor may be considered more or less important than any other, as multivariable models do not describe any additional variability in light of the added uncertainty (by including an additional parameter which AIC penalizes). The model that utilized the "time since fire" variable had the lowest AIC_c relative to all other possible models. Given these data (Table 2), time since fire is the most important predictor ($w_i = 0.104$), however, it is only slightly better than the %WFPS model ($w_i = 0.097$).

Nitrous oxide

My investigation of how time since fire and topography affect N_2O flux rates revealed a significant interaction between time and aspect at these sites. The likelihood approach revealed somewhat different patterns (Table 2). First, of all the models, fire severity best descried the N_2O flux rates at these sites. Fire severity emerged in each of the top five models for N_2O flux rates. All five variables were included in at least one of the top five models, such that knowledge of each variable is important to understand post-fire N_2O fluxes at these sites.

Controls of soil trace gas flux rates

I used regression analyses to investigate the amount of variability that each factor independently described for each gas by calculating partial r^2s. These analyses revealed very similar patterns to what was found with the AIC_c approach, however, partial r^2s describe the absolute amount of variability described rather than providing relative rankings. Using the five variables time since fire, aspect, soil moisture, soil temperature, and fire severity, I was able to describe ~90% of the total variability in CO_2 flux rates at these sites (Figure 4). In these terms (partial r^2s) I found that for CH_4, local scale factors (%WFPS, soil temperature, fire severity) described nearly 20% of the total variability (Figure 3) while the landscape factors (time since fire and aspect) described an additional 15% of the variability. Fire severity and aspect described approximately 30% of the total variability in N_2O flux rates (Figure 3).

Soil moisture (%WFPS) described the most variability of any factor I considered for both CO_2 and CH_4 flux rates. Also important to biological activity, temperature described only 4, 9 and 1 % of the variability in CO_2, CH_4, and N_2O flux rates (Figure 3). While soil temperature described a small proportion of the variability in each gas flux rate, closer inspection revealed a negative relationship with CO_2, a positive effect on CH_4 uptake, and no effect on N_2O flux.

Fire severity was an important descriptive variable for CO_2 and N_2O. I found a negative relationship between CO_2 flux rates and fire severity. This same trend was seen for N_2O. The largest fluxes of N_2O occurred on north-facing slopes, and particularly at those locations that experienced a lower severity wildfire. My study found that aspect independently described 10, 4 and 8 % of the variability in CO_2, CH_4, and N_2O flux rates (Figure 3). My data suggest that time is an important factor for understanding CO_2 and CH_4 flux rates over the period investigated here. There was a positive relationship between time and CO_2 fluxes.

Discussion

In considering these results it is useful to consider the hierarchical controls over trace gas flux rates. Each site was a recently burned ponderosa pine forest, however they were distributed in the region such that there was inherent variability within and between the sties. While this was the case I attempted to explore these relationships by examining variability in trace gas flux rates in response varying fire severities and topographical aspect. These two factors are strongly related in ponderosa pine forests for the two primary reasons. First, each fire burned independently of the others and in such a way that reflected differences in fire weather, fuel availability, and topography at each site. Second, fire severity is inversely correlated with fuel moisture whereas moisture is positively correlated with biomass (fuel) production. As a result there is a greater amount of fuel on north-facing slopes where fire severity is constrained by fuel moisture at the time of each fire which varied, respectively. These factors taken together greatly influence the amount of substrate that remains at a particular location within burned areas. Each of these factors (site, aspect, and fire severity) influence substrate availability, which is the primary constraint on soil CO_2 and N_2O fluxes. The physical factors, soil moisture and serve as secondary controls on soil CO_2 and N_2O fluxes, but are of primary importance for CH_4 uptake. I tested how these five factors described trace gas flux rates.

Site & aspect differences

The observed increase in CO_2 flux rates across sites (with time) suggests that heterotrophic respiration increases following fire, as detritus continues to accumulate for several years immediately following fire. This pattern corresponds with the pattern of total dead wood accumulation that Hall *et al.* (2006) found in a related study in the same region. This study described fuel accumulation across a 160-year chronosequence of wildfires in Front Range forests. Their findings show a peak in dead wood (~25 Mg C ha^{-1}) to occur between 10 and 20 years post-fire. My findings, in combination with those of Hall *et al.* (2006), suggest that CO_2 fluxes via decomposition may continue to increase for an additional 5 - 15 years in these forests before reaching a maximum.

I found CO_2 flux rates to be lowest (Figure 1) at the more recently burned sites and greatest at the older burn sites, a pattern also observed in other regions (Fritze *et al.* 1993; Pietikainen and Fritze 1993). As I will discuss later these results are correlated with fire severity in such a way that reflects substrate availability, which is altered within sites and possibly within aspects.

The overall mean for my sites (144 ± 43 mg CO_2-C m^{-2} h^{-1}) are large compared to other flux rates measured ponderosa pine forests (Law *et al.* 2001; Irvine and Law 2002; Conant *et al.* 2004) and fall within the range 40 – 160 mg C m^{-2} h^{-1} observed by Grady and Hart (2006). They Grady and Hart (2006) found reduced CO_2 fluxes rates for burned ponderosa pine forests in Arizona relative to unburned controls.

The significant site*aspect interaction for N_2O fluxes was driven by the greater rates observed on the N-facing, most recently burned transects at Picnic Rock. This finding implies that substrate availability was less limiting at this location and I expect that this was due to the lower fire severity generally experienced on this aspect at this, the most recently burned, location. My data suggest that any increase in N_2O flux rates following fire in these ponderosa pine forests is minimal and short-lived (no longer present at five years post-fire).

The overall mean N_2O flux rate measured at my sites was 0.25 ± 0.05 μg N_2O-N m^{-2} h^{-1}. Several studies examining the effects of fire on N_2O fluxes have failed to observe any change in rates following those fires. Levine *et al.* (1988) were unable to detect N_2O fluxes before or after a prescribed burn in California chaparral, and only after wetting the soil were fluxes detected. It is possible that substrate availability, which likely increases after fire, as indicated by the CO_2 results, is not the major limitation to N_2O fluxes, but rather soil moisture is the major control in persistently dry ecosystems. The data of Levine *et al.* (1988) support for this where in an even drier South African savanna no combination of burning or wetting was found increase N_2O fluxes to measurable levels (Levine *et al.* 1996).

Within this region at the Shortgrass Steppe Long Term Ecological Research site, prescribed fire was not found to have any effect (relative to controls) on N_2O fluxes at 1 or 5 weeks post-fire (Gathany *et al.* unpublished). In studying land use change along the Colorado Front Range, Kaye *et al.* (2004; 2005) measured fluxes from urban soils as high 350 μg N_2O-N m^{-2} h^{-1}, however, the fluxes measured from soils (crop and native) had rates that varied between 0 - 100 μg N_2O-N m^{-2} h^{-1}.

Upland soils are generally considered to be net sinks of atmospheric methane (Topp and Pattey 1997), due to methanotrophic activity. The long-term effect of fire on the strength of this sink is not well understood despite its potential to be a significant offset to factors that increase an ecosystem's radiative forcing. To date, many studies interested in fire and methane are focused on the pulse that is released as a byproduct of incomplete combustion during the fire (Laursen *et al.* 1992; Potter *et al.* 2002). While this pulse is an important atmospheric budget component of fire prone forests and associated CH_4 dynamics, a complete budget should account for the changes in the longer term CH_4 sink in these upland soils (Topp and Pattey 1997). Recent studies have begun to investigate the potential influence of fire on an ecosystem's CH_4 sink strength and how this may vary with time (Randerson *et al.* 2006). Notably, the source of reduced carbon for methanotrophs - the atmosphere - is not likely directly affected by fire after several years. However, there could be other impacts on methanotrophic activity in soils, including nutrient availability and microclimate.

The overall mean CH_4 uptake for these sites is 0.12 ± 0.06 mg CH_4-C m^{-2} h^{-1}. The lack of statistical differences ($p > 0.05$) for methane uptake at my sites suggests that fire in these forests has little effect on the methanotroph community responsible for the sink's strength. Similar to my findings, Castaldi and Fierro (2005) found no differences for CH_4 uptake between burned and unburned studying coastal shrubland (maquis). However, they noted that the greatest uptake rates occurred during the driest and warmest time periods with fluxes between 0.016 and 0.671 mg C m^{-2} h^{-1}. Castaldi and Fierro (2005) also noted high concentrations of ammonium in the upper 10 cm that did not reduce uptake, suggesting the possibility that maximum methanotroph activity may exist deep in the soil profile. This vertical distribution of methanotrophs may be help describe there being no change in uptake between treatments as these communities are likely not affected by soil heating and minimizing microbial mortality.

Global warming potentials

Kaye *et al.* (2004) found that the annual CH_4 GWP from urban soils along the Colorado Front Range didn't exceed -10 g CO_2 equivalents m^{-2} yr^{-1}. Furthermore, they found that compared to cropped or urban soils, native soils (shortgrass steppe) had the greatest methane uptake and least N_2O flux. In contrast this native forest soil had an extremely low contribution of N_2O (0.19 g CO_2 equivalents m^{-2} yr^{-1}) to the overall GWP for the gases I measured. Of the three soil trace gas fluxes investigated in my study CO_2 fluxes contributing 98% of their combined global warming potential.

Environmental controls of soil trace gas flux rates

Ponderosa pine forests of the Colorado Front Range are generally categorized as dry forests, receiving approximately 500 mm of precipitation annually. Given the relatively low water inputs, it is not surprising that soil moisture described the most variability of any factor I considered for both CO_2 and CH_4 flux rates. While I would expect N_2O production processes to occur within the temperature range that I measured, the soils were likely too dry (2-35 %WFPS) for large scale denitrification to occur and may have been limiting to nitrification rates.

I observed a negative relationship between temperature and flux rate for CO_2 flux rates. This may reflect the combined importance of substrate availability (that decreases with depth) and water (that increases with depth) such that at the highest temperatures water availability is minimal at the soil surface where most of the substrate exists (Smith *et al.* 2003). Contrastingly, CH_4 uptake exhibited the opposite pattern, with increased uptake at higher temperatures. These data show support for the greatest methanotrophic activity occurring deeper in the soil profile where soil moisture is greater, as suggested by Castaldi and Fierro (2005) and discussed earlier. Generally, the small amounts of variability described by temperature for my measurements are likely reflective of the timing of my sampling. My field collections were conducted during the summer months when temperature might not be expected to be limiting to biological activity (except at the highest temperatures). I expect that temperature would have described more variability if measurements had been over the course of the year and particularly during snow melt periods (Sommerfeld *et al.* 1993).

My study found that fire severity was negatively correlated with both CO_2 and N_2O such that fluxes decreased with increasing severity. I attribute these patterns to variability in fire severity within and among sample locations. The majority of the locations I sampled experienced an intermediate to high severity fire, which is influenced by available fuel, topography, weather, and their respective interactions (particularly as it relates to fuel moisture). The Bobcat Gulch and Hayman fires each burned during the month of June, when fuel moistures were low such that fuel amount became the limiting factor for fire severity. In this region, north facing slopes have considerably higher forest biomass. As a result, forest stands on these aspects tended to burn at greater severity, whereas fire severity in stands on south facing slopes was generally less. I observed lower soil CO_2 flux on north facing aspects where more forest biomass, as well as soil organic matter, was likely lost to combustion, such that less was available for decomposition in the years following.

In contrast, I observed the largest fluxes of N_2O occurred on north-facing slopes, and particularly at those locations that experienced a lower severity wildfire. This more recently burned site, Picnic Rock, burned in early April, when fuel moistures in this region tends to be greater, such that combustion and subsequent loss of biomass from the system may be less. As a result, more of the forest biomass remains in the ecosystem, and being subject to post-fire decay. This trend has been noted in other studies (Covington and Sackett 1986; Covington and Sackett 1992); low severity fires can produce a pulse of mineral N in the soil, a portion of which is released to the atmosphere as N_2O. Several other studies have found that soil N levels are greatest at locations the burned at lower severity such as occur during prescribed burns (Covington and Sackett 1986; Covington and Sackett 1992; Hamman 2006; Hamman *et al.* 2007). However, this trend is short lived (Wan *et al.* 2001). Fire severity did not describe any of the variability observed for methane uptake, suggesting that within this post-fire timeframe fire had a minimal direct effect on methanotrophs.

Landscape position has frequently been shown to be an important determinant of soil organic matter and microclimate (Burke *et al.* 1995; Boerner *et al.* 2000; Likens *et al.* 2002; Izaurralde *et al.* 2004) and how these variables can be changed by fires along such gradients (Neary *et al.* 1999; Wan *et al.* 2001; Certini 2005). While only important independently for one trace gas flux (CH_4 uptake), topographic aspect appeared in the top five candidate models for all three trace gases. As an easily measured variable (in the field or remotely), its inclusion is useful in making predictions regarding post-fire gaseous exchanges between the soil and atmosphere.

The increasing CO_2 flux rates with time since fire are supported by findings of others in a variety of ecosystems that experience fire: boreal forest (Burke *et al.* 1997; Kim and Tanaka 2003; Czimczik *et al.* 2006), northern Rocky Mountain USA lodgepole (Litton *et al.* 2003), 50-150 mg m^{-2} h^{-1}), African savanna and woodland (Zepp *et al.* 1996), and mixed conifer in Sierra Nevada (Concilio *et al.* 2006). Randerson *et al.* (2006) considered the net effect of GHGs and aerosols on the net radiative forcing of burned landscapes. One year post-fire, they found that burned areas had strong net positive radiative forcing. However, after 80 years (one fire return interval) the post-fire landscape had a net negative radiative forcing for that period. For their ecosystem, they found that changes in albedo were most important in directory the net trajectory of all the variables' forcings. However, their model suggests that the importance of trace gas fluxes and their net radiative forcing will increase as the fire return interval shortens, as it is expected to in the coming centuries. The relatively low importance of time in predicting N_2O flux rates may be indicative of the ephemeral nature of the N pulse that is frequently observed within one year following fire (Wan *et al.* 2001).

Conclusions

Ponderosa pine forests compose 22% of all the forests in the American West (Powell *et al.* 1993). Despite this wide distribution, and sensitivity to change in climate and fire regime, relatively few studies have addressed trace gas fluxes in ponderosa pine forests. My data show that an understanding of fire and its associated effects is important for understanding the source-sink balance of CO_2, CH_4, and N_2O following wildfire. I found that CO_2 fluxes were greatest in magnitude as well as importance (relative to global warming potentials of CH_4 and N_2O). Across the span of five years since fire, I found that CO_2 fluxes increased with time, consistent with the data of Hall *et al.* (2006). My work shows that CO_2 flux rates can be predicted using the easily calculated and measured environmental variables; time since fire, aspect, fire severity, soil moisture, and soil temperature.

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Table 1. Global warming potentials (g CO_2 equivalents m^{-2} yr^{-1}± SE) calculated from soil trace gas fluxes that I measured on north- and south-facing aspects at each of my four post-fire locations along the Colorado Front Range. Values indicate soil-atmosphere exchange of methane, nitrous oxide and the total (summing methane uptake, nitrous oxide flux, and carbon dioxide flux). Negative values indicate net uptake by the soil whereas positive values indicate a net release from the soil.

		Global warming potentials (g CO_2 equivalents m^{-2} yr^{-1})		
Site	**Aspect**	**Methane ± SE**	**Nitrous oxide ± SE**	**Total (including CO_2) ± SE**
Bobcat Gulch	North	-56.14 ± 14.11	0.15 ± 0.06	5688 ± 1868
	South	-46.20 ± 44.49	0.09 ± 0.03	7222 ± 1895
Hayman	North	-75.97 ± 38.88	0.20 ± 0.05	1842 ± 472
	South	-66.93 ± 23.33	0.27 ± 0.06	3008 ± 912
Hewlett Gulch	North	-55.92 ± 54.11	0.09 ± 0.02	3861 ± 986
	South	-134.33 ± 30.11	0.29 ± 0.19	6966 ± 2484
Picnic Rock	North	-154.94 ± 115.98	0.39 ± 0.40	3972 ± 1215
	South	-54.56 ± 10.70	0.04 ± 0.01	3732 ± 1257
Overall		-80.62 ± 42.80	0.19 ± 0.10	4537 ± 1386

Table 2. The results of the likelihood analysis for CO_2, CH_4, and N_2O flux rates. The top five models (lowest AIC_c of 32 models) are shown here in rank order for each trace gas flux. Each model's parameter(s) is given as well as the total number of parameters (includes intercept and error term for AIC calculation), AIC_c score, Δi (the difference in a particular model's AIC score relative to the lowest overall for that trace gas), and w_i (describes the strength of that model with respect to all other models).

