LABILE C CONSTRAINS SOIL RESPIRATION IN PONDEROSA PINE FORESTS DURING SHORT-TERM PRECIPITATION MANIPULATION AND LONG-TERM CROWN FIRE RECOVERY

A Thesis in
Ecology
by
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Abstract

Ponderosa pine forests in the Southwest United States historically experienced frequent, low intensity surface fires, which maintained relatively open forests by removing dead woody material and most pine regeneration. Following a century of fire suppression, however, these forests have become major carbon (C) sinks, due to greatly increased tree densities. Yet high tree densities also increase fuel loading, leading to stand-replacing wildfires, which greatly decrease the carbon stored in this system. Because stand-replacing fires are new to this ecosystem, it is unclear how forest C storage and fluxes recover from wildfires and how this recovery may vary with predicted changes in precipitation patterns. We quantified soil C dynamics in ponderosa pine forests near Flagstaff, AZ, and examined the effects of summer precipitation and wildfire history on soil respiration rates and soil C stocks. We hypothesized that recently burned forests would have lower soil respiration rates than unburned forests, because fire would reduce the amount of soil C available for microbial activity, but that the difference between burned and unburned sites would diminish with increasing time since the fire. Prior research has shown that summer monsoons stimulate soil respiration. We hypothesized that burned forests would respond less to monsoons than unburned forests, again due to lower labile C availability. Finally, we hypothesized that a longer monsoon season, as predicted by some circulation models, would increase soil respiration from burned and unburned forests. Although time since wildfire did not affect soil respiration, the other two hypotheses were supported. Soil respiration from unburned forests was ~ 1.1 g CO₂-C m⁻² d⁻¹ before the start of the monsoon season and ~ 4.8 g CO₂-C m⁻² d⁻¹ after, with burned forest respiration generally 25% lower. Burned forests had ~ 40% less total soil C, with the majority of that difference due to the loss of the O horizon after fire. Mineral soil C pools were not significantly affected by
fire. We artificially simulated an earlier monsoon season and found that soil respiration rates showed a dramatic initial increase in response to watering, but decreased to below control rates within weeks. Thus, watering did not significantly change the amount of C respired over the course of the experiment, suggesting that precipitation from an earlier monsoon season may not increase total CO₂ respiration. A laboratory incubation of soils collected at the end of the watering treatment showed ~45% less labile C in burned soils than unburned soils. Our results indicate that total soil C, labile C, and soil respiration remain low in southwestern ponderosa pine forests up to 35 years after crown fire. We attribute this poor ecosystem recovery to co-limitation of soil C processes by both water and labile C availability. Because these forests have limited potential for pine regeneration following crown fire, future recovery of soil C is uncertain.
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Chapter 1. Introduction

Over the past century, changing wildfire regimes have had a major impact on the ecology of western forests (Noss et al. 2006). In the Southwest US, ponderosa pine (Pinus ponderosa) forests that were historically maintained by surface fires now experience stand-replacing fires. Current global climate change models predict these fires will increase in frequency, severity, and size (Westerling et al. 2006), with potentially large effects on regional and continental C cycling (Pacala et al. 2001, Hall et al. 2006). Effects of fire on long-term and large-scale C cycling depends on post-fire recovery rates and interactions with future climate change. Post-fire recovery rates are well documented for forests with historical stand-replacing fire regimes. However, it is still unclear how ponderosa pine forests with historical surface fires will recover from the stand-replacing fires that are now common. Here we use a wildfire chronosequence to examine soil C processes on a decadal scale in ponderosa pine forests recovering from stand-replacing fires. We also examine how altered summer precipitation regimes may impact growing season soil respiration rates on a daily to monthly time scale.

Fire regimes can be divided into two major conceptual categories: infrequent, stand-replacing crown fires and frequent, low intensity surface fires (Covington et al. 1994). For example, ecosystems dominated by lodgepole pine (Pinus contorta) typically experience stand-replacing fires every 100-300 years (Kashian et al. 2006). Burned areas are characterized by nearly complete tree mortality, but regeneration often begins within one to four years (Turner et al. 2003) and net ecosystem production (NEP) could reach prefire levels within 40 years (Kashian et al. 2006). In contrast, ponderosa pine forests in the American Southwest historically experienced frequent (every 2-12 years), low intensity surface fires that maintained a relatively open forest by removing detritus and limiting pine regeneration (Covington et al. 1994). At
elevations from 2000 to 2500 m on the Colorado plateau, they were historically characterized by mixed age stands, low tree density, and a diverse grassy understory. The surface fire regime began to change following Euro-American settlement in the late 19th century. Overgrazing removed the grasses that had carried surface fires, while the U.S. Forest Service instituted a policy of total fire suppression in the 1910’s. A century of fire suppression has created unprecedented tree densities, ~727 trees/ha across AZ (O’Brian 2002) compared to historical averages of 30-140 trees/ha (Covington et al. 1994). As a result of these dense forests with high fuel loads, fires are now carried into the canopy, where they become stand-replacing wildfires. Severe fires can remove almost all of the soil organic material, making pine regeneration less successful (Pausas et al. 2003). Unlike the serotinous lodgepole pine, southwestern ponderosa pine may not easily recover from stand-replacing wildfires, and post-fire areas often experience arrested succession as grasslands or shrublands (Savage and Mast 2005). If pine regeneration occurs, it is dependent upon favorable climatic conditions that may not occur for decades (White 1985, Savage et al. 1996). Thus, while some forest ecosystems are known to quickly recover C after stand-replacing fires (Thornton et al. 2002, Litton et al. 2004), ponderosa pine forests may not.