Trace gas	Model Rank	Parameters	p	SSE	AICc	Δ_i	w_i
Carbon dioxide							
	1	wfps	3	1949637	511.396	0.000	0.219
	2	wfps,time	4	1906357	512.297	0.901	0.139
	3	wfps,aspect	4	1939516	513.195	1.799	0.089
	4	wfps,severity,time	5	1866686	513.290	1.894	0.085
	5	wfps,severity	4	1946985	513.396	2.000	0.080
Methane							
	1	time	3	7.727	-136.837	0.000	0.104
	2	wfps	3	7.750	-136.682	0.155	0.097
	3	severity	3	7.809	-136.287	0.550	0.079
	4	aspect	3	7.820	-136.213	0.624	0.076
	5	temp	3	7.823	-136.194	0.643	0.076
Nitrous oxide							
	1	severity	3	14.830	-88.311	0.000	0.159
	2	severity,aspect	4	14.539	-87.171	1.140	0.090
	3	wfps,severity	4	14.741	-86.518	1.793	0.065
	4	temp,severity	4	14.802	-86.322	1.989	0.059
	5	severity,time	4	14.826	-86.246	2.065	0.057

Figure Legends

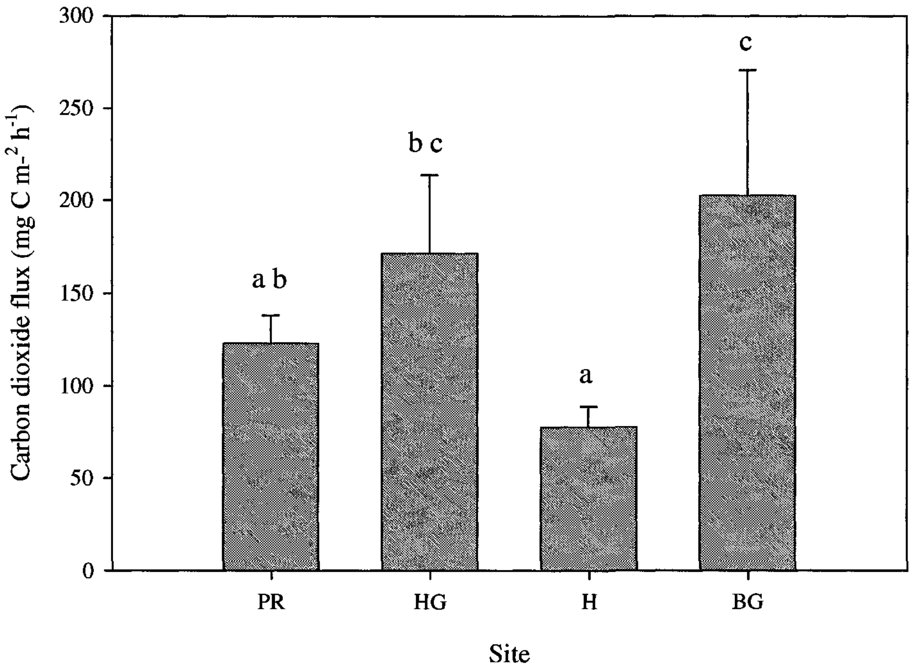
Figure 1. Mean CO_2 flux rates (mg C m^{-2} h^{-1} + SE) averaged over aspect and sampling cycle at each of the four sites studied during summer 2005 from the Front Range of Colorado. Sites include the following (figure abbreviation and years since fire) - Picnic Rock (PR, 1), Hewlett Gulch (HG, 3), Hayman (H, 3), and Bobcat Gulch (BG, 5). Fire severity was variable within and between sites. Letters above bars indicate significant differences ($p \leq 0.05$) between sites.

Figure 2. Bars represent mean CH_4 uptake rates (mg C m^{-2} h^{-1} + SE) averaged over aspect and sampling cycle at each of the four sites studied during summer 2005 along the Colorado Front Range. Sites include the following (site abbreviation, year(s) since fire) - Picnic Rock (PR, 1), Hewlett Gulch (HG, 3), Hayman (H, 3), and Bobcat Gulch (BG, 5). Fire severity was variable within and between sites. This factor is addressed in this paper that investigated the importance of environmental factors on predicting flux rates Letters above bars indicate significant differences between sites with different letters.

Figure 3. Each bar gives the proportion of variance that each factor explained with respect to the total variability that was observed for soil CO_2, CH_4, and N_2O flux rates. Open bars indicate a positive relationship and hatched bars indicate a negative relationship (aspect: S = 1 N = 2).

Figure 4. The proportion of variability that was described for each of the three trace gas species given the five environmental factors I measured. Refer to Figure 3 for positive or negative relationship of a particular factor.

Figure 1



300
250
200
150
100
50
0
Carbon dioxide flux (mg C m-2 h-1)
a b
b c
a
c
PR
HG
H
BG
Site

Figure 2

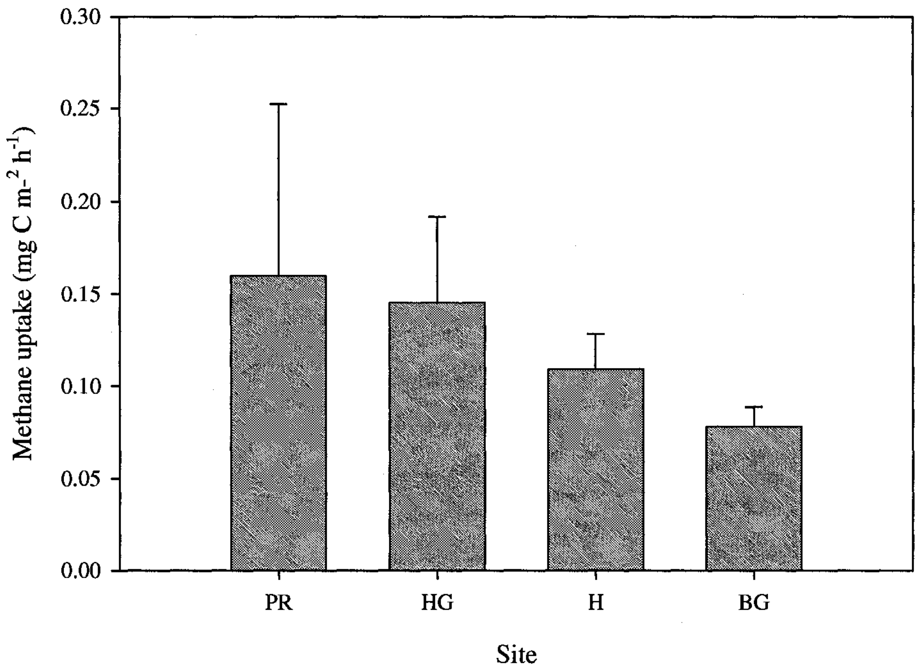
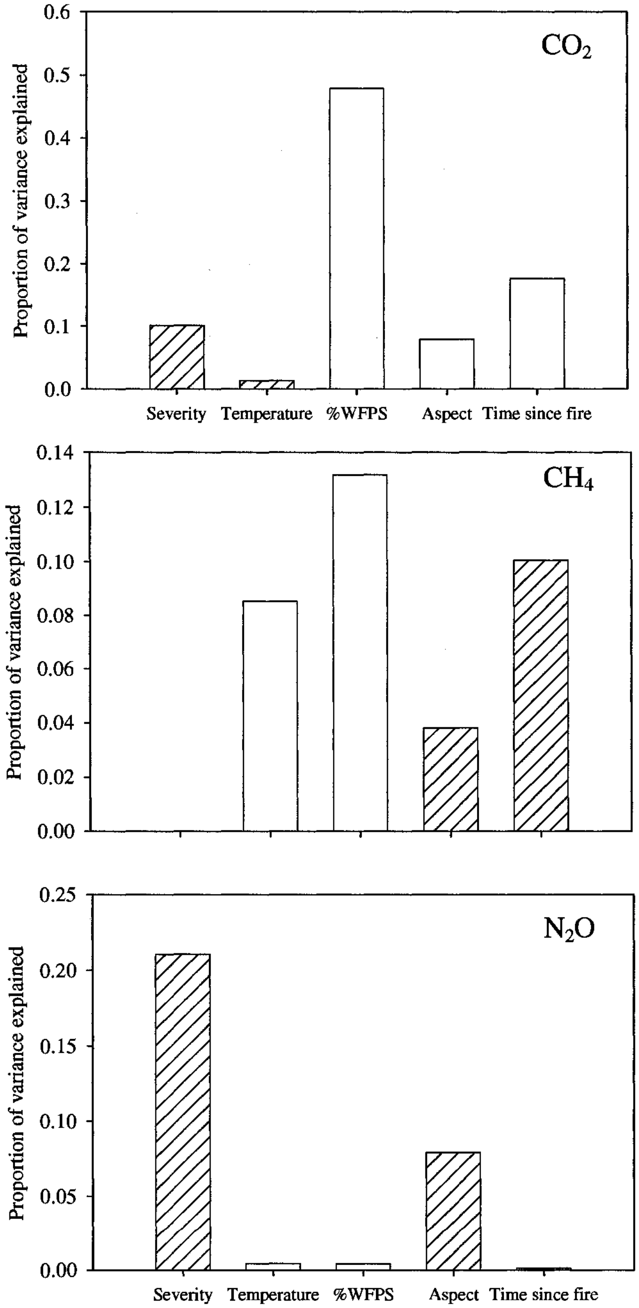
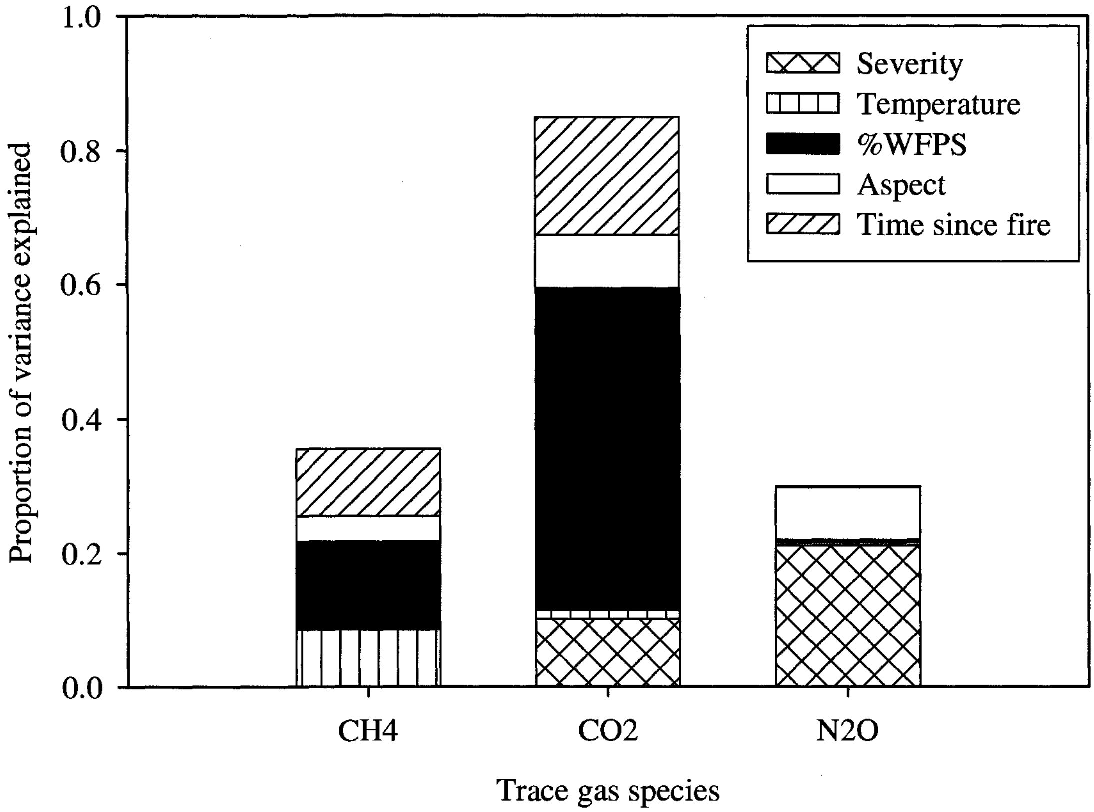

0.30
0.25
0.20
0.15
0.10
0.05
0.00
Methane uptake (mg C m-2 h-1)
PR
HG
H
BG
Site

Figure 3



CO2
CH4
N2O
Proportion of variance explained
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.00
0.02
0.04
0.06
0.08
0.10
0.12
0.14
0.05
0.15
0.20
0.25
Severity
Temperature
%WFPS
Aspect
Time since fire

Figure 4



1.0
0.8
0.6
0.4
0.2
0.0
Proportion of variance explained
Severity
Temperature
%WFPS
Aspect
Time since fire
CH4
CO2
N2O
Trace gas species

Chapter 3

THE EFFECTS OF FOREST THINNING PRACTICES AND ALTERED NUTRIENT SUPPLY ON SOIL TRACE GAS FLUXES IN COLORADO

Abstract

Increases in wildfire activity in the western United States have prompted land managers to reevaluate management practices. In the Colorado Front Range, where population density is high, there is often great concern regarding wildfire which leads to efforts that will reduce fire hazard. The most common method of achieving this goal is to thin the forest of small diameter trees. Oftentimes these practices are undertaken with little knowledge of the ecological consequences of such treatments. I investigated the effect(s) of three treatments (control, thinning-only and broadcast chipping) on trace gas fluxes (CO_2, CH_4, and N_2O), litter mass, and soil carbon and nitrogen. In a small plot study, I used a 2 x 3 x 3 randomized complete block design to determine the influence of nutrient amendments (woodchips, nitrogen, and phosphorus availability) on trace gas fluxes.

The stand-management study revealed that neither thinning-only nor broadcast chipping significantly affected soil carbon or nitrogen, while thinning-only significantly reduced the amount of forest floor litter. Each trace gas flux was significantly affected by the date of sampling (June or August). CO_2 and N_2O fluxes each had a significant interaction between treatment and sampling date. I attribute this to a difference in moisture availability between the sampling times. In the plot study I found that only the interaction between woodchip addition and phosphorus availability significantly affected CO_2 flux. Nitrous oxide fluxes were not significantly affected by any combination,

however, methane uptake was found to respond significantly to different nitrogen and phosphorus levels.

Introduction

Our knowledge of the complex interactions between fire and climate is steadily increasing (Moritz *et al.* 2005; Westerling *et al.* 2006). As fire activity has increased in recent decades (Westerling *et al.* 2006), so too has public awareness. Concerns have developed in light of last century's fire exclusion practices, how these now affect wildfire potential, and the uncertainty of how future climate change will affect fire regimes (Veblen *et al.* 2000). Forest managers in the Colorado Front Range and elsewhere in the American West have begun to use a variety of forest management practices to direct forests back to a natural range of variability that could be better buffered against future changes in climate (Kaufmann *et al.* 2005; Veblen and Donnegan 2005). These practices include prescribed burning and/or thinning each with the goal of reducing fire risk and hazard (Fule *et al.* 2001). Currently, there is relatively little ecological knowledge to use in evaluating the ecosystem consequences of these practices in the Colorado Front Range.

In southwestern U.S. ponderosa pine forests, these restoration practices have altered forest structure (Covington *et al.* 2001), microclimate (Hungate *et al.* 2007), substrate quality and availability (Grady and Hart 2006), and microbial communities (Boyle *et al.* 2005). Hungate *et al.* (2007) developed a general framework to depict how restoration treatments influence the properties and processes of the plant and microbial community in southwestern ponderosa pine forests. I apply that framework, and adapt it to explain how I expect restoration treatments in the northern Colorado to change trace gas flux rates that are regulated by biological activity that in turn is controlled by the physical environment (Figure 1).

Among the important ecological consequences of forest management practices are trace gas fluxes, which are the product of multiple biogeochemical processes that are sensitive to environmental change (Mosier 1998). Carbon dioxide (CO_2), methane (CH_4) and nitrous oxide (N_2O) act as greenhouse gases in the atmosphere (Conrad 1995; Conrad 1996) and knowledge of how forest management practices affect their flux rates is largely unknown. In addition, data about trace gas exchanges can provide insights into ecosystem functioning, carbon balance, nutrient cycling and microbial activity (Figure 1). Both CO_2 andN_2O fluxes are primarily by substrate availability and biological activity. Biological activity is constrained by two parameters, water availability and temperature, which have changed significantly in response to forest thinning. Methanotrophs are responsible for CH_4 oxidation in upland soils and the rate of CH_4 uptake is constrained by the biotic activity and the diffusion of atmospheric CH_4 into the soil (diffusivity). Both of which are sensitive to changes in soil moisture, that again has been found to be significantly altered following forest thinning.

In this study, my overall aim was to assess the effects of forest management practices on trace gas fluxes, with the general hypothesis that soil CO_2 and N_2O flux rates would increase with forest management practices that increased soil substrate (carbon or nitrogen) availability, or soil moisture, and soil CH_4 fluxes would be primarily affected by forest management practices that altered soil microclimate. In a first study, referred to hereafter as the "stand management" study, I had two objectives: 1) to measure changes in litter mass and soil carbon (C) and nitrogen (N) following forest thinning, and

2) to understand how thinning treatments affect the soil flux rates of methane, carbon dioxide, and nitrous oxide. In a second study, which I refer to as the "fertilization" study, I sought to determine nutrient (carbon, nitrogen, and phosphorus) controls of these gas fluxes from the forest soil.

Methods

Study site

Heil Valley Ranch is located approximately 15 kilometers north of Boulder, Colorado, and is owned and managed by Boulder County Open Space and Mountain Parks. Forest thinning practices began on the property in 1999 with the objective of reducing canopy fire risk. The forest canopy is dominated by ponderosa pine (*Pinus ponderosa*), with a Douglas-fir (*Pseudotsuga menzeii*) component. Soils are generally shallow (< 1 m), and described as coarse sandy loams common to the Typic Haplustalfs series in the region. According to the Soil Survey Staff (2007) of the Natural Resource Conservation Service (NRCS), the following series can be found at Heil Valley Ranch: Fern Cliff, Baller, Allens Park, Goldvale, & Nederland Series. All of my sampling locations were on a shallow slope (5-15%) and with the same aspect (southeast).