Fire regimes and soil C can also be modified by climatic variation. In addition to the effects of a century of fire suppression, western forest fires are increasing in frequency, severity and duration due to warmer spring and summer temperatures (Westerling et al. 2006). Severe fire seasons are also correlated with drought conditions related to the El Niño / Southern Oscillation (Swetnam & Betancourt 1998). Summer climate at our field sites near Flagstaff, AZ is defined by a monsoon season, which typically lasts from early July to mid-September and accounts for half the mean annual precipitation. In Arizona and New Mexico, the North
American monsoon transports moisture northward from the Gulf of California and releases it as afternoon and evening thundershowers due to orographic cooling of moist air as it rises up the Colorado Plateau (Sheppard et al. 2002). The onset date for the monsoon season can vary greatly, because it is strongly dependent on warm sea-surface temperatures, the air-sea temperature difference, and the location of a subtropical ridge (Zhang 1993, Ellis et al. 2004). If continued global climate change increases sea-surface temperatures earlier in the summer, this should stimulate an earlier onset and longer duration of the monsoon season (Mitchell et al. 2002). Because pre-monsoon soil respiration is strongly limited by soil moisture (Kaye and Hart 1998), an earlier and longer monsoon could increase total growing season soil respiration.

Uncertainties about future C storage have led us to address the following question: How do soil C dynamics in ponderosa pine forests historically maintained by surface fires and a July monsoon respond to crown fires and an earlier monsoon? Specifically, we examine how stand-replacing wildfire interacts with summer precipitation to influence soil respiration rates and soil C pool sizes in ponderosa pine forests in north central Arizona. Soil respiration measures the rate at which carbon dioxide (CO₂) is leaving the soil, and includes microbial (heterotrophic) respiration and plant root (autotrophic) respiration (Schlessinger and Andrews 2000). Both autotrophic and heterotrophic respiration are regulated by soil temperature and moisture, and heterotrophic respiration may also be controlled by the abundance of easily accessible (labile) soil C (Davidson et al. 2006). To understand the interaction between fire history and summer monsoonal precipitation, we designed a nested experiment looking at different spatial and temporal scales. First, we used a 35 year chronosequence of 7 fires to understand landscape variability and the effect of time since burning. We measured soil respiration rates monthly from May through August in burned forests and nearby unburned controls. We hypothesized that
respiration would initially be lower in burned forests than unburned forests due to C limitation, but that it would gradually increase as plants recolonize and begin adding labile C to the soil (Figure 1A). We also hypothesized that due to this C limitation, soil respiration rates from burned forests would have a smaller response to the monsoonal rains than unburned forests (Fig. 1B). Second, we established an artificial watering manipulation experiment at one fire site, where we sampled soil respiration at a finer temporal resolution to determine the effects of burn condition (i.e. burned or unburned) and an earlier onset of summer monsoonal precipitation on summer soil respiration rates and C pools. We predict one of two results: 1) If labile C does not limit microbial response to monsoonal rains and the watered plots maintain the same rate of respiration as unwatered plots throughout the growing season, an earlier monsoon season could result in a net increase of C released from soil by increasing the duration of high soil respiration rates (Fig. 1B). 2) If labile C does limit microbial respiration, the artificially watered plots will initially show higher respiration rates than the unwatered plots, but will run out of C earlier in the season, resulting in no net difference in total soil respiration between watered and unwatered treatments (Fig. 1C).
Fig 1. Hypotheses of C accumulation and soil respiration. (A) predicts soil C decrease with time since fire until plants colonize and begin replenishing C stocks. (B) predicts lower soil respiration at burned sites than unburned sites, with greater differences after monsoon season onset in July. The arrow indicates our prediction that earlier watering could shift the increase in soil respiration earlier, while maintaining the same post-monsoon levels of respiration. (C) alternatively predicts that artificial watering will increase soil respiration before monsoon season onset, but that labile C limitation will decrease respiration later in the season.
Chapter 2. Methods