Stand study

Boulder County Open Space and Mountain Parks initiated thinning treatments at Heil Valley Ranch in 1999 in response to increased wildfire activity in surrounding forests. All stems < 15 cm dbh (diameter at breast height) were selectively cut. As these small stems were not merchantable, the managers elected to dispose of the biomass using two methods, broadcast-chip and thinning-only. In the broadcast-chip plots, all of the cut stems were mechanically chipped and broadcast onto the forest floor with a 7.5 cm target depth. In the thinning-only plots all stems < 15 cm dbh were cut, subsequently removed from the plots, and mechanically chipped into large piles at specific locations on the property. I sampled the three broadcast-chip plots that were thinned in 2002. These broadcast-chip plots had an average size of 27 acres. Thinning-only plots were thinned in 2003 and had an average plot size of 27.5 acres. I randomly selected control plots from the untreated area of the property while still being within 1 – 2 km of the thinning-only and broadcast-chip plots.

To compare the effects of the treatments, I established a 20-m transect in each of the three treated plots (thinning-only and broadcast-chip) and at four untreated control sites. I measured trace gas flux and associated soil properties in the summer of 2006. During June I sampled two transects from each treatment (thinning-only, broadcast-chip) and un-thinned controls, and in August I sampled one transect in both thinning-only and broadcast-chip and two in my control, un-thinned forest. June and August sampling dates were separated by no more than 42 days.

At the time of sampling I placed five 20 cm diameter chambers every 5 m along transects. I used a landscaping tamper to drive PVC chamber bases into the soil until secure; I recorded heights at three points within each chamber base to calculate chamber volume. At time zero I placed the chamber lid on the base, sealed it with a rubber gasket and collected a 25 mL air sample from the chamber headspace. Similar samples were collected at 10, 20, and 30 minutes after chamber closure. Each air sample was collected with a 30 mL BD nylon syringe and then injected into pre-evacuated (200 millitorr) serum vials sealed by rubber septa. Vials were stored at 25 °C until gas chromatographic analysis.

Upon completing air sampling, I removed chamber covers and collected soil cores (to 5 cm) and all litter (including woodchips where present) within each chamber base (0.0314 m^2). I dried all litter and soil at 55 °C for 24 hours, or to a constant weight. I calculated soil moisture for both the soil and litter as the % change between field moist and dry mass. Soils were then sieved through a 2mm mesh and analyzed for total soil C and N using a Leco analyzer. I converted soil C and N data to a volume basis using bulk density estimates. Litter mass was corrected to a per area basis (m^2).

Fertilization study

I utilized an ongoing small plot fertilization study that measured the responses of understory plant community to the addition of woodchips, and the manipulation of nitrogen and phosphorus levels that included either increased, ambient or decreased levels. These plots were established in an area of the forest that had been thinned in the early winter of 2004, approximately 2 years prior to this study.

The woodchip addition was meant to serve as a carbon addition that would result in N immobilization; a 7.5 cm thick layer of woodchips was placed on half of the plots (n = 36). Woodchips were added to the 2.25 m^2 plots at the beginning of the 2005 growing season. These chips were from an adjacent thinned stand that had been piled in 2003. The chips applied to these small plots were taken from the interior of the large (~5 m diameter) chip pile so as to access "fresh" chips that had experienced relatively little decay. At the time of this study, the chips had been on the treated plots for nearly two full growing seasons with nutrient amendments being added to the plots during that same time period. For the nitrogen treatments, NH_4^+/NO_3^- fertilizer (10 g N m^{-2} yr^{-1}) was applied to increase N availability, sucrose (500 g C m^{-2} yr^{-1}) to decrease N availability, and I refer to plots receiving no manipulation as ambient, or control N. Similarly to N, P availability was increased with phosphate fertilizer (2 g P m^{-2} yr^{-1}), decreased with gypsum (10 g Ca m^{-2} yr^{-1}), with untreated plots as ambient P controls. Nutrient amendments were made monthly through the 2005 and 2006 growing seasons. I collected air samples for trace gas analysis in September 2006, two weeks after the last amendments were made for that season. At each plot (n = 72), I placed a single chamber, collected and stored air samples as described above.

Gas chromatography and lab analyses

Trace gas concentrations were measured using a Shimadzu GC 14B with electron capture detector (ECD for N_2O) and flame ionization detector (FID for CH_4 and CO_2). Nitrogen gas (N_2) was used as the carrier gas. Oven and column temperatures were set at 280 °C and 60 °C, respectively, for CH_4 and CO_2. I utilized a linear, 3-point calibration curve for each of the three gases of interest and standardized chamber gas samples with field standards (Hutchinson and Mosier 1981; Hart 2006) which underwent the same sampling procedures and served as a control against collection and storage bias. Flux rates (mg C or μg N m^{-2} h^{-1}) were derived from the change in concentration over the 30-minute sampling period (Robertson *et al.* 1999).

Statistical methods

I used a one-way analysis of variance to determine the effect of treatments (broadcast chipping, thinning only & control) on three environmental variables; litter mass, soil C & soil N. If a significant ($p \leq 0.05$) treatment effect resulted, I used the LSD post-hoc analyses to determine which treatments were different from one another.

Other variables I measured, such as flux rates and soil moisture, are more sensitive to inter-annual changes in the environment (local weather). To address my second objective – the effect of treatments on trace gas fluxes - I analyze the effects of treatment and sampling date on CH_4 uptake and CO_2 and N_2O flux. I used a two-way analysis of variance to examine the effect and relative importance of treatments and date on trace gas fluxes. To compare significant ($p \leq 0.05$) treatment or date effects (or their interaction), I used LSD post-hoc analyses.

To test the effects of nutrient amendments on trace gas fluxes in the fertilization plots described above, I treated the results as a randomized complete block (4 blocks as reps) experimental design. This setup allowed me to evaluate direct and interacting nutrient controls on CH_4 uptake and CO_2 and N_2O flux. I conducted all analyses with $\alpha = 0.05$, using SPSS Version 15.0 (SPSS-Inc. 2006).

Results

Stand treatments

My first objective for the stand management study was to measure changes in the litter mass and soil C and N following forest thinning. I did not find broadcast chipping or thinning-only to have any significant effect on soil carbon ($p = 0.973$) or nitrogen ($p = 0.856$) relative to controls. I did, however, find that the treatments differed ($p = 0.05$) in forest floor litter (g m^2). Post-hoc analyses show that sampled locations within the thinning-only treatment had significantly less litter (g m^{-2}) than sampled locations within broadcast-chip ($p = 0.026$) and controls ($p = 0.05$), which were not significantly different ($p = 0.599$) from one another (Figure 2). Soil moisture, but not soil temperature, was significantly different between time periods. Averaging over treatments, which were not significantly different, soil moisture (mean % ± SE) for June and August was 3.1 ± 0.5

and 8.5 ± 0.5, which were respectively significantly different ($p < 0.05$). Similarly, litter moisture (%) was 6.6 ± 0. 8 and 9.8 ± 0.9 during June and August sampling, respectively.

Date of sampling had a strong impact on CO_2 flux rates ($p < 0.001$) where they increased between June and August. In addition, the interaction between treatment and sampling date was significant ($p = 0.02$) for CO_2 flux rates, suggesting that differences among treatments were dependent on the sampling date. CO_2 fluxes were higher in August than in June for each of the three treatments. This most likely reflects the significantly higher moisture content of both the soil ($p < 0.000$) and litter ($p = 0.01$) during August. The greatest increase in CO_2 flux rates between June and August sampling dates was observed for the broadcast-chip plots (Figure 3).

Methane uptake rates were most significantly affected by the month in which measurements were made. In the month of June, I found significantly less ($p < 0.001$) methane uptake (0.012 ± 0.003 mg C m^{-2} hr^{-1}) than in August (0.032 ± 0.003 mg C m^{-2} hr^{-1}). I did not observe any significant differences for methane uptake between treatments or for the interaction term.

I found no significant differences for N_2O flux rates between treatment types or sampling date. However, the interaction of the two factors was significant ($p = 0.027$), suggesting that the magnitude and/or directionality of the treatment effects were dependent on the date of sampling. In control plots, there was no difference among sampling dates (Figure 4). In contrast, the broadcast-chipping led to an increase in N_2O flux from June to August, whereas thinning-only had lower N_2O fluxes between the two sampling dates.

Flux rates of the fertilization study

In the full RCB analysis of variance, no main factor (wood chip, nitrogen, or phosphorus) had a significant influence on CO_2 flux rates. The addition of wood chips did, however, interact significantly ($p = 0.03$) with the altered phosphorous availability (Figure 5). Increasing phosphorous availability on chipped plots caused a positive linear increase in CO_2 flux. In contrast, un-chipped plots showed a slightly negative response to increasing levels of phosphorous. Post hoc analyses showed that plots with added woodchips had significantly ($p = 0.002$) greater CO_2 flux rates (310.2 ± 50.0) than plots without woodchips (193.1 ± 19.4).

Methane flux rates at the small plots were significantly ($p = 0.028$) affected by an N*P interaction (Figure 6). At reduced levels of P, there was a positive relationship of increasing N on methane flux (decreased uptake). At control levels of P, the opposite pattern occurred, with a negative relationship of increasing N with methane flux (increased uptake). Last, with increased P levels, there was no effect of N on methane flux. N_2O Flux rates ranged between 18.7 – 107.3 $\mu g\ N\ m^{-2}\ h^{-1}$ with no significant main or interaction effects of nutrient treatments.

Discussion

Ponderosa pine forests are distributed widely across the western United States. The stand structures vary greatly with respect to the climate and fire regime of a particular area. Therefore, restoration strategies vary by region (Shinneman and Baker 1997). A large quantity of the current understanding of ponderosa pine ecosystems has been developed in the southwestern U.S. and particularly in Arizona. In a recent study, Hungate *et al.* (2007) proposed and experimentally tested the effects of forest restoration (thinning and burning) on nitrogen cycling in those ecosystems. Here I present a modified version of their "framework" as it applies to this forest with respect to the influence of management practices on trace gas exchanges (Figure 1).

Forest management and restoration practices, such as thinning and broadcast chipping, can have significant effects on forested ecosystems (Resh *et al.* 2006), though the changes are not always as expected and often the mechanisms have yet to be tested. Forest thinning can have immediate impacts on plant communities, soil organic matter, and forest microclimate (Figure 1). These impacts may be enhanced in the case of broadcast-chipping treatments where there is a large amount of substrate rapidly made available for decay. Reduction of the canopy cover directly reduced canopy photosynthesis and indirectly changes the water and energy balance of the ecosystem. For instance, I expect greater differences in maximum and minimum temperatures at the soil surface relative to untreated controls and alteration of the soil water balance (reduced transpiration, increased evaporation and throughfall). The changes in the canopy structure and microclimate are expected to affect the quantity and quality of soil resources available to plant and microbial communities, consequently affecting trace gas fluxes.

Forest floor, soil C & N – stand management study

My study found that thinning-only significantly reduced litter mass relative to broadcast-chipping and controls. The litter mass was not different between broadcast-chip (which included chips) and control treatments. However, the horizontal and vertical structures of the forest floors were different, as the chipped layer of the broadcast-chip areas had a more compact layer of woodchips on the forest floor. While even distribution was the goal, there was great variability in both the depth of woodchips and their patchiness. In contrast, control plots were more uniform in the distribution of litter. These patterns are likely associated with the distribution of trees. For the purposes of restoration with respect to litter, thinning-only treatments may be most effective in these forests.

Forest managers have long been interested in soil carbon and nitrogen as they influence forest productivity (Ballard 2000; Birdsey and Lewis 2002). With an increasing awareness of carbon storage (and credits) managers are interested in the effects of their management decisions on the ecosystem and economic budget. In their review of the effects of forest thinning (and broadcast chipping), Resh *et al.* (2006) found mixed results for positive, negative, or no change in soil C and N stocks. My data show that 5 years after thinning any changes that may have occurred during that period were short-lived.

Flux rates in managed forest – stand management study

I conducted all of my fieldwork during June and August 2006. I found no difference in soil temperatures among sampling dates. However, soil moisture was significantly different between June and August sampling. This relationship has been found elsewhere in the American West (Boyle *et al.* 2005; McLain and Martens 2006b). In semi-arid vegetation of southeastern Arizona McLain and Martens (2006b) described the ability of soil temperature and moisture to control CO_2 and N_2O fluxes and CH_4 uptake.

I observed a similar correlation in my study since differences between June and August moisture levels reflected the differences in CO_2 flux rates. The treatment effect was dependent on the sampling date (Figure 3). For the summer season (averaging across sampling date), I found no significant difference in CO_2 flux rates between treatments. The most dramatic increase in CO_2 flux was seen in broadcast-chip where the flux tripled between sampling dates, which correlated with increased moisture availability. Carbon substrate availability is the initial limitation to soil CO_2 fluxes, but my data suggest water availability is of primary importance and supports the assertion of Smith *et al.* (2003) that CO_2 flux from soils is a "function of water content as soils dry out."

This forest is described as "dry" or "semi-arid" with ~ 500 mm of precipitation each year. I observed a difference between wet and dry conditions with respect to methane uptake. My data showed greater uptake during months when soil moisture was greater. According Del Grosso *et al.* (2000) maximum CH_4 uptake (0.05 mg C m^{-2} h^{-1}) in coarse soils occurs at 7.5 % WFPS (water filled pore space). At my sites, soil moisture increased to a level that appeared to stimulate biological activity (Figure 4), whereas further increases of soil moisture should be expected to decrease the uptake rate. Castaldi *et al.* (2006) reviewed the literature research on CH_4 flux rates in seasonally dry savannas. They examined the influence of land management as well as determining the effect of wet and dry seasons on the soil to atmosphere exchange of these trace gases. They found that CH_4 fluxes were significantly different among managed (0.005 mg CH_4 m^{-2} h^{-1}, net source), burn only (-0.020 mg CH_4 m^{-2} h^{-1}) and control (-0.086 mg CH_4 m^{-2} h^{-1}). Within each land use type, they found a significant difference between wet and dry seasons.

Thinning treatments did not directly affect methane uptake. Other studies have examined the direct effects of forest management on the rates of CH_4 exchange. Teepe *et al.* (2004) found that soils that had been compacted by heavy equipment and trucks had significantly lower methane uptake relative to adjacent undisturbed soils. As methanotrophic bacteria rely on the atmosphere for their substrate (methane) the rate of diffusion through the soil exerts a strong control on the rate at which methane oxidation may occur (Smith *et al.* 2003). My sample collections were made three to four years after heavy equipment had been used to thin these areas. I was unable to visually identify areas that may have had compacted soils and may therefore be a potential source of variability in my data.

Nitrous oxide flux rates were greatest in the broadcast-chip treatment during August. The significantly higher moisture content of the soil and litter also had a positive effect on CO_2 flux and CH_4 uptake. While I can easily attribute a similar correlation between N_2O fluxes and greater water availability, my observations only support that conclusion for a single treatment, broadcast-chip (Figure 4). Castaldi *et al.* (2006) did not find any significant effect of wet versus dry season on N_2O flux rates in seasonally-dry ecosystems. In the cases they reviewed, intra-site and intra-season variability was greater than the variability among sites or seasons. Other studies have been inconclusive in trying to determine the effect(s) of management on N_2O fluxes at the site level (Castaldi *et al.* 2006).

Flux rates and nutrient amendments – plot level study

Fertilizer additions to forests are a common practice throughout the world (Papen and Butterbach-Bahl 1999; Palm *et al.* 2002) and the United States (Johnson 1992;

Johnson and Curtis 2001). To my knowledge, there has not been any research on the response of soil trace gas fluxes to fertilization in northern ponderosa pine forests. I had predicted that wood, as a C substrate for heterotrophs, would increase CO_2 fluxes, and that N and P would increase CO_2 and N_2O fluxes as I expected microbial community to respond with increases in activity. I expected methane uptake would be directly influenced by nitrogen and phosphorus additions and indirectly by wood chip additions and changes in soil moisture availability.

The significant interaction between woodchip addition and phosphorus showed support for the idea that substrate availability is of primary importance. This finding is different from my stand management study suggesting that newer chips may undergo a short period (0-4 years) of decomposition, but stabilizing when most labile compounds have been accessed. I found that wood addition, like water addition for Illeris *et al.* (2003), made the greatest difference, but appeared to then be enhanced in some manner by phosphorus manipulation. Interestingly, I found the greatest difference for wood and phosphorus manipulation to be between the wood additions versus no wood additions at control levels of phosphorus (Figure 4) indicating the greater importance of carbon substrate availability.

Other studies have found the same directional responses to nutrient additions for CO_2 flux. Schaeffer and Evans (2005) found the greatest CO_2 flux rates in plots with added C and N (360 mg C m^{-2} h^{-1}), or just added C in the Canyonlands National Park of Utah. These differences were greatest just three days after precipitation and nutrient pulses, both of which were undetectable after seven days. These soils show greater activity; without water additions, I observed significant differences between treatments in which fertilizers had last been added two weeks prior to my sampling. Maljanen *et al.* (2006a; 2006b) examined the affect of ash and nitrogen additions in coniferous forests of Finland. They did not observe any in situ differences in CO_2 fluxes in soils where ash, nitrogen, or ash + N had been added. Like my study, they found that sampling times were significantly different from one another, suggesting that environmental controls, particularly soil temperature in their case, were more important than nutrient addition.