Chronosequence study sites

In order to understand the effects of time since wildfire and the timing of summer precipitation on soil carbon and respiration at the landscape level, we created a chronosequence of post-wildfire sites in ponderosa pine forests near Flagstaff in northern Arizona. We began by examining 60 years of wildfire records at the Coconino and Kaibab National Forests. Fires that had not burned ponderosa pine forests, were not on basalt parent material, had experienced more than one recorded fire, or could not be accurately identified as stand-replacing crown fires were eliminated. To give us the broadest age span, we chose seven wildfires, ranging from 2 to 35 years since fire (Table 1). Each wildfire “site” consisted of two paired “patches,” designated by burn condition as either “burned” or “unburned.” By pairing burned and unburned patches we test the assumption that the main difference among sites is the time since burning because we account for other types of environmental variation that may occur across landscapes (Johnson and Miyanishi 2008). Burned patches were areas that had experienced a stand-replacing crown fire (i.e. greater than 95% tree mortality.) The size of the patch equaled the burned area (Table 1). The Sanderson and Wild Bill burned patches were salvage logged after the fire and replanted. Unburned patches were in the nearest accessible unburned forest (outside the burn perimeter) that had similar slope and aspect to the burned patches. At each patch, we established three transects. Although the unique shape of each burned patch prevented the uniform layout of all transects at each site, we attempted to cover a similar spatial extent. Along each transect we sampled at three plots, giving n = 9 replicate plots per patch. All plots were >100 m away from other plots or drivable roads, and >20 m from trails and abandoned logging roads. We attempted to place all plots >100 m from transition zones between burned and unburned forests, although
the size of the Leroux and Wedding fires meant several plots were as little as 25 m away from edges. All unburned patches were dominated by ponderosa pine (>95%) with occasional Gambel oak (*Quercus gambelii*) at lower elevations or mixed conifers at higher elevations. All sampling occurred between May and August, 2007.

**Chronosequence carbon storage measurements**

To determine the amount of carbon stored in soil, we collected the organic horizon down to mineral soil at two 30x30 cm quadrats in each of the 9 plots per patch. This material was homogenized, air-dried, weighed, and ground to <1 mm on a Wiley mill. Subsamples were oven-dried for 48 hours at 60 °C to determine gravimetric water content (GWC). A 15-cm mineral soil core was taken from the center of each quadrat using a 5.1-cm diameter slide hammer core sampler (AMS Inc., American Falls, ID, USA). These cores were homogenized by hand, air-dried, weighed, sieved to <2 mm to remove rocks, and reweighed. Subsamples were oven-dried for 48 hours at 105 °C to determine GWC. Mineral soil bulk density was calculated using the mass of soil in the core (<2mm), GWC, and the known volume of the corer. Uniformly mixed subsamples were ground on a roller mill and then analyzed for total C concentrations by thermal conductivity detection after combustion at temperatures up to 1200 °C on an elemental analyzer (ThermoElectron Flash EA 1112, Carlos Erba, Milan, Italy).

**Soil respiration measurements**

Soil respiration was measured using a LiCor 6200 Portable Photosynthesis System (Li-Cor Inc., Lincoln, NE, USA), using a 962 cm³ chamber (Model #6000-09), programmed to take three respiration measurements based on a change of 5 ppm CO₂. A soda lime scrub was used to
decrease the chamber’s initial CO2 concentration, allowing us to bracket these three measurements around ambient CO2 concentrations. The instrument was calibrated weekly at 400 ppm CO2 and was zeroed and calibrated for ambient air pressure daily. Three days before the first measurement, we placed one thin PVC collar (10 cm inside diameter x 5-10 cm tall) 3 cm into the mineral soil at each plot to prevent lateral CO2 flow and ensure repeated sampling of the same location. The variable height of the collars accommodated variability in O horizon thickness. Soil respiration rates were measured in May and June to get a pre-monsoon baseline and in July and August to examine the effect of the monsoon season. Due to the distance between sites, it was not possible to sample all sites on the same day. We simultaneously measured soil temperature at a depth of 10 cm and used an Oakfield sampler to collect ~25 g of the top 10 cm of mineral soil, which was then dried in the lab to determine GWC.

Manipulation study sites

The chronosequence allowed us to look at a variety of burned forests in different stages of regeneration over a large spatial extent. The logistics of working at such a broad scale, however, restricted us to monthly measurements over the course of the summer. To examine the effects of altered summer precipitation on soil respiration rates and C concentrations at a much finer temporal scale, we conducted a manipulative experiment at one site. We chose the 1996 Horseshoe fire site so we could compare our results to an eddy covariance tower located there (Dore et al. 2008, Sullivan et al., in review) as well as data collected from the chronosequence. We created a two factor experiment, looking at burn condition (burned vs. unburned) and precipitation (artificially watered & unwatered). To test the effect of an earlier onset of the summer monsoon on soil C, we created 10 paired plots in the burned and unburned patches,
where each plot consists of one 1 m² subplot that was artificially watered and one subplot that was not watered. We used a backpack sprayer to deliver 0.6 cm of water to each watered subplot once every three days. At the start of the monsoon season, the frequency and amount of precipitation can be highly variable. Our watering regime was designed to represent historically typical rain events during the start of the monsoon season (Staudenmaier, Jr. et al. 2005). Between 1898 and 2005, average July precipitation was 6.1 cm. This usually occurs over the three weeks after the monsoon season begins on approximately July 7th, averaging 0.6 cm of precipitation over a three-day period. Measureable precipitation occurs on approximately 12 days, with >0.25 cm rain on 7 days, >0.63 cm on 4 days, and >1.27 cm on 2 days. We determined that 0.6 cm of water every three days would be the most practical way to approximate the historical frequency and total amount of monsoon precipitation. We began watering on June 26th and continued through four 3-day cycles before the first rain event on July 6. We then ceased watering but continued measuring soil respiration, thus lengthening the monsoon season by 10 days without increasing precipitation once the monsoon began.

*Manipulation measurements*

Soil respiration was measured in all plots before each watering event and repeated up to three times per day after watering. Measurement frequency varied from several times per day at the start of the experiment to several times per week by the end. At half of the plots at each patch, we recorded soil moisture and temperature at five minute intervals using ECHO-TM probes (Decagon Devices, Inc., Pullman, WA, USA). Although we buried the sensors to measure conditions 5-10 cm into the mineral horizon, very high soil temperatures caused the soil
moisture sensors to fail during the day at the burned patch. Thus, we present only nighttime soil moisture data.

Mineral soil samples were collected from each plot at the end of the experiment in August and analyzed for total C by dry combustion and for labile C with a 28-day laboratory incubation. Approximately 10 g of air-dry, rock-free mineral soil were placed in a 120 mL sealable glass jar. Distilled water was added to maintain soil at 60% water holding capacity. The samples were incubated at 22ºC for 28 days. Jars remained open except during measurement periods, which occurred daily at the start of the experiment and weekly by the end. Headspace CO$_2$ concentration was analyzed by drawing a 0.5 mL sample into a syringe, which was then injected into the ‘sample’ loop of a LiCor 7000 (Li-Cor Inc., Lincoln, NE, USA) set in Reference Estimation Mode. Labile C concentrations per g soil were calculated by graphing the rate of CO$_2$ increase during each measurement period and integrating the area under to calculate the total C respired over the course of the incubation.

**Statistical analysis**

We used paired t-tests to determine differences in soil temperature and moisture between burned and unburned patches on the chronosequence. To test the effects of time since wildfire on soil respiration, we performed a repeated measures analysis of variance (ANOVA) on log-transformed soil respiration values from the chronosequence sites and assessed interactions between month and burn condition (burned vs. unburned areas) in SAS (version 9.1, SAS Institute, Inc., Cary, NC, USA). Finding no interactions, we averaged soil respiration on the plot level in May and June for a “pre-monsoon” data set and in July and August for “post-monsoon” data. We then ran ANOVAs and mean comparisons within each data set (pre- and post-
monsoon), comparing burned and unburned patches for a given fire year. Similar ANOVAs were used to compare C pools at burned and unburned patches. We then used simple linear regression to test for correlations between time since fire and the difference in soil respiration and C pools between burned and unburned patches at the site level. This analysis accounts for site-to-site variability that results from landscape variation unrelated to fire. Linear regression was also used to test for correlations between total soil C pools and our averaged pre- or postmonsoon soil respiration at the patch level. At the manipulation experiment, soil temperature, moisture, and respiration were recorded simultaneously at paired watered and unwatered plots, allowing us to use paired t-tests to determine differences in respiration and microclimate between watering treatments. Cumulative C respired during the manipulation experiment was calculated using the “area under the curve” macro in SigmaPlot (version 6.00, Systat Software Inc., San Jose, California, USA). Because sampling and watering could not occur at exactly the same time at both of the manipulation patches, we do not compare total C respired between the burned and unburned patches for our 43-day field study. All samples were measured simultaneously for our 28-day laboratory incubation, so results can be compared across burn conditions. We acknowledge that having only one site for our manipulation and only one site per year at the chronosequence constitutes pseudo-replication, but we were limited by fire history and the logistics of large-scale experiments. This small scale work was complemented by true large-scale replication across the chronosequence at a coarser temporal resolution. Prior to analysis, we chose \( \alpha < 0.05 \) for all statistical significance.
Table 1. Chronosequence site characteristics.