In my study, the smallest CH_4 uptake rate was observed at high N and low P availability. These results confirm the observations of others where increased N availability can decrease CH_4 oxidation (Mosier *et al.* 1996; Gulledge and Schimel 1998; Bowden *et al.* 2000). Maljanen *et al.* (2006a) found that long term additions of wood ash increased CH_4 uptake. They found no effect of N addition or ash*N interaction. These findings differ from my observations, where wood addition had no direct effect on CH_4 uptake which was significantly affected by N*P (Figure 6).

Nitrous oxide fluxes were not significantly affected by any nutrient amendment. This result was somewhat surprising, as these plots had received monthly N additions for two full growing seasons, which I would have expected to increase both nitrification and denitrification rates (Davidson and Verchot 2000). The same results have been observed in various locations. In Canyonlands National Park of Utah, Schaeffer and Evans (2005) found soil N_2O flux measurements on day 7 (following N addition and moisture pulse) were not significantly different from one another from day zero. They concluded that the microbial community is most limited in these dry systems by water. Other studies have suggested that C and N may accumulate during dry periods (Davidson *et al.* 1993; Austin *et al.* 2004) which may then generate a flush of available soil resources once water becomes available (Hungate *et al.* 1997; Fierer and Schimel 2002). The same pattern was observed in Finland where neither ash or N affected N_2O production, whereas sampling date did (Maljanen *et al.* 2006a). Extensive studies have been conducted in Germany, particularly at Hoglwald Forest, to investigate the effects of N deposition (ButterbachBahl *et al.* 1997; Brumme *et al.* 1999), forest type and management (Butterbach-Bahl *et al.* 2002a), and distance to trees (Butterbach-Bahl *et al.* 2002b) on N-gas fluxes. In their continuous 4-year study of gaseous N fluxes, Butterbach-Bahl *et al.* (2002a) found that of the gaseous N fluxes, N_2O fluxes exhibited the greatest inter-annual variability (> 7-fold).

Conclusions

I found no direct effect of forest thinning on soil trace gas fluxes. In my study, soil moisture was highly correlated with sampling dates, and sampling date interacted significantly with treatments for CO_2 and N_2O suggesting that moisture levels exert a strong level of control over biological activity. This suggests that broadcast-chipping and thinning-only treatments may significantly impact soil CO_2 and N_2O fluxes, but only at times when soil moisture is high. Similarly, CH_4 uptake rates tripled among sampling dates (Figure 4), but was not influenced by management treatments. Since forest thinning practices impact trace gas fluxes only when soil microclimate is not limiting, substrate availability may not be the main limitation. In the fertilization study, I found that nutrient manipulation significantly affected CO_2 flux and CH_4 uptake.

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Figure captions

Figure 1. This diagram depicts the potential consequences of forest thinning practices at these sites (modified from (Hungate *et al.* 2007). Primary consequences are alterations to plant processes and the forest microclimate. Changes in these lead to secondary changes in soil resources and soil processes.

Figure 2. Bars represent mean litter mass measured in thin-chipped, thin-removed, and controls (error bars are the standard error of treatment means). Lower cased letters that differ indicate treatments that are significantly ($p \leq 0.05$) different from one another based upon LSD post-hoc analyses.

Figure 3. Carbon dioxide flux rates with respect to sampled treatments. Bars represent means measured in June (dark) and August (light).

Figure 4. Nitrous oxide flux rates with respect to sampled treatments. Bars represent means measured in June (dark) and August (light) for each of the measured

Figure 5. Interaction of wood chip additions, phosphorus, and soil carbon dioxide flux in a recently thinned ponderosa pine forest in the Front Range of Colorado. Bars are treatment means and error bars are standard error of the mean.

Figure 6. Interaction between phosphorus and nitrogen as they control methane flux (net uptake) in a ponderosa pine ecosystem. Error bars represent standard error of the mean.

Figure 1.

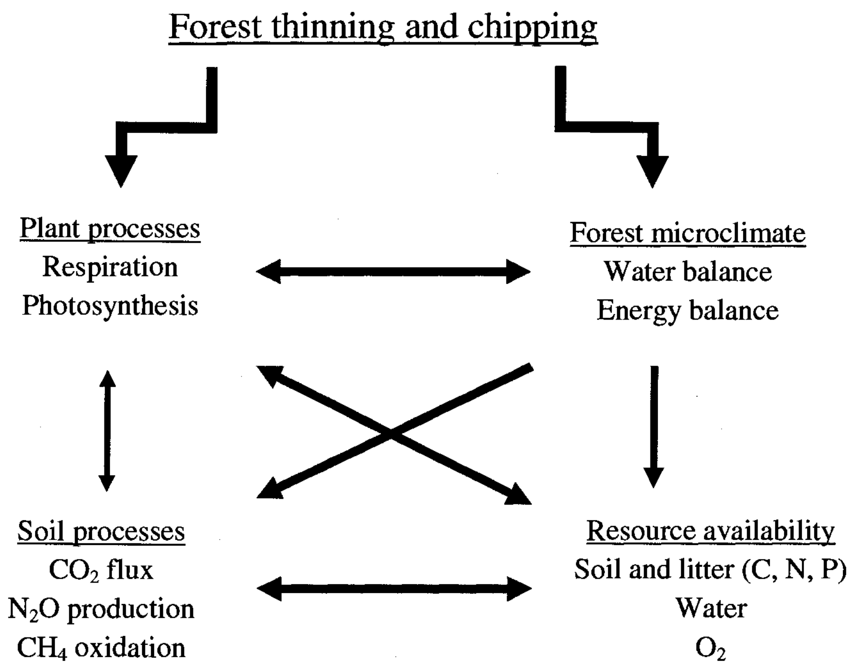
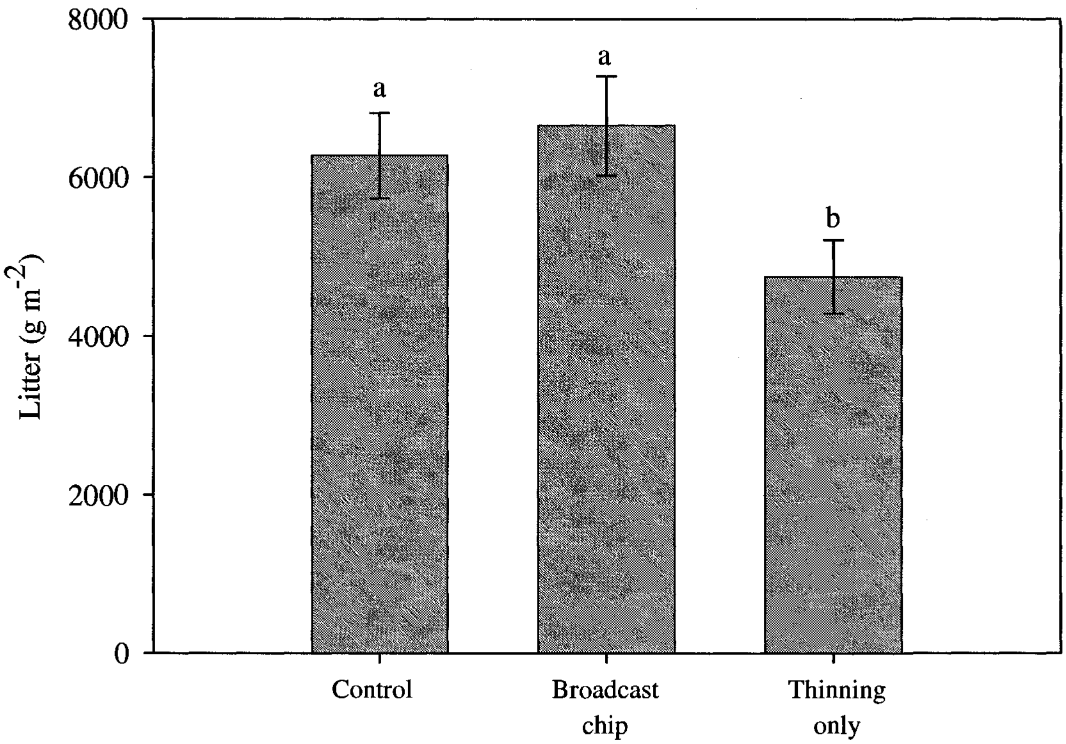
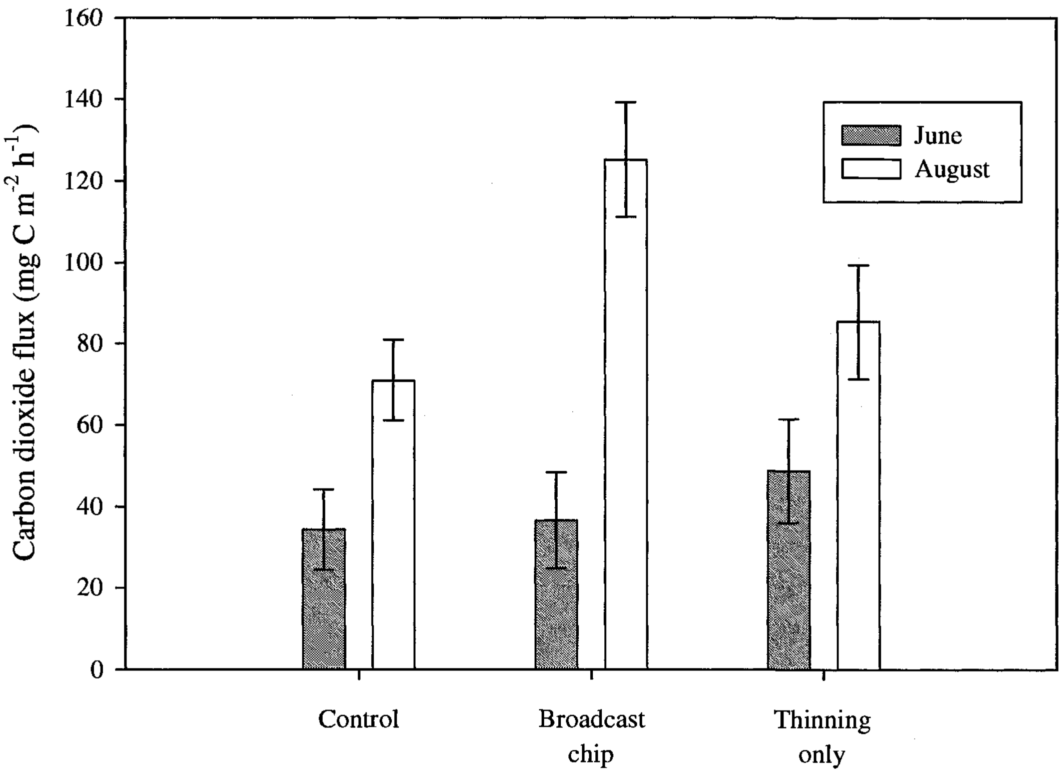

Forest thinning and chipping
Plant processes
Respiration
Photosynthesis
Forest microclimate
Water balance
Energy balance
Soil processes
CO_2 flux
N_2O production
CH_4 oxidation
Resource availability
Soil and litter (C, N, P)
Water
O_2

Figure 2.



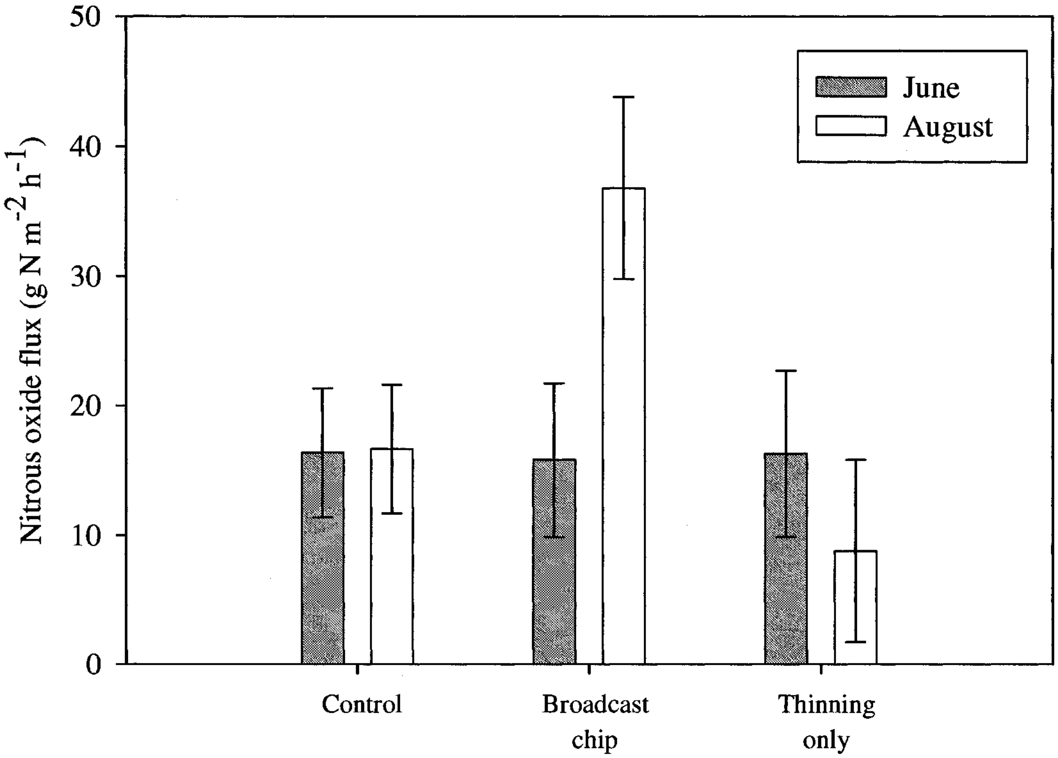
8000
6000
4000
2000
0
Litter (g m-2)
a
a
b
Control
Broadcast chip
Thinning only

Figure 3.



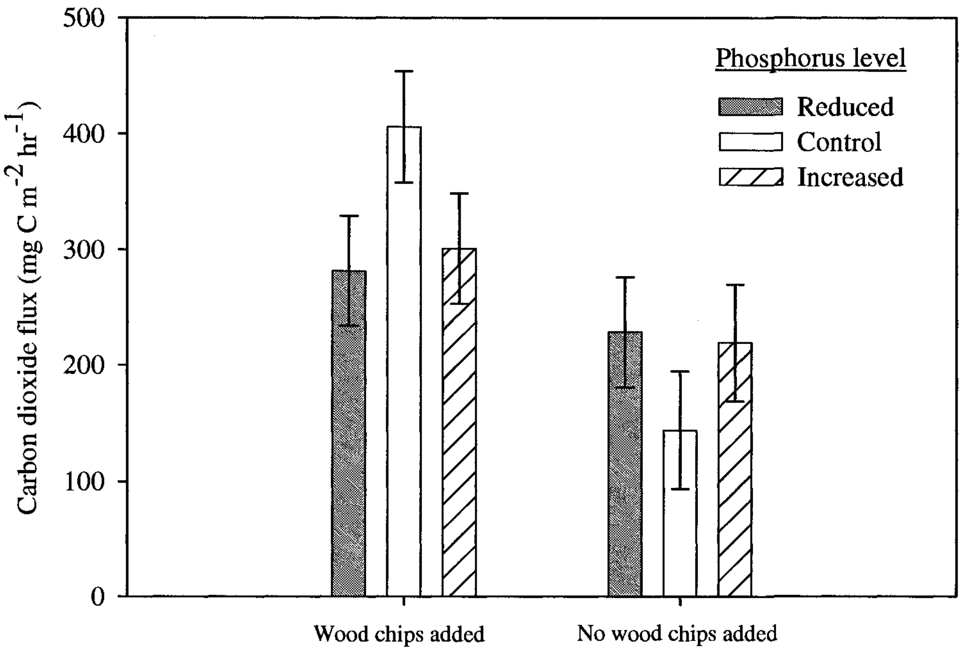
160
140
120
100
80
60
40
20
0
Carbon dioxide flux (mg C m-2 h-1)
June
August
Control
Broadcast chip
Thinning only

Figure 4.



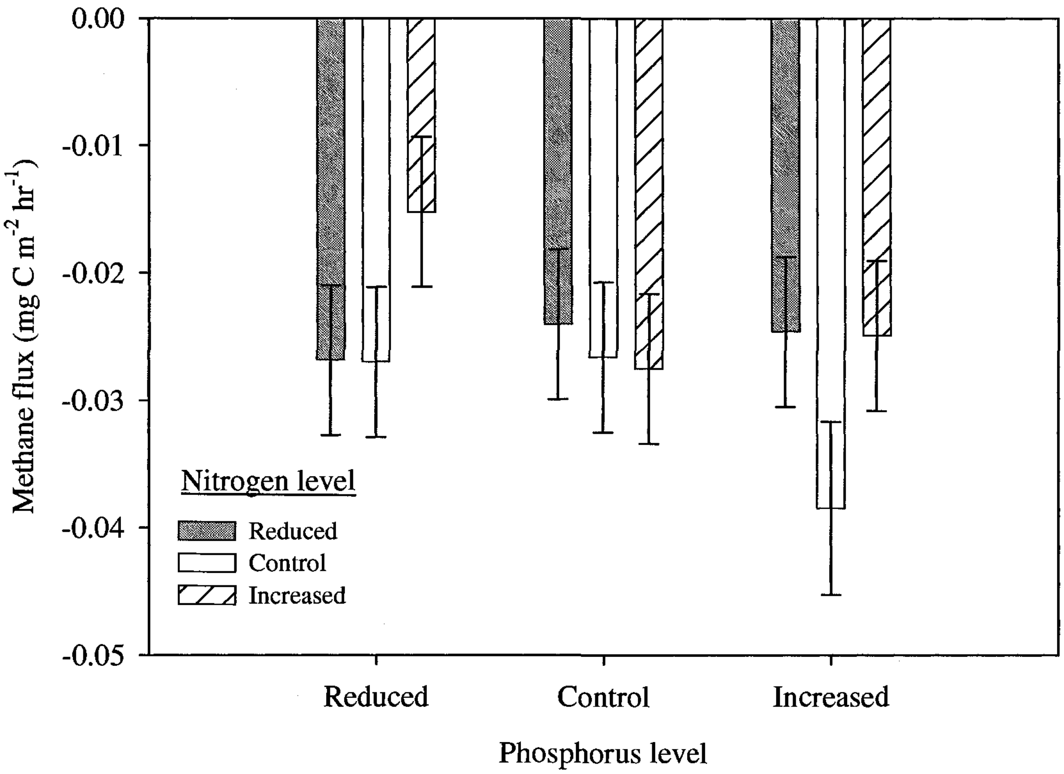
June
August
Nitrous oxide flux ($g\ N\ m^{-2}\ h^{-1}$)
0
10
20
30
40
50
Control
Broadcast chip
Thinning only

Figure 5.