<table>
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<tr>
<th>Site Name</th>
<th>Patch Type</th>
<th>Years Since Fire†</th>
<th>Mean Elevation (m)</th>
<th>Burned Area (ha)</th>
<th>GPS Coordinates Easting, Northing</th>
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† Years since fire in 2007.
Chapter 3. Results

Chronosequence

Soil temperature and moisture did not significantly differ between burned and unburned patches within months (p>0.05). Paired summer soil temperature and moisture differences were also not significant (p=0.180 and p=0.311, respectively). Across all sites, soil respiration at burned patches was generally lower than unburned patches (Fig. 2). Within-month comparisons show a significant effect of burn condition at all months except June, when soil moisture (Table 2, Fig. 6B) was low. Before the monsoon season, soil respiration rates at unburned patches were ~1.1 g CO$_2$-C m$^{-2}$ d$^{-1}$ and were approximately 25% lower at burned patches. After the onset of the monsoon season, soil respiration increased to ~4.8 g CO$_2$-C m$^{-2}$ d$^{-1}$ at the unburned patches, while the burned patches remained ~25% lower. Because an ANOVA showed no significant differences within burn conditions between May and June or July and August, plot level monthly values in May and June were averaged together as “pre-monsoon,” while July and August were averaged as “post-monsoon.” ANOVA and mean comparisons were then performed within each season. Both the pre-monsoon and post-monsoon data showed significant effects for burn condition (p=0.001 and p<0.001, respectively) and fire year (p=0.041 and p<0.001, respectively) (Fig. 3). Although the treatment-by-year interaction was significant (p=0.008) for the post-monsoon data set, this seems to be driven by site-to-site variability rather than an overall trend with time. Significant differences between treatments were found for all post-monsoon sites except at 7 and 23 years since fire, while significant pre-monsoon differences were only found at 2 and 11 years. Regressions performed between soil respiration and years since fire for pre- and post-monsoon burned patches and pre- and post-monsoon unburned patches were all found to be not significant (p=0.427, p=0.786, p=0.439, and p=0.156, respectively). The difference in soil
respiration between paired burned and unburned sites was not significantly correlated with years since fire for pre- and post-monsoon (p=0.638 and p=0.390, respectively) data. Organic horizon and total (organic plus mineral) soil C pools were affected by burn condition (p<0.001 and p<0.001, respectively) while mineral soil C pools were not (p=0.158) (Fig. 4). Regressions between time since fire and organic, mineral, and total soil C pools at burned patches were not significant (p=0.347, p=0.468, and p=0.610, respectively). Linear regressions between time since fire and the difference between organic, mineral, or total soil C pools at unburned and burned patches were also not significant (p=0.226, p=0.633, and p=0.383, respectively). The organic soil horizon at unburned patches averaged 1700 g C m⁻², while burned areas contained only ~225 g C m⁻². Burned and unburned patches had significantly different O horizon C storage for all burn years. The loss of O horizon at the burned patches was also apparent in total soil C, which showed significant differences for all burn years. Burned patches generally held ~ 40% less C than unburned patches. Mineral soil C pools ranged from 1850-3000 g C m⁻² but did not differ significantly between burned and unburned patches (p=0.158) when all fire years were examined. For individual fire years, unburned patches had more mineral soil C at years 2 and 30, while burned patches contained more mineral soil C at year 23. There was a positive (p<0.001, r²=0.708) correlation between total soil C pool and post-monsoon soil respiration rates, but not between total soil C pool and pre-monsoon soil respiration (p=0.265) (Fig. 5).

Manipulation

Mean soil temperature during the times we measured soil respiration was ~ 2.6°C lower in watered plots than paired unwatered plots (p< 0.001) at the burned patch and ~ 2.9°C lower than unwatered plots (p<0.001) at the unburned patch between 6/25 and 7/5 (Fig. 6A, 6B). After
7/22, there were no differences in soil temperature between watered and unwatered plots (p=0.550 and p=0.070 at burned and unburned patches). Watering treatments significantly increased nighttime volumetric water content between 6/25 and 7/5 by ~ 0.034 m$^3$/m$^3$ (p<0.001) at the burned patch and by ~ 0.046 m$^3$/m$^3$ (p<0.001) at the unburned patch (Fig. 6B). This difference persisted until after the major increase in soil water content on 7/22, when the watered plots remained an average of 0.005 m$^3$/m$^3$ wetter than paired unwatered plots at the burned patch (p<0.012) while there were no significant differences at the unburned patch (p=0.224). The first rain event occurred on 7/6, at which time we discontinued watering. Significant rain events occurred on 7/12 and 7/18 before a major thunderstorm dramatically changed soil water content on 7/22. Soil respiration in watered plots at the burned and unburned sites showed immediate responses to our artificial watering (Fig. 6C, D). Soil respiration rates increased within minutes after watering and remained elevated for several days compared to the unwatered controls. Respiration at unwatered plots averaged ~ 1 g CO$_2$-C m$^{-2}$ d$^{-1}$ (Fig. 6C, 6D) and was consistent with our pre-monsoon chronosequence data (Fig. 2, 3). Watered plots showed peak respiration rates approaching ~ 10 g CO$_2$-C m$^{-2}$ d$^{-1}$ and even 24 hours after watering, they often remained double the unwatered plots. After artificial watering ceased, the watered plots maintained elevated soil moisture levels and increased respiration rates. Watered plots had greater soil respiration than unwatered plots at both burned and unburned patches between 6/24 and 7/6, the time period that corresponded to our artificial watering (burned p<0.001, unburned p=0.001, Fig. 7A). After artificial watering ceased, we found no further differences between soil respiration at the watered and unwatered plots in the unburned patch. At the burned patch, however, unwatered plots had significantly greater respiration than watered plots from 7/6 to 7/20 and from 7/20 to 8/6 (p=0.015 and p=0.010, respectively). Over the
course of this 43-day experiment, there was no significant difference between soil respiration at watered and unwatered plots at either of the patches (burned \( p=0.372 \), unburned \( p=0.979 \)). A 28-day laboratory incubation of mineral soil collected at the end of the manipulation experiment showed \( \sim 45\% \) lower soil respiration in burned sites than in unburned soils, but found no effect of watering within patches (Fig. 7B).

![Soil Respiration Graph](image)

**Fig 2.** Monthly soil respiration by burn condition. Bars are means (\( n=63 \)) across all sites for a given burn condition ± 1 standard error. Lowercase letters denote significant differences (\( p<0.05 \)).
Table 2. Chronosequence soil temperature (°C at 10 cm depth) and gravimetric water content (g H₂O g⁻¹ dry soil from 0-10 cm mineral soil depth). Values are means (n=9) with SE in parentheses. No significant differences were found (p>0.05).

<table>
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<tr>
<th>Site</th>
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<th>May</th>
<th>June</th>
<th>July</th>
<th>August</th>
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<tr>
<td></td>
<td></td>
<td>T (°C)</td>
<td>GWC</td>
<td>T (°C)</td>
<td>GWC</td>
</tr>
<tr>
<td>Wedding</td>
<td>Unburned</td>
<td>18.7 (1.6)</td>
<td>-</td>
<td>17.8 (1.2)</td>
<td>-</td>
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<tr>
<td></td>
<td>Burned</td>
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<td>-</td>
<td>16.7 (0.6)</td>
<td>-</td>
</tr>
<tr>
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<td>Unburned</td>
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<td>-</td>
<td>16.0 (0.9)</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Burned</td>
<td>12.5 (0.4)</td>
<td>-</td>
<td>14.8 (0.4)</td>
<td>-</td>
</tr>
<tr>
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<td>Unburned</td>
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<td>-</td>
<td>20.4 (0.7)</td>
<td>0.03 (0.00)</td>
</tr>
<tr>
<td></td>
<td>Burned</td>
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<td>-</td>
<td>20.6</td>
<td>-</td>
</tr>
<tr>
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<td>16.0 (1.0)</td>
<td>0.06 (0.01)</td>
</tr>
<tr>
<td></td>
<td>Burned</td>
<td>16.7 (0.6)</td>
<td>-</td>
<td>19.7 (0.7)</td>
<td>0.03 (0.00)</td>
</tr>
<tr>
<td>Sanderson</td>
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<td>-</td>
<td>16.4 (0.5)</td>
<td>-</td>
</tr>
<tr>
<td></td>
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<td>-</td>
<td>21.2 (0.6)</td>
<td>-</td>
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<tr>
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<td>-</td>
<td>16.4 (0.4)</td>
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<tr>
<td></td>
<td>Burned</td>
<td>16.8 (0.5)</td>
<td>-</td>
<td>20.0 (0.6)</td>
<td>-</td>
</tr>
</tbody>
</table>

† Dashes indicate no data collected.
Fig. 3. Pre- and post-monsoon soil respiration at burned and unburned sites for a chronosequence of 7 wildfires. Sampling dates were averaged (May & June = Pre-monsoon, July & August = Post-monsoon.) Squares indicate means (n=9) ± 1 standard error. ANOVA and mean comparisons were only performed within each season. * denotes significantly different (p<0.05) means between burn conditions pre-monsoon, while ** denotes significant differences post-monsoon.
Fig. 4. Carbon pools in (A) organic, (B) mineral, and (C) organic and mineral soils. Means (n=9) are shown ± 1 standard error. * indicates significant differences (p<0.05) between burned and unburned sites.
Fig. 5. Correlation between mean total soil C stocks and mean soil respiration for burned and unburned patches (n=14). Each point is the mean of 18 soil respiration measurements and 9 soil C measurements. Circles denote post-monsoon soil respiration (p<0.001, $r^2=0.708$) while triangles denote pre-monsoon soil respiration (p=0.265).
Fig. 6. (A) Soil temperature (10 cm mineral soil depth), (B) soil water content (5-10 cm mineral soil depth, 11:00pm – 7:00 am) and soil respiration at watered and unwatered plots at the (C) burned and (D) unburned patches. Means are shown ± 1 standard error (temperature & VWC n=5, soil respiration n=10 at burned site, n=9 at unburned site). (B) shows irrigation and rain events in Sampling Periods (SP) 1 and 2. Frequent precipitation in SP 3 is not depicted.
Fig. 7. Cumulative C released for (A) a 43-day in situ watering manipulation, broken into 3 sampling periods and (B) a 28-day laboratory incubation. Means (n=10, except n=9 at (A) unburned) ± 1 standard error. Lowercase letters indicate significant differences (p<0.05) between watered and unwatered plots. * in (A) show significant differences between watered and unwatered plots for the sampling period indicated.
Chapter 4. Discussion