Carbon dioxide flux (mg C m-2 hr-1)
0
100
200
300
400
500
Phosphorus level
Reduced
Control
Increased
Wood chips added
No wood chips added

Figure 6.


0.00
-0.01
-0.02
-0.03
-0.04
-0.05
Methane flux (mg C m-2 hr-1)
Nitrogen level
Reduced
Control
Increased
Reduced
Control
Increased
Phosphorus level

Chapter 4

DAYCENT SIMULATIONS TO TEST THE INFLUENCE OF FIRE REGIME AND FIRE SUPPRESSION ON TRACE GAS FLUXES AND NITROGEN BIOGEOCHEMISTRY OF COLORADO FORESTS

Abstract

Biological activity and the physical environment regulate greenhouse gas fluxes (CH_4, N_2O & NO) from upland soils. Wildfires impact forested ecosystems directly as biomass burns and indirectly through alterations in the physical environment and the subsequent feedbacks to the biota. Fire regimes, varying in frequency and severity, were once regulated primarily by environmental variability in climate, available fuels, and ignitions. I utilize climate records at each of four sites that span 58 to 108 years of daily weather data. I obtained fire return intervals, or fire years when available in the scientific literature. These and soil data were used as primary inputs into Daycent, the daily timestep version of the ecosystem simulation model, Century. In this paper I test the ability of Daycent to simulate four forested sites in this area and to address two objectives: 1) to evaluate the short-term influence of fire on trace gas fluxes from burned landscapes, and 2) to compare trace gas fluxes among locations and between pre-/post-fire suppression. My model simulations indicate that CH_4 oxidation is relatively unaffected by wildfire on the short-term, or by fire suppression over the long-term (< 2% change). In contrast, gross nitrification rates were reduced by 13.5 – 37.1% during the fire suppression period. Daycent calculates N_2O and NO fluxes as a proportion of the nitrification rate such that N-gas flux rates followed the same pattern. At two of the four sites, I calculated large increases in mean gross nitrification rates (> 100%), and N_2O and NO fluxes during the year of fire relative to the year before a fire. Simulated fire suppression has decreased gross nitrification rates presumably as N is immobilized as

biomass. This finding concurs with other studies in coniferous forests that highlight the importance of fire to maintain soil N availability.

Introduction

Fire regimes are determined by the interaction of climate, fuels/plant community, and ignitions (Donnegan *et al.* 2001; Moritz *et al.* 2005). Regional to local climate dictates biomass accumulation and fuel ignitions, which taken together, determine a location's fire regime (Moritz *et al.* 2005). A moist climate may allow for greater fuel accumulation while simultaneously making that fuel less likely to be ignited, whereas the opposite would be expected to occur in a dry climate: lower fuel accumulation, but more easily ignited. The interplay among these three factors is of great interest as scientists continue to try and discern the importance of human influence on Western U.S. forests and their fire regimes (Brown *et al.* 1999).

In the western U.S., we have the most extensive and detailed fire history records in the world (Swetnam *et al.* 1999). However, knowledge of fire activity does not always translate into an understanding of forest structure and function for those same periods of time. In particular, there is great interest and concern regarding the consequences of fire suppression and exclusion (which includes grazing effects) over the past century (Fule *et al.* 1997) on ecosystem structure and function, relative to the natural range of variability.

Despite its importance, relatively little research has related biomass accumulation and Colorado Front Range fire regimes. Warmer and drier conditions in the American West have increased wildfire frequency and extent over the past three decades (Westerling *et al.* 2006). Global circulation models (GCMs) predict that these conditions will continue as greenhouse gases continue to accumulate in the atmosphere (Lauenroth *et al.* 2004; Seager *et al.* 2007). I am interested in understanding the extent to which natural variability and fire suppression practices affect the source-sink strength of greenhouse gases, and how important the two-way interaction between fire and climate may be (Randerson *et al.* 2006).

Ecosystem modeling is particularly valuable for evaluating the sensitivity of ecosystem structure and functions to natural variability and management (such as fire suppression), especially for dynamic and highly variable processes that are difficult to estimate in the field, such as trace gas fluxes. Simulation models allow one to extrapolate across spatial variability and through time, and to evaluate historical situations that no longer occur. My objectives in this chapter are to examine the Daycent model's ability to simulate (Parton *et al.* 1998; Del Grosso *et al.* 2000; Parton *et al.* 2001) a ponderosa pine forest, and then:

1. Evaluate the short-term impact of fire on trace gas fluxes and N biogeochemistry from burned landscapes.
2. Examine trace gas fluxes and N biogeochemistry in response to hypothetical fire regimes among locations and pre-/post- fire suppression.

Model description

The Daycent model (Parton *et al.* 1998) is the daily time step version of the Century model (Parton *et al.* 1987; Parton *et al.* 1988). Both models simulate the flow of carbon (C), nitrogen (N), phosphorus (P), and sulfur (S), as they cycle with production and decomposition of organic matter (plant and soil) through a simulated ecosystem. The

Daycent 4.5 model includes daily representations of soil moisture, temperature, and N availability. Required model inputs include daily precipitation (cm) and maximum/minimum daily temperatures (°C), soil depth (divided into as many as 10 layers), and soil characteristics (texture and bulk density). This high temporal resolution of these submodels allows for daily output of trace gas fluxes (nitrous oxide, nitric oxide, and methane), which are greatly variable and dependent upon rapid changes in the soil environment driven by weather variability as well as biotic processes.

The Daycent submodels include plant production, decomposition, methane oxidation, nitrification, and denitrification. The plant production subroutines simulate production, nutrient allocation, and death. These processes are regulated by soil water content, temperature and nutrient availability. Dead and decomposing material enters the soil organic matter (SOM) pools (active, slow, and passive) that are also regulated by the factors that affect production.

The N-gas submodel (Parton *et al.* 2001) utilizes the "hole-in-the-pipe" model (Davidson and Verchot 2000) to represent denitrification (NH_4^+ to NO_3^-) and nitrification (NO_3^- to N_2) processes. N_2O and NO are intermediate molecules for both processes, and each is lost during metabolism to the environment. The rate of these gas losses is dependent upon environmental factors that the N-gas submodel accounts for, including soil water status, temperature, NH_4^+ and NO_3^- availability, and respiration rates to drive calculations of daily N_2O and NO_x emission rates. The denitrification and nitrification submodels are driven by soil water status, temperature, pH, NH_4^+ and NO_3^- availability, labile C availability, O_2, soil diffusivity, and respiration rates. No denitrification occurs within the model if the % water-filled-pore-space (% WFPS) falls below 55%.

Denitrification rates increase exponentially between 55 and 90% WFPS. Nitrification rates are constrained by the size of the soil NH_4^+ pool, soil temperature, % WFPS, and pH. Nitrous oxide production is considered to be a constant proportion of the nitrification rate (g N m^{-2} d^{-1}). NO_x production is proportional to N_2O production, but also regulated by soil gas diffusivity and % WFPS.

Upland soils are generally found to be sinks for atmospheric CH_4 (Conrad 1995). Del Grosso *et al.* (2000) created a submodel within Daycent to simulate this biological process based upon field data collected in a variety of ecosystems, including grasslands, agricultural land, and forests. Methane oxidation is calculated within the submodel based upon soil water status (field capacity), soil texture, and soil bulk density. Each of these factors influence soil gas diffusivity, however, as this becomes less limiting the importance of soil temperature increases.

Study sites

Fire history and climate data

I selected four sites to evaluate response to fire events and fire exclusion practices, both of which are common in the region (Keane *et al.* 2002): Boulder, Allenspark, Cheesman and Fort Collins, with the intention of capturing a large range of variability in the Front Range of Colorado and maximize the realm of inference. Each site had complete weather records, fire history documentation in the scientific literature, and field observations of trace gas flux rates.

Weather data were readily available and complete for each location (Center 2008). At three sites, the daily weather records exceeded 100 years with the fourth site

(Allenspark) having 58 years of record (Table 1). The long period of observation provided a wide spectrum of variability in weather and climate. The climate of the northern Front Range is dry, with lowest precipitation in winter. Precipitation is unimodal (Fort Collins and Boulder) to weakly bimodal (Allenspark and Cheesman) with peaks in the late spring (April and May) and/or summer (July and August) (Figure 1). Even during these times of increased moisture vegetation can remain stressed due to the greater temperatures that occur concurrently. Mean annual temperature ranged between 4.7 and 11.0 °C at the four sites (Table 1) while mean annual precipitation ranged from 384 – 520 mm (Table 1).

At each of these four sites I found estimates for fire return intervals (Table 2). Brown *et al.* (1999) found that composite fire return intervals generally ranged between 6 and 12 years for Cheesman, though there were long periods (1723 2000, fires in 1723 and 1851) where fires were much less frequent. Two of my sites, Boulder and Allenspark, are found in Boulder County, Colorado where Veblen *et al.* (2000) conducted an extensive fire history study. Boulder had an average fire return interval of 14 years with exact fire scar dates back to 1679. Sites near to Allenspark had an average fire return interval of 40 years based on fire scar chronologies dating back to 1541. I constrained the number of fires at these sites by selecting only the fire years during which at least 10% of the examined trees had recorded a fire scar. In order to make a good estimate of fire return interval for the Fort Collins site, I interpolated the fire return interval from an equation developed by Brown and Shepperd (2001) in the region that relates fire return interval with latitude. I then pooled that with information from Rocky Mountain National Park (Sherriff and Veblen 2006). These patterns of fire return interval are dictated in large part by the climate of the region and the individual sites that vary both in latitude and altitude.

Study sites - vegetation and soils

A dynamic ecotone is formed as the grasslands of the Great Plains merge into the forests of the foothills of the Colorado Front Range. I focused on two forest types within this ecotone, lower elevation ponderosa pine stands (tend to be open with substantial grass, 1800 – 2100 m) and mid-elevation ponderosa pine (some canopy closure, mixed with Douglas fir, 2100 – 2400 meters) (Peet 1978; Peet 1981; Mast *et al.* 1998; Mast and Veblen 1999).

I used site-specific soil data from the online NRCS Soil Survey. The Northern Front Range and Larimer County, Colorado are dominated by with a sandy loam texture. A typical soil profile is 0.90 m thick with bedrock at 1 m depth. Soils of Boulder County, Colorado are gravelly loamy sand with soil depths of approximately 1.5 m. At Allenspark, soils profiles are 1.5 m deep with cobbly and stony sandy loam soil texture. Soils that surround the Cheesman Reservoir are shallow with weathered bedbrock at 0.75 m depth and the soil texture is gravelly throughout the profile. Using the soil texture triangle I converted texture descriptions from the NRCS Soil Survey to % sand, silt, and clay (Table 3).

Model parameterization

Daycent requires input for daily weather (precipitation and temperature) and soils (texture and number of layers). These data are fundamental to the land surface submodel that simulates soil water content and soil temperature for each soil layer. I used Daycent to estimate wilting point, field capacity, and hydraulic conductivity (K_s) based on soil texture data for the sites.

I parameterized the model (CROP.100 and TREE.100 plant production subroutines) to simulate grass and tree production, nutrient allocation, and death in a temperate forest ecosystem (Keogh, personal communication). Plant death is regulated by temperature and soil water content. Dead and decomposing material enters the soil organic matter (SOM) pools. I used fire return intervals (FRI) from the scientific literature (Table 2) as the basis for my scheduling of fire events at each site. FRI and fire severity (and intensity) vary inversely (Shinneman and Baker 1997). I expressed this relationship in the model by allowing more severe fires when the time since the last fire was great relative to the mean fire return interval. Conversely, I modeled a low severity fire when the most recent fire was less than the mean fire return interval for that site. In the model, at the time of each fire event, biomass pools are multiplied by the specified coefficient and that portion is removed from the simulation.

Simulation procedure

Model simulations were initiated with the site-specific soil and weather data described above. I ran a total of four separate simulations, or one per site. I initialized the Daycent model as a forest ecosystem with a grass component, and simulated plant production with two subroutines: one for the grass understory (CROP.100), and a second for the tree component (TREE.100). I used literature values for other ponderosa pine forests as estimates for initial conditions (pool sizes) for biomass and soil carbon, and ran simulations for each site, for 2000 simulation years. Between year 1 and 1500, I scheduled regular fires to reflect the fire return intervals at each site (Table 2). The length of these simulation runs have been found to bring other modeled ecosystems into equilibrium (Li *et al.* 2006). I examined total soil organic matter pools at each site to verify steady state that I define as having less than a 5% change in total soil organic matter from year to year. Each of the four simulated sites met this criterion.

At the time of each fire, Daycent ran two subroutines, TREM.100 (Table 4) and FIRE.100 (Table 5). The TREM routine removed biomass from trees (and constituent pools) for either a low or high severity fire. The FIRE routine worked in a similar fashion except that rather than removing biomass from tree pools, it removed the grass and litter components at rates that correlated to the fire severity. At year 1500, I began to analyze the simulated fluxes (g m^{-2} yr^{-1}) of CH_4, N_2O, and NO as well as gross nitrification rates (g N m^{-2} yr^{-1}) with the intent of observing how they respond to simulated fire events and more recent (circa 1920) fire suppression practices common to the region (Keane *et al.* 2002).

Comparison of model output and statistical analyses

I used two methods to verify the model output and its ability to simulate biogeochemical processes in these forests. First, I compared the model output of plant production (NPP) and total ecosystem and soil carbon with values in the scientific literature for ponderosa pine ecosystems (Law *et al.* 2001; Irvine and Law 2002; Hicke *et al.* 2004; Law *et al.* 2004; Hall and Burke 2006; Hall *et al.* 2006). Law *et al.* (2004) estimated total carbon stocks to be 10 to 21 kg m^{-2} in Oregon where simulations of my sites yield estimates between 4 and 12 kg C m^{-2}. Mean NPP for the four simulated sites ranged between 56 - 200 g C m^{-2} yr^{-1}. This falls in the range (76 – 236 g C m^{-2} yr^{-1}) of NPP estimates by Law *et al.* (2001) in ponderosa pine forests of Oregon and carbon accumulation (90 – 281 g C m^{-2} yr^{-1}) estimated by Hicke *et al.* (2004) in ponderosa pine forests of the Colorado Front Range.

In addition, I compared short-term, infrequent, trace gas flux measurements at locations near to each of these sites (Chapters 2 and 3, this volume) to modeled output. I calculate the mean, minimum, maximum, and coefficient of variation (%) for simulated methane oxidation, N_2O and NO production, gross nitrification (g m^{-2} yr^{-1}), and annual precipitation (cm) for each site. I isolated the years that fires were simulated at each site, and collected the data for that year and the year before and after. From these data, I calculated means and the standard error of the mean for the variables mentioned above (Figure 2) in order to determine the short-term influence of fire. Following the same procedure, I grouped model output into two categories; pre-fire suppression (1500 – 1920, with hypothetical fire return intervals) and post-fire suppression (1920 – 2000, no fires). I evaluated the potential influence of large-scale management by comparing means (± SE) within and among sites.

Results and Discussion

Simulated and observed biogeochemistry of Front Range forests

Daycent simulated CH_4 uptake rates as consistent across all four sites. Of the four sites I modeled, means ranged between 0.377 and 0.448 g CH_4 m^{-2} yr^{-1}, while all had CV (%) for CH_4 uptake of < 15% (Table 5). This correspondence among modeled sites reflects the similarity in the climate and soil texture (sandy loams). The CH_4 oxidation submodel is largely controlled by soil water content, which interacts with soil texture to control gaseous diffusion through the soil profile. Del Grosso *et al.* (2000) calculated that maximum CH_4 uptake (~0.438 g CH_4 m^{-2} yr^{-1}) occurs at 7.5% soil volumetric water for coarse textured soils such as I used in these simulations. Field observations in the region (Chapters 2 and 3, this volume) were made at soil moisture levels between 2 and 18 % and associated flux rates agreed well with those predicted by the beta function used in the CH_4 oxidation submodel.

My simulation output suggests that Daycent captured this dependence of CH_4 uptake on soil moisture levels; Fort Collins, with intermediate levels of precipitation (Table 5) had the greatest CH_4 oxidation. In contrast Cheesman (driest site), and Allenspark (wetter site) were (on an annual basis) below and above, respectively, the optimum soil moisture levels for CH_4 oxidation and thus showed lower rates. In his study of coniferous forest soils in Arizona, Hart (2006) measured mean methane uptake rates between 0.229 and 0.479 mg C m^{-2} h^{-1} that were significantly correlated with soil temperature, not soil water content. While at a slightly lower elevation, the simulated sites in Colorado received approximately half the precipitation that occurred at Hart's study sites. Elsewhere in the Front Range, methane uptake rates were measured in urban/agriculture/native (Kaye *et al.* 2004), alpine (Sommerfeld *et al.* 1993) and shortgrass steppe (Mosier *et al.* 1996; Mosier *et al.* 1997; Epstein *et al.* 1998) ecosystems. My simulated rates of methane oxidation, ~0.4 g m^{-2} y^{-1} (Table 6), are intermediate to the rates measured at these sites. Smith *et al.* (2000) reviewed the scientific literature and calculated that the mean methane uptake rate of 0.24 g m^{-2} y^{-1} from "natural/semi-natural", or non-agricultural soils around the globe.

Nitrous oxide flux rates were also similar among all four modeled sites. However, each exhibited greater variability than CH_4 uptake as coefficients of variation

(CVs) were > 49% within all sites. Means (g N m^{-2} yr^{-1}) of Daycent simulations for N_2O in decreasing order are Allenspark (0.029) > Cheesman (0.014) > Fort Collins (0.011) = Boulder (0.011). These model estimates are similar to the observations of Kaye *et al.* (2004) for native grassland and cropped wheat systems in northern Colorado where both had mean N_2O fluxes less than 0.05 g N m^{-2} yr^{-1}. In contrast, they found fluxes to be an order of magnitude greater from urban and agricultural ecosystems that had received N fertilizer. In the southwestern U.S., others observed N_2O flux rates of approximately 0.05 g m^{-2} yr^{-1} (Hart 2006), 0.01 g m^{-2} yr^{-1} (Matson *et al.* 1992), and between 0.05 and 0.20 g m^{-2} yr^{-1} (McLain and Martens 2006).

Nitric oxide fluxes were an order of magnitude greater than the N_2O fluxes from all but the Allenspark location. I found the following pattern of decreasing NO fluxes (g m^{-2} yr^{-1}): Allenspark (0.198 > Fort Collins (0.152) > Boulder (0.129) = Cheesman (0.129). Coefficients of variation (CV, %) for NO fluxes followed a similar pattern and fell within the same range (43.6 – 85.9 %) as I observed for the N_2O flux rates. The simulated NO flux estimates fall within the range of field measurements from the western U.S. (Levine *et al.* 1988; Stark *et al.* 2002). In an Oregon ponderosa pine forest Stark *et al.* (2002) report NO fluxes of 0.009 g N m^{-2} yr^{-1} whereas Levine *et al.* (1988) reported a flux rate of 0.63 g N m^{-2} yr^{-1} in California chaparral.

Nitrification rates, or the rate of conversion from NH_4^+ to NO_3^-, were greatest for the Allenspark simulation (Table 5). Means of gross nitrification rates ranged between 0.558 and 0.861 g m^{-2} yr^{-1}. The maximum rate of nitrification across all sites and years was Cheesman with a value of 3.866. Minimum values of nitrification were generally ¼ of the mean; whereas maxima were 4 – 5 times the site mean (Table 2). Patterns of variability were identical (in rank order) to that which was observed for NO fluxes (Table 5). Gross nitrification rates measured in ponderosa pine forests of Oregon and New Mexico (Stark and Hart 1997; Stark *et al.* 2002) were an order of magnitude greater than those calculated from my Daycent simulations.

Effects of fire on trace gas fluxes

Year before, of and after fire

Simulated methane uptake was minimally affected by fire. All four of the sites I modeled exhibited a slightly increasing trend over the three-year periods that included the year prior to, the year of and the year after a fire (Figure 2). Allenspark departed most from pre-fire years, when methane uptake increased by a mean of 0.05 g CH_4 m^{-2} during the year of a fire. At one-year post-fire, the mean CH_4 uptake had decreased though still being slightly greater than the mean for one year pre-fire. Allenspark also exhibited the greatest variability of the four sites I modeled. This is best explained by the longer fire return interval (40 years), greater fire severity (high), and climate variability. In contrast, each of the other three sites showed much less variability, suggesting that fire only has a minor affect on CH_4 oxidation. None of the factors that control the rate CH_4 oxidation in the Daycent submodel such as field capacity, soil texture and bulk density are directly impacted by my modeled fire events. If I extrapolate my estimate to incorporate my knowledge of a fire's burn area I may use these data to estimate the change in sink strength as a result of a single fire event. In 2002, the Hayman fire burned ~55,000 ha. Using these data, I estimate that the net reduction in sink strength between one year before and one-year after the fire would be approximately 55,000 kg CH_4.

Each of these simulated sites exhibited a large increase in gross nitrification during a fire year relative to the year prior. Simulated N availability following fires was increased at two of my sites, Fort Collins and Allenspark (Figure 2).This increase persisted into the year after the fire for Allenspark only, while Fort Collins returned to pre-fire levels within a year. Gross nitrification rates were relatively unaffected by fire at both Boulder and Cheesman (Figure 2). I attribute this primarily to the lower severity fires (less N lost, Table 4 & 5) that were simulated at these sites as compared to Allenspark and Fort Collins, which generally had longer fire return intervals and consequentially greater fire severity (greater N lost).

Generally, greater fire severity leads to an increase in gaseous loss of N from the forest during the fire. However, this effect of reduced substrate availability decreased as competition for nutrients with plants was also greatly reduced as the high severity fires at Allenspark and Fort Collins removed a large portion of the live vegetation. The model compares well with field data; Hamman *et al.* (2006; 2007) found that fire severity and altered fire regime can directly influence the soil microbial community structure and biogeochemistry in ponderosa pine forests of the Colorado Front Range. Carreira *et al.* (1994) investigated the effect of a single fire and found that it significantly increased N availability and net nitrification rates. Similar findings have been documented in southwestern U.S. ponderosa pine (Covington and Sackett 1986; Covington and Sackett 1992) and a variety of other ecosystems (Wan *et al.* 2001).

I observed three patterns for means of gross nitrification (Figure 2): no change (Boulder), response and return (Cheesman and Fort Collins) and persistent change (Allenspark) over the three-year time period for each fire event. Nitrogenous gas (N_2O

and NO) fluxes are the result of incomplete oxidation during nitrification or reduction during denitrification. Of the four modeled sites, none had average rainfall greater than 530 mm yr^{-1}. The N-gas submodel is driven by soil moisture and no denitrification occurs when %WFPS < 55% (Parton *et al.* 2001). This was supported by model observation of very low to absent N_2 flux, the end product of denitrification (Parton *et al.* 2001).

Nitrous and nitric oxide fluxes (Figure 2) followed a nearly identical pattern to simulated gross nitrification rates. Both are by-products of nitrification, and together, they accounted for up to 25% of the gross nitrification N. In a related study (Chapter 2, this volume) I measured N_2O fluxes along a chronosequence of fires in the Colorado Front Range, and calculated a mean flux of 0.002 g N m^{-2} yr^{-1}. Other sites in the Front Range were found to have N_2O flux rates between 0.164 g N m^{-2} yr^{-1} (Chapter 3, this volume). Averaging across all four sites, Daycent calculated annual N_2O fluxes of 0.016 g N m^{-2} yr^{-1}, which is an order of magnitude above and below these field measurements. These field based studies were limited in their spatial and temporal coverage, whereas Daycent appears to have integrated variability observed in those studies producing an intermediate estimate of N_2O fluxes from these systems.

Pre- versus post-fire suppression

Fire suppression practices did not alter methane uptake rates in the Daycent simulations (Figure 3). Within site variability was low for these two time periods. I calculated percent difference for pre- and post-fire suppression to be less than 1.2 % at all 4 sites. Where methane uptake showed a short term increase immediately following a fire, the response appears to be insignificant when considering longer time scales such as a single (hypothetical) fire return interval. While I saw a minor decrease in CH_4 uptake, I had expected greater differences to become apparent as fire suppression allowed tree biomass (or tree densities) to increase and consequently nutrient competition. My simulation data suggest then that either methanotrophic bacteria are not in direct competition with plants for nutrients, or that the model fails to capture this interaction.

Nitrous oxide fluxes were greatest at Allenspark, which had nearly 3-fold the rates observed at Cheesman, Boulder, and Fort Collins. Based on the model, this outcome is the result of differences in precipitation and soil properties between Allenspark and the other three simulated sites. Daycent first partitions N_2O fluxes from nitrification and denitrification processes and then sums these values into the single value reported as the N_2O flux. At Allenspark, precipitation events stimulated pulses of N_2O flux denitrification, whereas similar events at the other three sites were only great enough to stimulate N_2O flux from nitrification. Changes in N_2O fluxes in response to fire suppression (Figure 3) were greatest at Fort Collins (-36.7%), Cheesman (-25.2%), Boulder (-14.5%), and Allenspark (10.3%). N_2O flux rates at these four sites accounted for < 1% of gross nitrification. Nitric oxide flux rates (Figure 3) followed the same pattern though the fluxes were an order of magnitude greater than N_2O fluxes. Fire suppression reduced NO fluxes by 39.7% at Fort Collins, 28.6% at Cheesman, 19.0% at Boulder, and 15% at Allenspark. Since the climate wasn't different during the fire suppression period relative to before, the changes in N_2O and NO flux reflect a change in substrate availability as continued plant uptake during this the fire suppression period led to N immobilization.

I found Allenspark to have the greatest rate of nitrification both before and after fire suppression that I simulated to begin in 1920. Fire suppression decreased gross nitrification rates there by 13.5% that was the least compared to the other three sites that also experienced decreases: Boulder (-15.2%), Cheesman (-25.3%) and Fort Collins (-37.1%). Stark and Hart (1997) measured gross nitrification rates of 25 to 79 mg N m^{-2} d^{-1} (9.1 g N m^{-2} yr^{-1} to 28.8 g N m^{-2} yr^{-1}) in New Mexican and Oregon ponderosa pine, respectively. Stark and Hart (1997) suggest that C and N supplies and microbial activity control gross nitrification rates. They suggest that internal cycling of NO_3^- is strongly controlled by microbial uptake that can be rapid relative to plant uptake in forested ecosystems. My Daycent simulations seem to capture this short-term dynamic as gross nitrification rates increase during the year of the fire (Figure 2). Over longer time scales, my Daycent simulations predict that fire suppression has led to a decrease in gross nitrification rates relative to pre-1920 rates (Figure 3).

The Daycent simulations indicate that fire is important for maintaining N availability in ponderosa pine ecosystems. Covington and Sackett (1986; 1992) found fire to increase NH_4^+-N immediately in ponderosa pine forests of varying ages in Arizona. Within a year that NH_4^+ pulse had dissipated through nitrification processes leading to a pulse in NO_3^-- N that was detected one year after fire. In a review of N response to fire (Wan *et al.* 2001) documented a similar pattern across multiple ecosystems for NH_4^+ and NO_3^-. Long-term decreases in gross nitrification observed in Daycent may be indicative of leaching losses of NO_3^- from these forested ecosystems that may have consequences for production in the future.

Conclusions

Daycent simulations indicate that CH_4 uptake in ponderosa pine forests of the Colorado Front Range is unaffected by wildfire over the short-term, or by fire suppression over the long-term. Field observations made in the same region show support for this conclusion as it relates to changes that occur over the short-term following a fire (Chapter 2). It remains unclear as to what effect(s) climate change and changes in fire management practices will have on these forests that have had fire actively excluded for nearly a century. Specifically, it is interesting to consider how the microbial community responsible for methane uptake might respond to such changes (Schimel and Gulledge 1998).

Nitrogen gas fluxes were tightly coupled with rates of gross nitrification at both short and long time scales. My Daycent simulations estimated mean N_2O fluxes that fell within the range of field-based observations in the Colorado Front Range. Gross nitrification rates were lower during the simulated fire suppression period, which concurs with other studies that suggest wildfire maintains N cycling and availability. These data also suggest that management of these systems back to their natural fire regime may lead to increased rates of N cycling and in turn N-gas fluxes to the atmosphere. However, such changes appear to be temporary as N-gas fluxes return to average values within a year after a fire.

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Table captions

Table 1. Weather stations with daily weather data to be used in the Daycent model. (National Climatic Data Center, http://www.ncdc.noaa.gov/oa/ncdc.html).)

Table 2. Time period(s) modeled using Daycent, including fire return intervals (years) or fire dates (year A.D.) for a particular time period at a specific site. Fire record data for each of these sites were retrieved from the literature source cited. These data were coded into the Daycent schedule file (*.sch) to reflect the same event chronology as that site had experienced in the past.

Table 3. A description of the site specific soil parameters used for each of the four simulated locations. Data shown include the number and thickness of soil layers, bulk density, and soil texture.

Table 4. A description of Daycent input paramaters for tree removal (TREM.100) events for two fire severity scenarios: surface (low severity) or canopy (high severity) fire.

Table 5. A description of Daycent input paramaters for fire events (FIRE.100) events for either a low fire severity or high severity fire scenario. This subroutine removed mass from litter and grass pools.

Table 6. Mean, minimum, maximum and coefficient of variation (%) for CH_4 uptake, N_2O and NO fluxes, nitrification rates and annual precipitation (cm). Mean, maximum and minimum values for fluxes and nitrification are given as g m^{-2} yr^{-1}. These descriptive data are derived from the years 1500 – 2000.

Table 1

Location	Station name	Years of record	Data years	Latitude (°N)	Longitude (°W)	Elevation (meters)	MAP (cm)	MAT (°C)
Boulder	Boulder	1898-2006	108	40:00	-105:16	1671	48.6	11.0
Cheesman	Cheesman Reservoir	1903-2006	103	39:13	-105:17	2097	41.2	7.2
Allenspark	Allenspark	1948-1993 1994-2006	45 13	40:12	-105:32	2606	52.8	4.7
Fort Collins	Fort Collins	1900-2006	106	40:37	-105:08	1525	38.4	8.9

Table 2

Location	Modeled period	Fire return interval (years) or fire date (year	Source
Cheesman	1 - 1285	9	Brown *et al.*(1999)
	1286 - 1500	12	
	1501-1600	6	
	1601-1715	10	
	1715 - 2000	1723, 1851 (no fires after this)	
Boulder	1 - 1650	14	Veblen *et al.* (2000)
	1651 - 1920	1679,1691,1703,1708,1713,1716, 1722, 1725, 1732, 1737, 1747, 1786, 1789,1795, 1813, 1841, 1847, 1851, 1860, 1868, 1870, 1880, 1884, 1886, 1908, 1910	Sites 15 (1853-1914 m, > 10% of trees scarred)
	1921 – 2000	Fire suppression	
Allenspark	1 - 1500	40	Veblen *et al.* (2000)
	1501 - 1920	1541, 1602, 1654, 1745, 1768, 1814, 1859, 1880	Sites 18,19 (2414-2682 m, > 10% of trees scarred)
	1921 – 2000	Fire suppression	
Fort Collins	1 -1920	30	Sherrif and Veblen (2006)
	1921 - 2000	Fire suppression	Brown and Shepperd (2001)

Table 3.

Layer thickness (cm)	Bulk density (mg cm^3)				Sand and clay (%)			
	Allenspark	Boulder	Cheesman	Fort Collins	Allenspark	Boulder	Cheesman	Fort Collins
0 to 2	1.5	1.33	1.33	1.25	0.80, 0.13	0.74, 0.11	0.71, 0.21	0.70, 0.20
2 to 5	1.5	1.33	1.5	1.25	0.80, 0.13	0.74, 0.11	0.75, 0.15	0.70, 0.20
5 to 10	1.5	1.33	1.5	1.35	0.80, 0.13	0.74, 0.11	0.75, 0.15	0.70, 0.20
10 to 20	1.5	1.33	1.5	1.35	0.80, 0.13	0.74, 0.11	0.75, 0.15	0.70, 0.20
20 to 30	1.5	1.33	1.6	1.5	0.80, 0.13	0.74, 0.11	0.80, 0.10	0.70, 0.20
30 to 45	1.5	1.33	1.6	1.5	0.80, 0.13	0.74, 0.11	0.80, 0.10	0.75, 0.15
45 to 60	1.5	1.33	1.6	1.7	0.80, 0.13	0.74, 0.11	0.80, 0.10	0.75, 0.15
60 to 75	1.5	1.33		1.7	0.80, 0.13	0.74, 0.11		0.75, 0.15
75 to 90	1.5	1.33		1.7	0.80, 0.13	0.74, 0.11		0.75, 0.15
90 to 105	1.5	1.33			0.80, 0.13	0.74, 0.11		
105 to 120	1.5	1.33			0.80, 0.13	0.74, 0.11		
120 to 150	1.5	1.33			0.80, 0.13	0.74, 0.11		

Table 4.

Surface fire	Canopy fire	Parameter	Definition
1	1	EVNTYP	event type flag (=0 for cutting event, =1 for fire event)
0.5	0.99	REMF(1)	fraction of leaf component removed
0.5	0.90	REMF(2)	fraction of live branch component removed
0.2	0.90	REMF(3)	fraction of large wood live component removed
0.8	0.99	REMF(4)	fraction of fine branch dead component removed
0.4	0.99	REMF(5)	fraction of large wood dead component removed
0.3	0.99	FD(1)	fraction of fine root component that dies
0.1	0.99	FD(2)	fraction of coarse root component that dies
0.5	0	RETF(1,1)	fraction of C in killed live leaves that is returned to the system (ash or litter)
0.5	0.3	RETF(1,2)	fraction of N in killed live leaves that is returned to the system (ash or litter)
1	1	RETF(1,3)	fraction of P in killed live leaves that is returned to the system (ash or litter)
0	0	RETF(1,4)	fraction of S in killed live leaves that is returned to the system (ash or litter)
0.5	0	RETF(2,1)	fraction of C in killed fine branches that is returned to the system (ash or dead fine branches)
0.5	0.3	RETF(2,2)	fraction of N in killed fine branches that is returned to the system (ash or dead fine branches)
1	1	RETF(2,3)	fraction of P in killed fine branches that is returned to the system (ash or dead fine branches)
0	0	RETF(2,4)	fraction of S in killed fine branches that is returned to the system (ash or dead fine branches)
0.3	0	RETF(3,1)	fraction of C in killed large wood that is returned to the system (ash or dead large wood)
0.3	0.3	RETF(3,2)	fraction of N in killed large wood that is returned to the system (ash or dead large wood)
1	1	RETF(3,3)	fraction of P in killed large wood that is returned to the system (ash or dead large wood)
0	0	RETF(3,4)	fraction of S in killed large wood that is returned to the system (ash or dead large wood)

Table 5

Fire severity			
Low	**High**	**Parameter**	**Definition**
0.6	0.8	FLFREM	fraction of live shoots removed by a fire event
0.6	0.8	FDFREM(1)	fraction of standing dead plant material removed by a fire event
0.2	0.9	FDFREM(2)	fraction of surface litter removed by a fire event
0.6	0.9	FDFREM(3)	fraction of dead fine branches removed by a fire event
0.4	0.9	FDFREM(4)	fraction of dead large wood removed by a fire event
0.1	0.01	FRET(1,1)	fraction of C in the burned aboveground material (live shoots, standing dead, and litter) returned to the system following a fire event
0.4	0.4	FRET(1,2)	fraction of N in the burned aboveground material (live shoots, standing dead, and litter) returned to the system following a fire event
1	0.4	FRET(1,3)	fraction of P in the burned aboveground material (live shoots, standing dead, and litter) returned to the system following a fire event
1	0.4	FRET(1,4)	fraction of S in the burned aboveground material (live shoots, standing dead, and litter) returned to the system following a fire event
0.003	0.003	FRET(2,1)	fraction of C in the burned dead fine branch material returned to the system following a fire event
0.2	0.2	FRET(2,2)	fraction of N in the burned dead fine branch material returned to the system following a fire event
0	0.4	FRET(2,3)	fraction of P in the burned dead fine branch material returned to the system following a fire event
0	0.4	FRET(2,4)	fraction of S in the burned dead fine branch material returned to the system following a fire event
0.003	0.003	FRET(3,1)	fraction of C in the burned dead dead large wood material returned to the system

			following a fire event
0.2	0.2	FRET(3,2)	fraction of N in the burned dead dead large wood material returned to the system following a fire event
0	0.4	FRET(3,3)	fraction of P in the burned dead dead large wood material returned to the system following a fire event
0	0.4	FRET(3,4)	fraction of S in the burned dead dead large wood material returned to the system following a fire event
0.2	0.2	FRTSH	additive effect of burning on root/shoot ratio
10	10	FNUE(1)	effect of fire on increase in maximum C/N ratio of shoots
30	30	FNUE(2)	effect of fire on increase in maximum C/N ratio of roots

Table 6

Variable	Site	Mean	Minimum	Maximum	CV (%)
CH_4 uptake	Fort Colllins	0.448	0.378	0.501	4.2
	Allenspark	0.377	0.248	0.511	14.8
	Boulder	0.427	0.356	0.468	5.2
	Cheesman	0.398	0.331	0.432	5.2
N_2O flux	Fort Colllins	0.011	0.002	0.048	49.3
	Allenspark	0.029	0.004	0.099	52.4
	Boulder	0.011	0.003	0.066	82.7
	Cheesman	0.014	0.004	0.077	78.6
NO flux	Fort Colllins	0.152	0.030	0.674	52.1
	Allenspark	0.198	0.058	0.694	43.8
	Boulder	0.129	0.033	0.676	85.9
	Cheesman	0.129	0.036	0.637	80.0
Nitrification	Fort Colllins	0.558	0.106	2.422	49.2
	Allenspark	0.861	0.205	2.348	37.5
	Boulder	0.564	0.148	3.304	83.1
	Cheesman	0.678	0.188	3.866	78.2
Precipitation	Fort Colllins	38.9	19.4	72.6	27.2
	Allenspark	49.1	23.2	87.3	32.5
	Boulder	47.1	22.0	75.5	23.7
	Cheesman	35.4	33.8	49.1	20.0

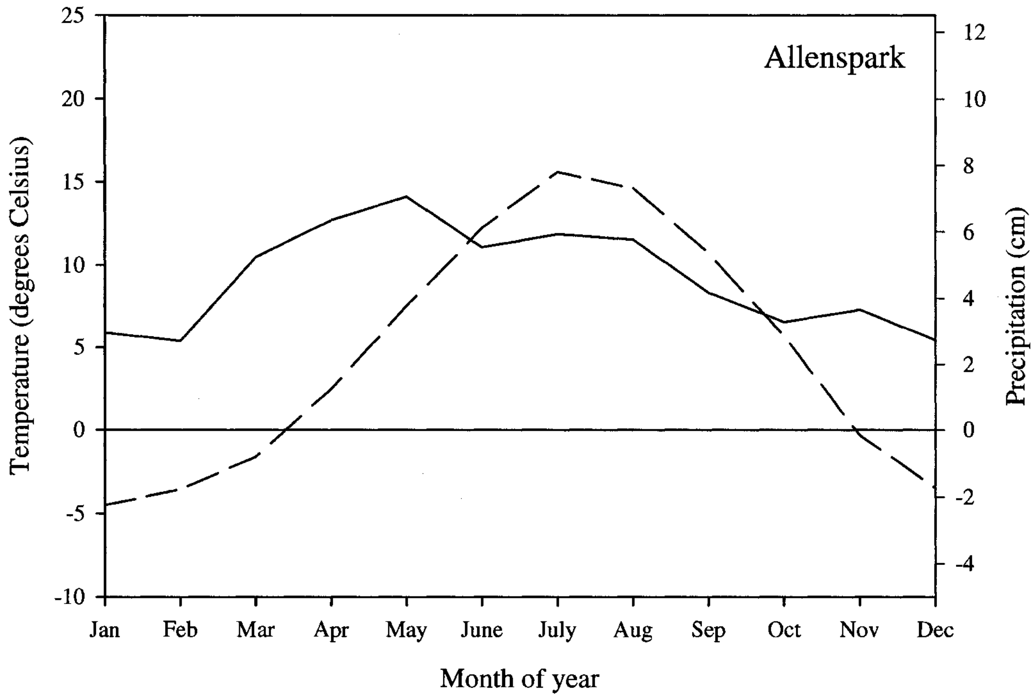
Figure captions

Figure 1. Monthly precipitation (cm, solid line) and mean temperatures (°C, dashed line) for Fort Collins, Boulder, Allenspark, and Cheesman weather stations.

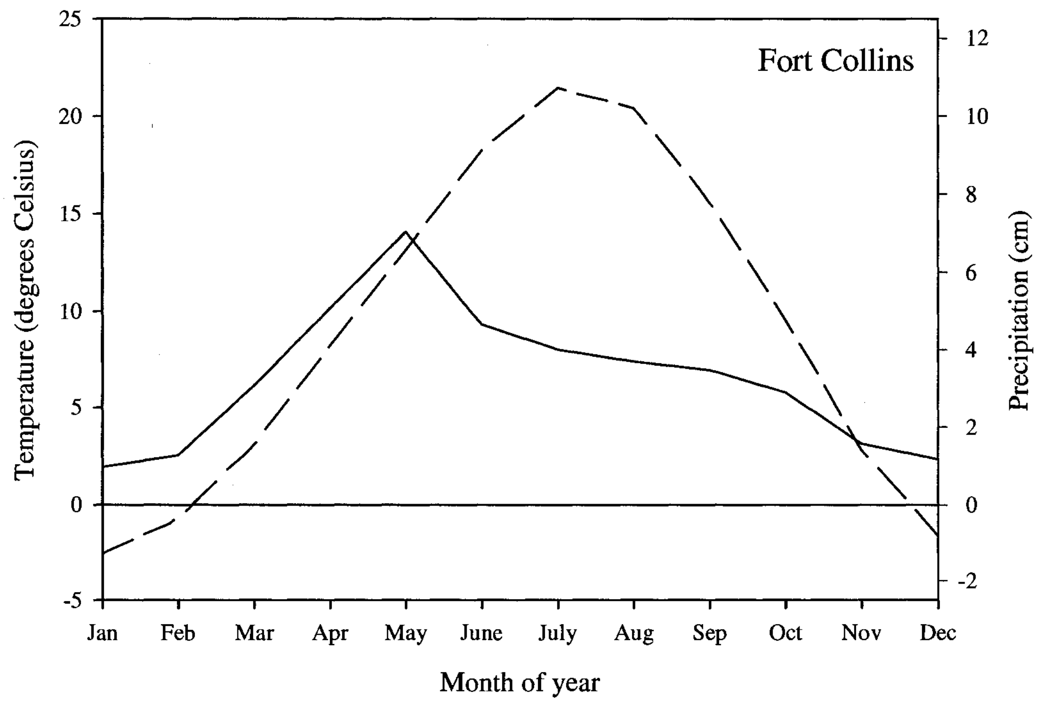
Figure 2. a) Methane uptake rates (g CH_4 m^{-2} yr^{-1}), b) gross nitrification (g N m^{-2} yr^{-1}), c) nitrous oxide fluxes (g N_2O m^{-2} yr^{-1}), and nitric oxide fluxes (g NO m^{-2} yr^{-1}), for each of the four simulated locations. Points represent the means of methane uptake one year prior to, during the year of, and one year after a fire occurred for each site. Error bars are the standard error of the mean.

Figure 3. Means and standard error of a) methane uptake rates (g CH_4 m^{-2} yr^{-1}), b) gross nitrification (g N m^{-2} yr^{-1}), c) nitrous oxide fluxes (g N_2O m^{-2} yr^{-1}), and nitric oxide fluxes (g NO m^{-2} yr^{-1}), for each of the four simulated locations. Gray bars depict the respective values for the fire suppression period (after 1920) whereas the black bars represent the pre-1920 (no fire suppression) period.

Figure 1



Allenspark
Temperature (degrees Celsius)
Precipitation (cm)
25
20
15
10
5
0
-5
-10
12
10
8
6
4
2
0
-2
-4
Jan
Feb
Mar
Apr
May
June
July
Aug
Sep
Oct
Nov
Dec
Month of year



Fort Collins
Temperature (degrees Celsius)
Precipitation (cm)
25
20
15
10
5
0
-5
12
10
8
6
4
2
0
-2
Jan
Feb
Mar
Apr
May
June
July
Aug
Sep
Oct
Nov
Dec
Month of year

Figure 1 (continued)

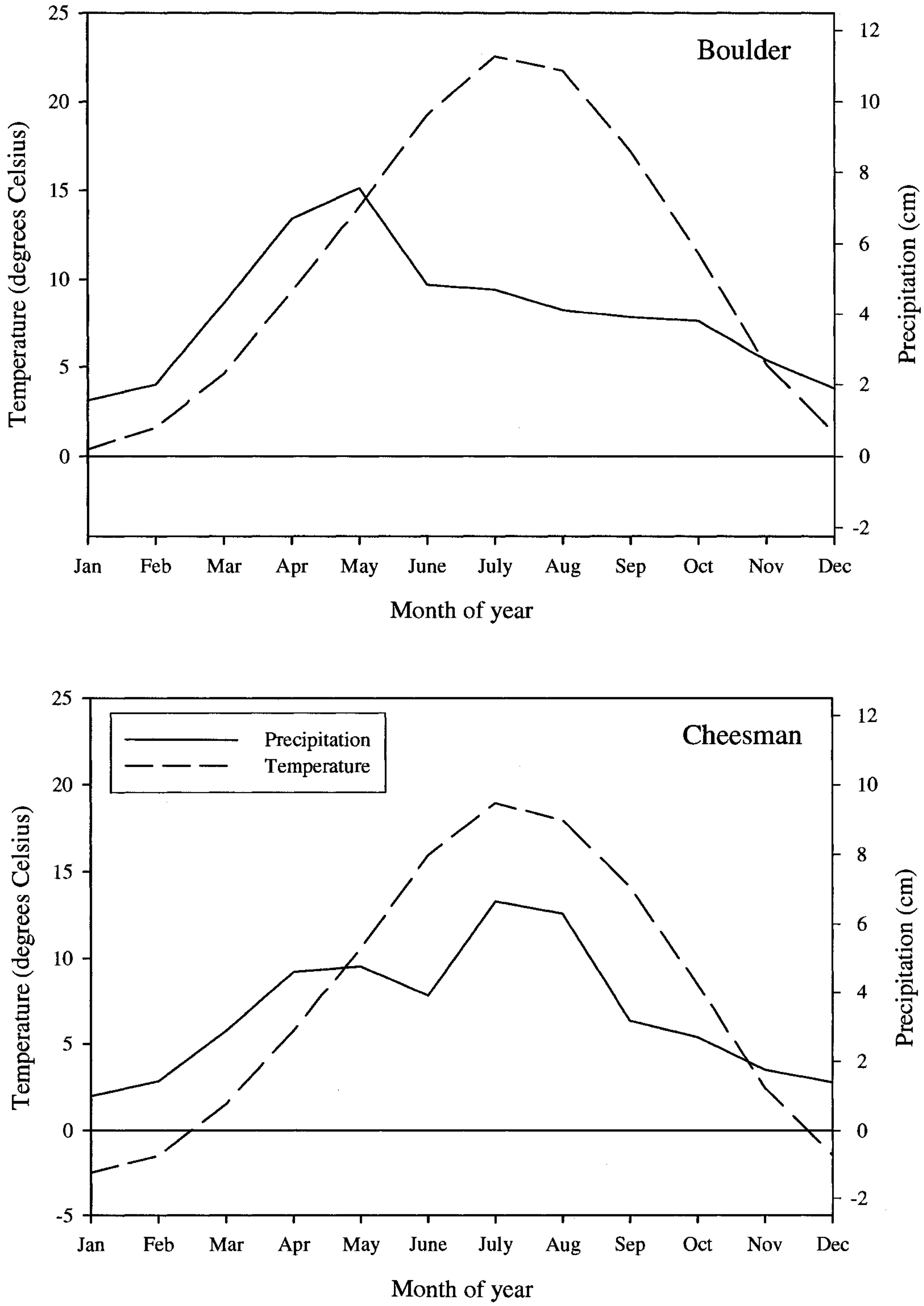


Figure 2

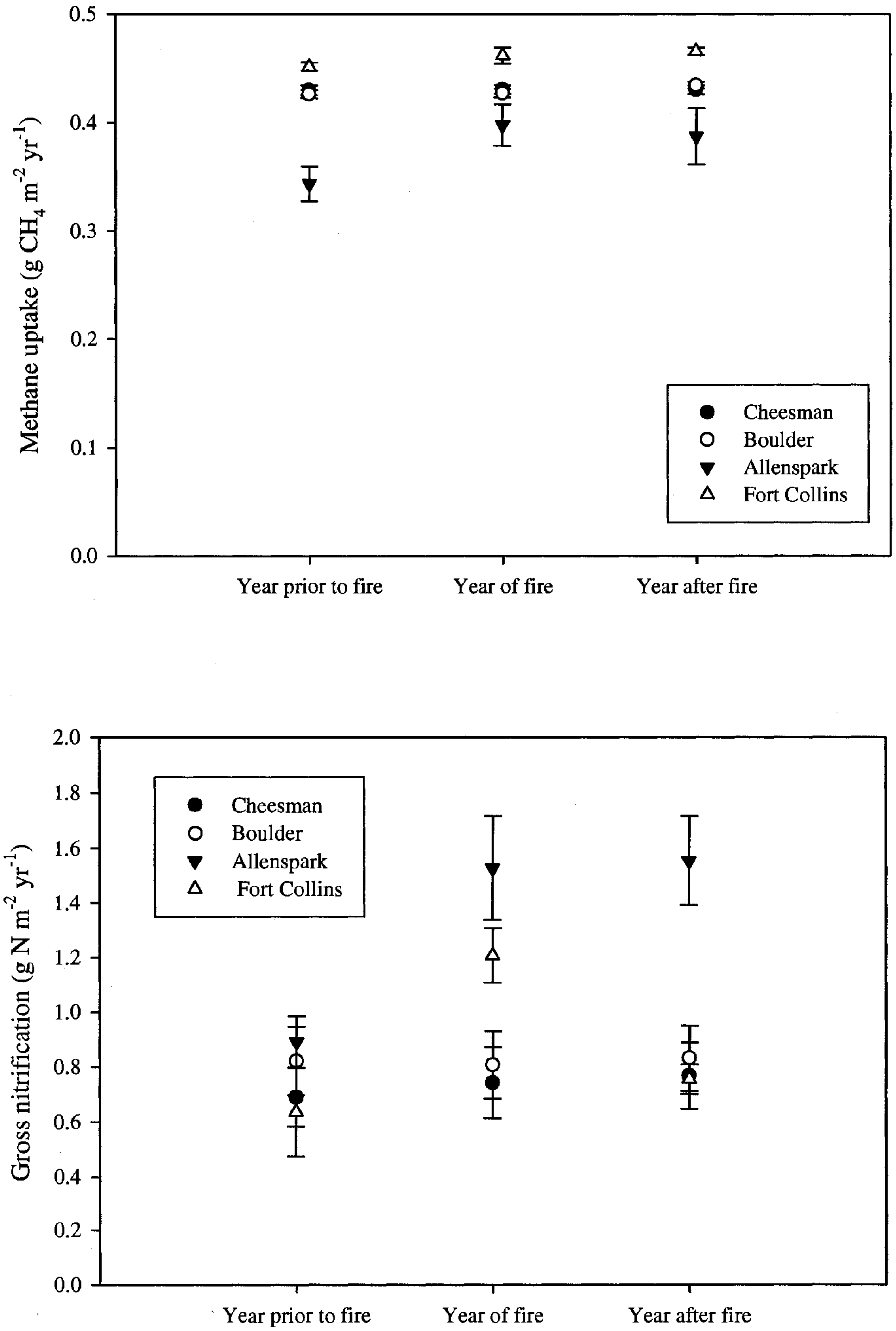
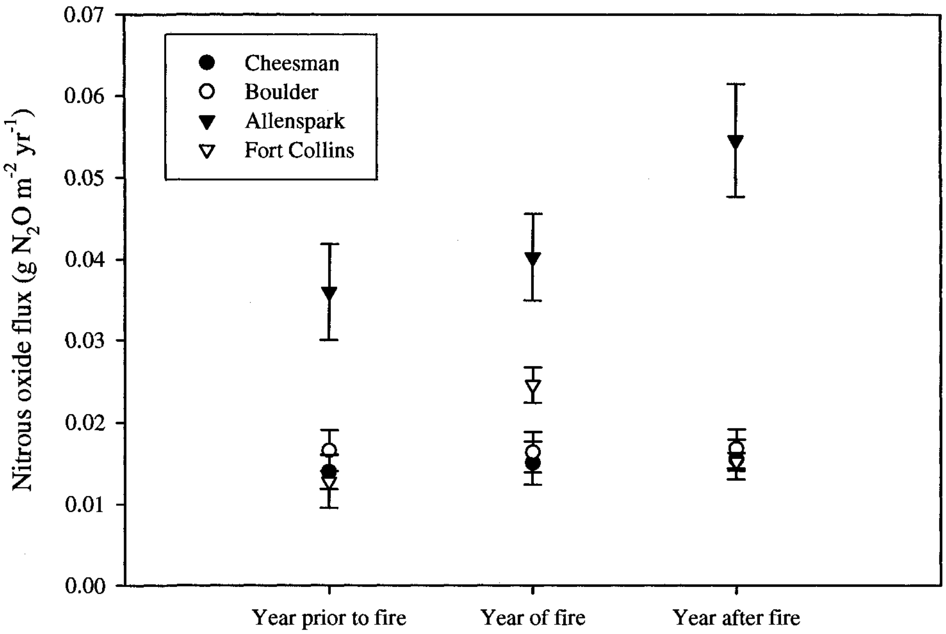

Methane uptake (g CH4 m-2 yr-1)
0.5
0.4
0.3
0.2
0.1
0.0
Cheesman
Boulder
Allenspark
Fort Collins
Year prior to fire
Year of fire
Year after fire
Gross nitrification (g N m-2 yr-1)
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
Cheesman
Boulder
Allenspark
Fort Collins
Year prior to fire
Year of fire
Year after fire

Figure 2 (continued)



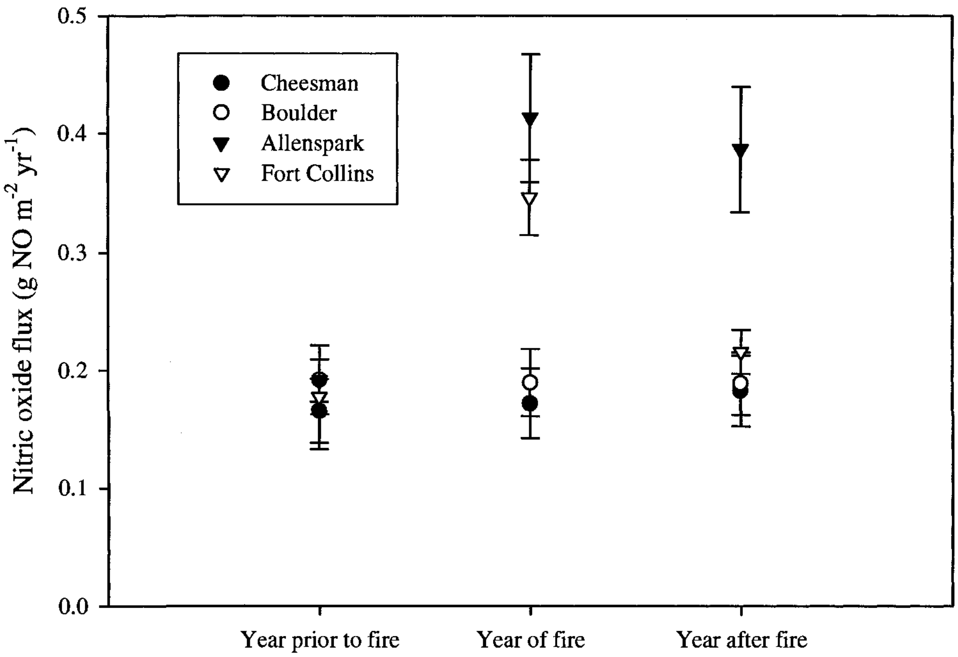


Figure 3

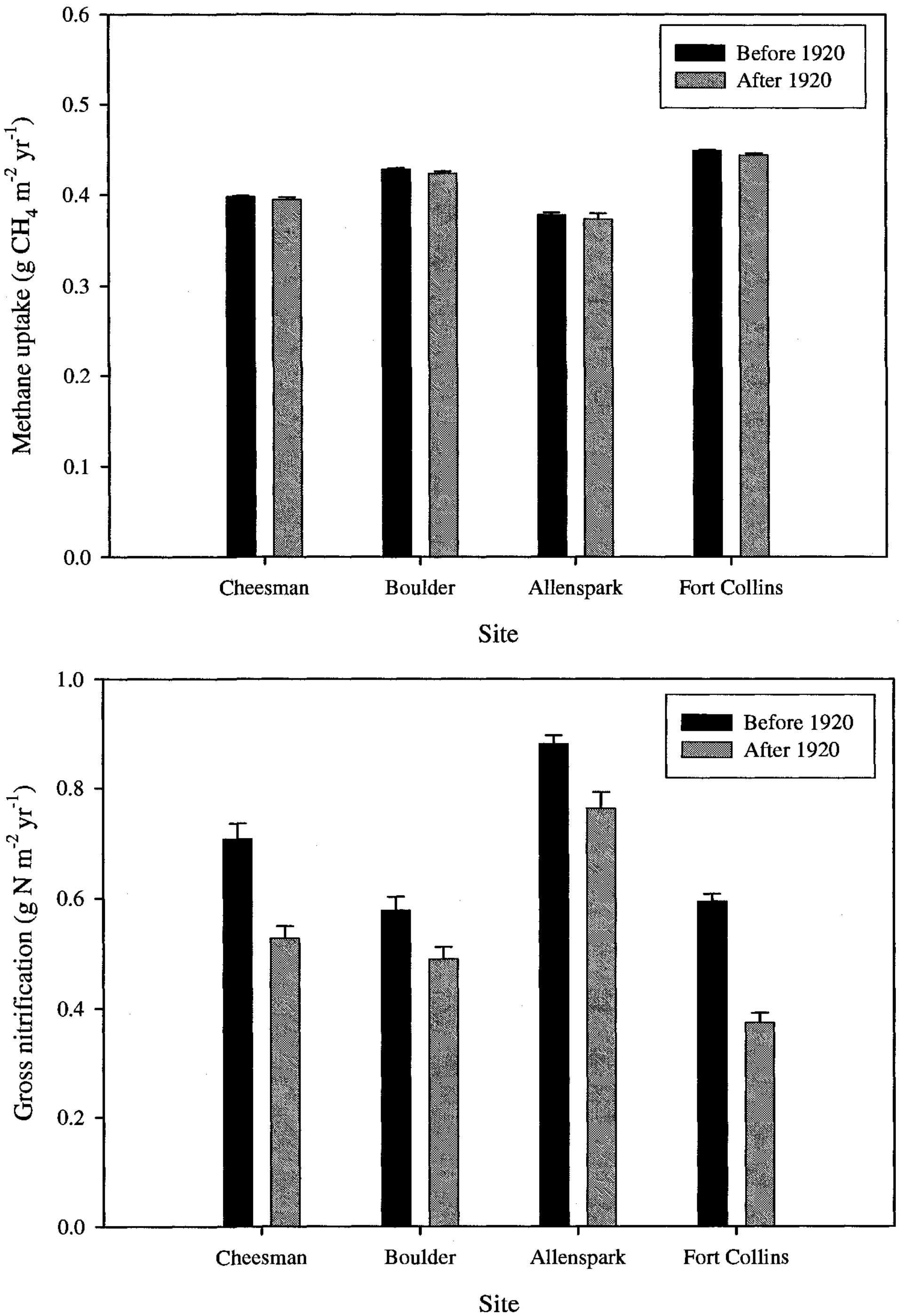
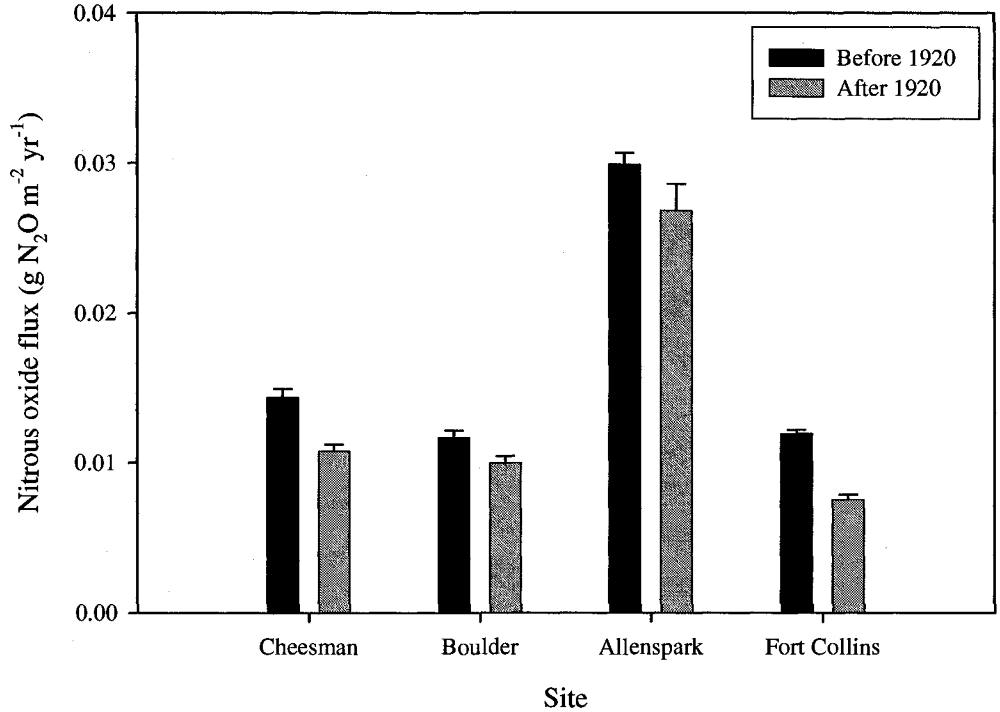
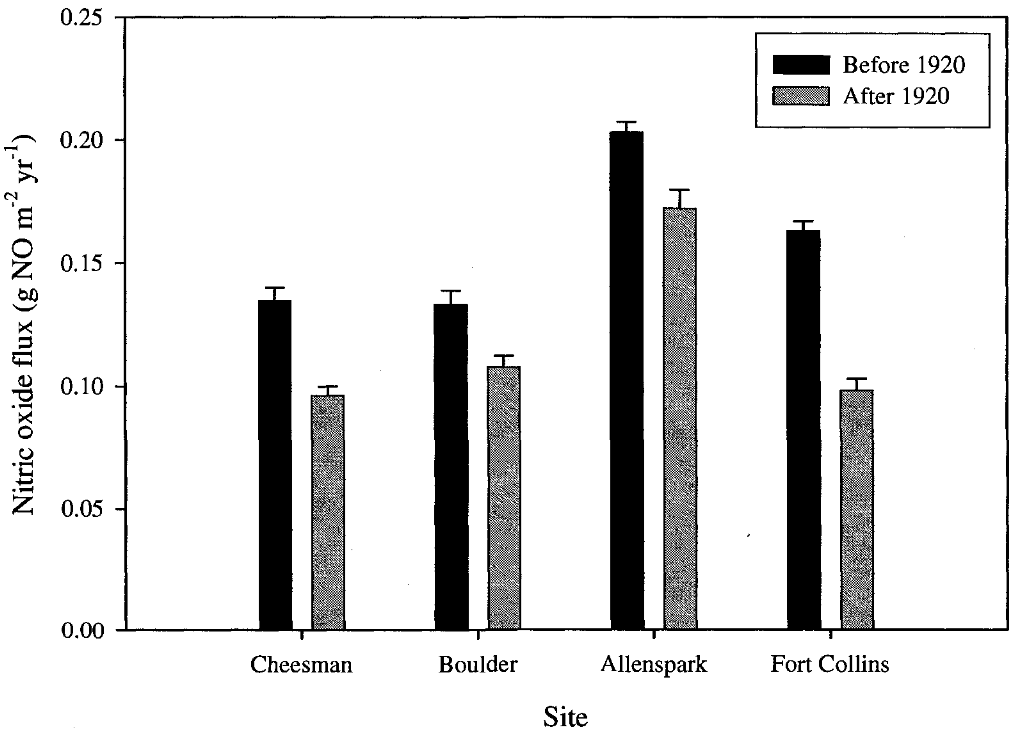

0.6
0.5
0.4
0.3
0.2
0.1
0.0
Methane uptake (g CH_4 m^{-2} yr^{-1})
Before 1920
After 1920
Cheesman
Boulder
Allenspark
Fort Collins
Site
1.0
0.8
0.6
0.4
0.2
0.0
Gross nitrification (g N m^{-2} yr^{-1})
Before 1920
After 1920
Cheesman
Boulder
Allenspark
Fort Collins
Site

Figure 3 (continued)





Chapter 5

CONCLUSIONS

Using the greenhouse gases CO_2, CH_4, and N_2O as my primary variables of interest, I investigated an array of factors that I expected to influence their rate of exchange between the soil and atmosphere.

In Chapter 2, I report that CO_2 fluxes increased significantly with time since fire, while aspect was not found to be significant. Methane uptake was not influenced by either of these factors, but N_2O fluxes had a significant interaction between time since fire and aspect. The greatest N_2O release occurred on north facing aspect at one year post-fire. In order to better understand how fires affect trace gas fluxes I chose to test the ability of five easily measured variables to predict flux rates. I used a likelihood approach to evaluate the strength of support in the data for model combinations of soil moisture, soil temperature, fire severity, topographical aspect, and time since fire. Of these the single variable models, soil moisture, time, and severity best described the CO_2 CH_4, and N_2O flux data, respectively. I found that CO_2 accounted for > 98% of the combined global warming potential of CO_2, CH_4, and N_2O soil fluxes, suggesting its importance for future study.

I also addressed the biogeochemical impact of forest thinning in the Colorado Front Range as these practices are becoming increasingly common. From Chapter 3, I learned that neither thinning-only nor broadcast chipping had significantly affected soil carbon or nitrogen, while thinning-only had significantly reduced the amount of forest floor litter. CO_2 and N_2O fluxes each had a significant interaction between treatment and sampling date indicating that the thinning-only and broadcast-chipping treatments do affect flux rates. However, the magnitude and/or direction of that relationship likely dependent upon soil moisture that varied by sampling date. Chapter 2 also revealed that CO_2 fluxes were affected by carbon and phosphorus availability (a wood*phosphorus interaction). Methane uptake was not affected by wood additions as methanotrophs gain carbon through the oxidation of atmospheric CH_4. The levels of nitrogen and phosphorus availability significantly affected CH_4 uptake.

In Chapter 4, I departed from field-based studies to a modeling approach using Daycent. Daycent simulations supported previous field findings that CH_4 uptake remains relatively unaffected by wildfire or fire suppression. Daycent calculated mean N_2O fluxes that fell within the range of field-based observations presented in Chapters 2 and 3. These simulations suggest that managing these systems back to their natural fire regime may lead to short term increase N-gas fluxes to the atmosphere before returning to average ranges within a year after a fire.

From field based studies and simulation modeling, my research shows that wildfire, forest thinning, and fire exclusion does impact the soil-to-atmosphere exchange rates of CO_2, CH_4, and N_2O. However, in each case, the response depends upon an array of other factors. Some of these were investigated as part of the research I presented here in my dissertation such as moisture, temperature, time since fire, soil C, N & P, and topography.