Fire history and soil C

Previous research has suggested that soils from patches that have experienced wildfires have lower respiration rates than unburned sites (Sullivan et al in review, Grady & Hart 2006). However, these studies compared single fires to controls without landscape replication or variation in time since fire (Fig. 1A). We predicted that soil respiration in burned areas would decrease with time since fire as the labile C pool declined, and would then begin to increase again as grasses, shrubs, and trees recolonized burned areas and began adding new litter and root respiration to the organic soil pool. Our results confirmed that burned patches had ~ 25% lower soil respiration rates than unburned plots. However, we did not find our predicted trend of decreasing and then increasing soil respiration rates at the burned patches (Fig. 3). Instead, both burned and unburned patches showed significant variability among fire years, suggesting that site-to-site variability had a greater influence on soil respiration within a burn condition than any trends through time. This was confirmed by the organic and mineral soil C pools at the burned patches, which did not show any trend of changing C storage with time (Fig. 4). However, our overall hypothesis that post-fire soil C content would be correlated with soil respiration was supported (Fig. 5). Previous research has shown that soil respiration can be correlated with aboveground net primary production (Irvine et al. 2007) and aboveground, belowground, and microbial biomass (Litton et al. 2003). These correlations suggest that primary productivity increases soil respiration through both autotrophic and heterotrophic pathways. The ability of grasses, shrubs and trees to recolonize following a stand-replacing fire controls how quickly autotrophic respiration rates can recover to pre-fire levels. In ponderosa pine forests in central Oregon, autotrophic respiration accounts for ~45% of soil respiration in mature stands and can
return to this proportion in as little as 2 years after a severe fire (Irvine et al. 2007). However, this recovery is not due to ponderosa pine regeneration but rather a very dense herbaceous understory, which does not typically occur in forests in northern Arizona. By contrast, lodgepole pines have the ability to regenerate very quickly after stand-replacing fires and can reach densities of >50,000 trees ha\(^{-1}\) within 13 years after fire (Litton et al. 2003). This immediate recovery of net primary production also initiates the accumulation of C in the forest floor; thus only 13 years after a stand-replacing fire, these lodgepole pine forests show no significant difference between organic soil C storage in burned and unburned sites. Decomposition of this material provides labile C for heterotrophic respiration. We found neither of these recovery trajectories occurring at burned sites in ponderosa pine forests in northern Arizona. For example, intensive sampling of the fire used in our precipitation manipulation reveals no natural pine regeneration, low herbaceous production, and negative net ecosystem C exchange within 11 years of burning (Dore et al. 2008). Regeneration at older sites was due to post-fire replanting, and even this was not enough to substantially increase organic soil C storage within 35 years after a stand-replacing fire. We conclude that the lower aboveground production and lower soil C storage at burned patches results in lower autotrophic and heterotrophic respiration rates compared to unburned patches.

A chronosequence relies on the assumption that all variation among sites is due to differences in the time since disturbance (Johnson and Miyanishi 2008). In our case, we assume that all sites had the same soil C and soil respiration prior to fire, that all fires burned with the same intensity (due to similar fuel and climatic conditions), and that each burned area experienced the same post-fire recovery trajectory. We used paired burned and unburned plots to help account for violations in the first assumption; if sites differed in soil C and respiration
due to inherent landscape variability, then we expected to capture that variability in the paired unburned patches. One significant violation of chronosequence assumptions is that the 23 and 34 year-old burned patches had been salvage logged and replanted within several years post-fire, while other burned patches were not salvaged logged or replanted. While salvage logging caused an immediate loss of ecosystem C, the planted seedlings allowed the forest to begin accumulating tree C again. Soil respiration and C pools at these two sites were similar to those at the 30 year-old fire, which was neither salvage logged nor replanted, suggesting that this violation did not have a major impact on soil C pools. Other violations pertain to possible differences in burn intensity between the earliest and most recent fires. Forests burned by the most recent fires have had an additional 35 years of fuel accumulation compared to the oldest fires in our chronosequence. Combined with a prolonged drought over the past decade, these forests have greater stocks of drier fuels, suggesting that more recent fires may have experienced higher intensity fires. Cumulatively, these violations may mean that more ecosystem C could have survived a stand-replacing fire 35 years ago, compared to the amount that may have survive a current fire. If this were the case, we would expect to find artificially high levels of soil C at the older sites, which may have falsely shown an increase in C with time since fire. Since we found no such trend, these violations cannot produce interpretations that are inconsistent with our conclusions.

*Interactions with precipitation*

Precipitation from the summer monsoon season greatly affects ecosystem C cycling in ponderosa pine forests in northern Arizona (Kaye and Hart 1998, Grady and Hart 2006). We hypothesized that low soil water content would limit soil respiration rates in May and June by
restricting microbial activity at both the burned and unburned sites, and that C limitation would cause a lower response of soil respiration to the monsoon season at the burned sites than at the unburned sites (Fig. 1). Post-monsoon soil respiration rates at our unburned sites increased ~350% relative to pre-monsoon levels, compared to a ~310% increase at the burned sites. The smaller increase at the burned site could be due to labile C limitation or the effects of the monsoon season on autotrophic respiration. Eddy covariance data suggest limitation of heterotrophic respiration, because measured gross primary production (Dore et al. 2008) did not change during the early monsoon season, while soil respiration was increasing (Fig. 6C). Our manipulation simulated an earlier monsoon season on 1 m² plots and increased the total pre-monsoon C respired at watered plots relative to unwatered plots (Fig. 7). Likewise, autotrophic respiration cannot account for lower soil respiration rates in the watered plots later in the season; we would expect watered plots to have greater autotrophic respiration than unwatered plots. Lower soil respiration from watered plots is consistent with our hypothesis that labile C was limiting heterotrophic respiration.

Our manipulation suggests that labile C can constrain soil respiration responses to altered precipitation. However, further large-scale testing needs to be done to understand the impact of an earlier monsoon season on ecosystem function. Eddy covariance towers show net C uptake due to photosynthesis at an unburned forest immediately after the major increase in soil water content in late July (Dore et al. 2008). Shifting this increase in soil water content and the resulting photosynthetic response earlier in the summer could increase the total growing season net primary productivity, which could increase autotrophic respiration immediately and eventually add more plant litter to the organic soil horizon.
Importance of labile C

No single test or experiment can fully explain soil C dynamics, particularly when changing multiple environmental factors at once. However, our results include several different lines of evidence that converge to support our hypothesis that labile C limits soil respiration response to water inputs in ponderosa pine forests. Across chronosequence sites, we found soil C pools and respiration rates were significantly lower at burned patches than nearby unburned controls. We found these two factors were strongly correlated regardless of burn condition, suggesting that the same controls apply at both burned and unburned patches. Because we were unable to differentiate heterotrophic and autotrophic respiration in the field, we performed a laboratory incubation of mineral soil, without live roots. We found that under controlled temperature and moisture conditions, microbial respiration was still ~45% lower in soils from burned patches compared to soils from unburned areas. Our manipulation of summer precipitation patterns also suggests that labile C is limiting cumulative soil respiration at both burned and unburned patches over the growing season. Rather than increasing the total C respired, we found that the increased respiration prior to the onset of the monsoon season was balanced within weeks by lower respiration rates (even though soils were still wet and warm), suggesting that labile C had become limiting. While each of these individual measures of labile C-soil respiration linkages has limitations, the intersecting lines of evidence from large and small-scale field experiments and laboratory incubations combine to provide strong support for our hypothesis that labile C constrains soil respiration responses to both fire and precipitation.
Chapter 5. Conclusions

At a 35 year chronosequence of stand-replacing fires, we found that soil respiration and C pools are still significantly lower than at unburned stands. We suggest that soil respiration is limited by labile C availability, due to the delayed recovery of net primary production and the organic soil horizon. We were limited to a 35 year chronosequence because no older fires exist, so we suggest continued monitoring of these wildfires, to determine how long this recovery may take, and to determine what factors are limiting pine regeneration in burned areas. We also examined the effect of the summer monsoon season on soil C pools and found that labile C availability constrains the soil respiration response to monsoon precipitation. These results support the conclusions of Davidson et al. (2006), that we need to move beyond ‘Q10’ and recognize the importance of substrate and moisture constraints on soil respiration. We suggest that further research be done to determine the proportions of autotrophic and heterotrophic respiration, to better understand the immediate effects of the onset of the monsoon season. Because our precipitation manipulation occurred on 1-m² plots, we suggest further large-scale testing to examine ecosystem effects of changing precipitation patterns. Additionally, global climate change is predicted to increase spring and summer temperatures, which could affect ecosystem production and decomposition rates, especially when combined with increased moisture from an earlier monsoon season.

Warmer temperatures and increasingly variable precipitation patterns are also predicted to increase fire frequency and severity. Stand-replacing wildfires are a necessary component of lodgepole pine ecosystems, which have certain characteristics that allow them to almost immediately begin the recovery process. Ponderosa pine forests in wetter regions also recover quickly. Our research shows that in ponderosa pine forests in northern Arizona, however, the
occurrence of stand-replacing fires in an ecosystem historically dependent upon surface fires can disrupt C cycling processes for decades. We have shown that total soil C, labile C, and soil respiration remain low in southwestern ponderosa pine forests for up to 35 years after crown fire. Because ponderosa pine regeneration can be slow or non-existent after crown fires (Savage et al. 1996, Savage and Mast 2001), severely burned areas may remain in a state of arrested succession indefinitely, or may shift to grasslands or shrublands. Thus, increasing frequency of stand-replacing fires will have a lasting negative impact on C storage across the southwestern United States.
References:


