Quantifying the effects of prescribed burning on soil carbon efflux in an Ohio oak woodland

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The University of Toledo
A Thesis

Entitled

Quantifying the Effects of Prescribed Burning on Soil Carbon Efflux

in an Ohio Oak Woodland

by

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Submitted as partial fulfillment of the requirements for

The Master of Science in Biology, Ecology-track

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College of Graduate Studies

The University of Toledo

May 2007
An Abstract of

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Prescribed burning is a major management technique used to restore oak woodlands to previous oak savanna conditions. Burning alters biotic and biophysical variables by combusting the litter layer and heating the soil; however, the net effects of these cool fires on ecosystem processes like soil respiration (SR) are not well understood. This study examined immediate and seasonal responses of biotic variables, biophysical variables, and SR to prescribed burning in Northwest Ohio successional oak woodlands. A chronosequence of treatments (0, 1, 3, and 5 years after burning) was compared with unburned woodland to estimate the duration of fire effects. A paired design limiting landscape variability was incorporated by maintaining a burn exclusion area within the freshly burned treatment (0yr). The relationship between SR and its biotic and biophysical predictors, and the temperature sensitivity of SR ($Q_{10}$) were also examined across treatments. Measurements were taken weekly between March 2005 and January 2006. Data were primarily analyzed with repeated measures analysis of variance.
This study suggested that repeated fires had persistent impacts on forest structure and species composition, and transitory impacts on litter biomass, soil temperature, soil moisture, soil nutrients, SR, and Q_{10}. Generally, changes caused by fire were not significantly different across the chronology; instead, fire effects were only visible within the first year after burning, and were most evident by comparing the paired sites. Fire effects changed by season so that spring SR at the freshly burned site was 18% higher than the paired site, summer SR was 36% lower, and fall SR recovered to unburned rates. Relationships between SR and its predictors changed slightly after burning, but soil temperature remained the dominant predictor across all treatments and seasons. Therefore, the effects of a single fire on successional woodland SR were seen to be weak and short-lived.
Acknowledgements

First, I must express my deepest gratitude for the unconditional love provided to me by family (Ma, Pa, Drewbert, Zach, Sabrina, Pepper, and Lucy). Without them, I surely would not have succeeded.

Additionally, my advisor, Jiquan Chen, and my committee, Hans Gottgens and Asko Noormets made this work possible with their continual support.

The LEES lab (Amy, Rachel, Nan, Ranjeet, Burkhard, Soung, Qinglin, Ili, Jacob), other UT students (Todd, Matt, Josh, Kerry, Ryan), and my auld and dear friends (Jason, Heather, Amy, Luke, Tosha, Monica, Kate, Johnny, Nick, Rob, Damian, Mac, Peggy, and Mutz) encouraged me when I complained, and made this project fun beyond the caffeine.

Toledo Metroparks staff (Tim Gallaher, Penny Hughes, and John Jaeger) do tremendous work to make the Oak Openings beautiful, and found time to help incorporate my research into their management plans.

Finally, my battles with statistics were made less bloody with the patience of many smart people (Ann Krause, Daryl Moorhead, Jim Harrell, and Chris Mayer).
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1.0 Introduction

Fire suppression has been the dominant fire management strategy of the last century in U.S. forests (Mouillot and Field 2005) which, along with land conversion, has reduced 11 million hectares of Midwestern oak savanna to just 0.02% of its historical coverage (Nuzzo 1986). In recent decades, management activities have changed, and fire has been reintroduced into many former savannas that had since become closed canopy woodlands (USDA 1995). In contrast to wildfires ignited by natural forces (i.e. lightning), prescribed fires are deliberately ignited in order to meet management goals. The land management practice of prescribed burning is defined as “the controlled application of fire to fuel buildups, in either their natural or modified state, in specified environmental conditions that allow the fire to be confined to a predetermined area and, at the same time, allow it to produce the fireline intensity and rate of spread required to attain the planned management objectives” (DeBano et al. 1998). The goals of prescribed fire management are generally to restore diversity, structure, and ecosystem functioning (Ruiz-Jaen and Aide 2005). In successional oak woodland, these goals are achieved with prescribed fires designed to burn only surface fuels without entering the canopy; consequently, fire intensities are low to moderate, and temperatures are relatively cool (DeBano et al. 1998). Despite the common usage of prescribed burning as a management tool, the responses of successional woodlands to these cool fires are still poorly understood.
Prescribed fire has been found to change tree species composition in oak savanna by favoring fire adapted Quercus species over such early successional species as Acer rubra and Prunus serotina (Boerner et al. 1988; Tester 1989; Peterson and Reich 2001), but results are not consistent, and Franklin et al. (2003) found no change in sapling species diversity after a prescribed fire. Fire is also known to reduce tree density by killing saplings (Reich et al. 1990; Peterson and Reich 2001; Franklin et al. 2003; Hutchinson et al. 2005) or changing germination patterns (Huddle and Pallardy 1999; Glasgow and Matlack 2007), but large overstory trees are generally not impacted by prescribed burns (Reich 1990; Elliot et al. 1999; Franklin et al. 2003; Abella et al. 2004). In former oak savannas where non-oak species have reached large enough size classes to become fire tolerant, the effects of prescribed fire on woodland diversity and structure are contentious. Some scientists suggest that, over the long-term, periodic fires and gap dynamics may be able to return oaks to dominance without further thinning (Hutchinson et al. 2005). Other researchers suggest that in successional woodlands, prescribed fires are not sufficient for sustainable oak forest management without additional management (Franklin et al. 2003). Currently, it is still uncertain whether low intensity prescribed fires will be adequate to restore successional oak woodland species composition and structure to previous oak savanna conditions.

Soil properties are important metrics for determining the effect of fire on forests; however, belowground responses to prescribed fire are not comprehensively understood (Knapp et al. 1998; Neary et al. 1999; Hubbard et al. 2004). Typically, post-fire soil temperatures increase after the litter layer is burned and the soil surface is blackened, while moisture levels and water retention decrease after a fire (Knapp 1984; Knapp and
Seastedt 1986; Neary et al., 1999; Bremer and Ham 1999). The availability of nitrogen often increases immediately after a fire (Dijkstra 2006; Wan et al. 2001), but with repeated burning over a longer scale, total N decreases (Knapp et al. 1988; Johnson and Curtis 2001; Reich et al. 2001; Boerner and Brinkman 2003; Dijkstra 2006). Other soil nutrients and cations volatize at higher temperatures than N, and are consequently slower to change with soil heating; however, elevated Ca, P, Mg, and K have been found after prescribed burning (Ahlgren and Ahlgren 1965; Shay et al. 2001; Knoepp et al. 2004; Franklin et al. 2003; Elliot et al. 2004). Even low intensity, cool fires lead to fine root mortality in upper soil layers (Overby et al. 2002), with a 17% decrease in fine roots still seen 2 years after prescribed fire in Ohio oak hickory (Dress and Boerner 2001). In general, cool prescribed fires do not significantly impact microbial biomass (Wuthrich et al. 2002; Michelsen et al. 2004), but acid phosphatase and β-glucosidase enzymes have been seen to decrease in Ohio oak hickory forests with repeated burning, suggesting that fires slow nutrient cycles and could thereby help return ecosystem functioning to oak savanna conditions (Boerner and Brinkman 2003). The process of ecosystem C cycling can be impacted by alterations of all or any of these soil properties, making C cycling a relevant process to study when evaluating the impact of prescribed fire on ecosystem functioning.

In its simplest form, C cycling is the process by which C is stored in plant biomass and soils, via photosynthesis, until it is released back into the atmosphere through respiration. Soil respiration (SR) is widely studied as a major component of C cycling, and represents about 70% of ecosystem respiration in temperate forests (Goulden et al. 1996; Law et al. 1999; Janssens et al. 2001). The release of CO2 from soil through
SR is divided into two parts: autotrophic and heterotrophic respiration. The only source of autotrophic SR is live roots, while heterotrophic respiration originates from microbial decomposition of both aboveground litter and belowground litter. Two similar studies, one in Massachusetts hardwoods by Bowden et al. (1993) and the other in Oregon conifers by Sulzman et al. (2005), estimated the components of total SR. The two studies found that the SR components of live roots, aboveground litter, and belowground litter contributed to total SR in ratios of 33:37:30 and 23:19:58 in OR and MA, respectively. Of aboveground litter, new litter inputs represented 12% of annual SR, which was 31% of aboveground litter respiration (Bowden et al. 1993). These proportions provide a range for the degree to which SR could be reduced, simply from the consumption of all (19-37%) or part (12%) of aboveground litter through prescribed fire.

Though litter is consumed to some extent in all forest fires, SR has been seen to increase, decrease, or be unchanged after prescribed fires (Knapp et al. 1998; Wuthrich et al. 2002; Hubbard et al. 2004) because of a suite of predictors and mechanisms governs SR. After fire, decreased C availability reducing aboveground heterotrophic SR might be offset by the simultaneous elevation of soil temperature and nitrogen increasing belowground heterotrophic SR and/or autotrophic SR, potentially leaving total SR unchanged despite alterations in component sources. In order to incorporate the many biotic and abiotic predictors of SR that have been identified, mathematical models are used to predict SR. SR model fit and predictors have been shown to change after burning, suggesting changes in SR sources because of fire. Ma et al. (2004) found lowered predictive ability of SR after burning and a shift in the best predictors of SR after burning, with soil temperature and litter depth significant before burning ($R^2=0.62$) and soil
moisture the only significant factor after burning ($R^2 = 0.48$). Though potentially powerful, these types of modeling results must be interpreted with caution because the specific mechanisms governing SR are not well understood, and therefore could not be incorporated into broad, correlative models (Davidson et al. 2006). Nevertheless, observing changes in total SR, SR model predictors, or SR model fit after prescribed fire would suggest alterations in ecosystem processes from burning.

Some studies have already examined the impact of burning on forest soil properties and processes. Most studies occurring in woodlands have described high intensity, stand replacing fires, or they have occurred in boreal forests where SR can drastically increase because large stores of boreal soil C are very sensitive to burning and temperature increase (Burke et al. 1997; Bergner et al. 2004; Czimczik 2006). Temperate forest studies focusing on fire adapted forests have largely focused on pine forests (Ahlgren and Ahlgren 1965; Sparks et al. 2002; Litton et al.. 2003; Tefkiolu 2006), not recovering oak savannas where fire impacts are likely to differ from higher density, coniferous stands. Iverson and Hutchinson (2002) looked at how prescribed fire changed soil temperature and moisture in Ohio oak-hickory forests, but did not examine other soil properties or processes. One recent study occurring in southeastern Ohio oak forest found no changes in soil temperature, soil moisture, or SRR after prescribed burning, though these parameters were found to be very similar at treatments with leaf litter removed and low intensity burn treatments (McCarthy and Brown 2006).

The current study was designed to determine how frequent, low-intensity prescribed fire influences SR and its predictors in a temperate oak woodland. A chronosequence approach was used so that recovery time of SR predictors could be
estimated as 0, 1, 3, or 5 years after prescribed burning. I expected to observe the following:

• **H1**: Fire will impact biotic variables through combustion; therefore, burned treatments will have lower biomass, a higher percentage of oaks, and lower litter biomass than unburned treatments.

• **H2**: Fire will impact biophysical variables both through litter removal, which will increase soil temperature ($T_5$) and lower soil moisture (GM), and through soil heating, which will be minimal so soil nutrients and cations will be unchanged after burning.

• **H3**: Soil respiration rates (SRR) will be higher in unburned treatments and recovered treatments (>1yr) than in recently burned sites (0yr) because the impacts of reduced organic matter and decreased GM will outweigh the impact of increased $T_5$.

• **H4**: After leaf fall, C will again be available; therefore, no significant difference in SRR will be observed between controls and treatments burned more than one year ago.

• **H5**: The relationships between SRR and its predictors, including the temperature sensitivity of SRR ($Q_{10}$), will not change because of burning treatment.
2.0 Methods

2.1 Study Area and Field Methods

The study was conducted in Oak Openings Metropark (41°33’17”N, 8°50’36”W), which is a 1,500 ha preserve within the greater 47,600 ha Oak Openings region of northwest Ohio and southeastern Michigan (Figure 1). The sand defining the Oak Openings region was deposited by a series of glacial lakeshores. At the time of Euro-American settlement, the regional vegetation of the Oak Openings was a matrix of 43% oak savanna, 27% wet prairie, 23% oak woodland, 7% oak barrens, and <1% floodplain forest (Brewer and Vankat 2004). According to Brewer and Vankat (2004) maps, the majority of the ~150 ha study area was historically oak savanna (>43 trees ha⁻¹). Modern tree densities are sufficiently high for all sites within the study area to now be classified as oak woodland (Table 1). The contemporary forest remains dominated by oak species (Quercus rubra, Q. velutina and Q. alba) and has an understory of red maple (Acer rubra), black cherry (Prunus serotina), and sassafras (Sassafras albidum) (Figure 2). Topography is flat with elevations ranging from 200-205 m. Soils are mixed, mesic, Spodic Udipsamments. The soils are udic because a perched (~2 m) water table keeps soils moist even in periods of little precipitation. Approximately 82% of total (0-20 cm) soil carbon (28.1 g C kg⁻¹) and soil
Figure 1: Locations of field measurements in the Oak Openings Metropark, Ohio. (A) Oak Openings Region boundary (47,600 ha) in Northwest Ohio. (B) Oak Openings Metropark boundary (1,500 ha) showing the study area as a square inset (~150 ha). (C) Site layout across the study area. The 16 sampling sites included four replicates of unburned (U), and three replicates of burned, which are shown by the number of years since the last application of prescribed fire (0, 1, 3, 5). A photograph characteristic of each treatment is also presented.

Nitrogen (1.6 g N kg⁻¹) is located in the top 10 cm (DeForest et al. 2006).

The fire regime of the Oak Openings region was historically characterized by regular and low-intensity fires; however, the fire regime of the last century has followed broader trends across the U.S., revealing a pattern of fire suppression and the consequential conversion of most Oak Openings’ oak savanna to oak woodland (Brewer and Vankat 2004). Two age classes of trees were distinguished within the study area. The majority of trees was 40-50 years old and represented regrowth during fire suppression, while the older group of trees was ~80 year old and predated fire suppression. Current management practices are again establishing a regular fire regime, and prescribed burns take place biannually at sites across the Metropark. These burning units were identified with the Metropark’s staff, and a chronosequence of treatments based on the length of time since a site was burned was established across the landscape. Treatments were 0yr, 1yr, 3yr, 5yr, and unburned. Each burned treatment was replicated with 3 sites, and the unburned treatment was replicated with 4 sites, totaling 16 sites across the landscape. Each site was 154 m², within which were 6 PVC collars (10 cm
wide x 5 cm high) arranged evenly on the circumference of a 10 m diameter circle, totaling 96 collars.

The soil respiration rate (SRR) was measured at each collar with a LI-6400 (Licor, Lincoln, NE.) portable infrared gas analyzer with an attached soil respiration chamber (6400-09). Measurements were taken from 19 March 2005 through 31 January 2006. Measurement seasons were divided into spring, summer, and fall based on Quercus phenological phases: spring includes dormancy (DOY 78-102) and pre-growth (DOY 103-150), summer is the growing season (DOY 151-290), and fall includes pre-dormancy (DOY 291-314) and dormancy (DOY 315-31). (For a more detailed description of phenological divisions see DeForest et al. 2006). During summer, SRR, soil temperature, and soil moisture were recorded at all of the 16 sites every week. In spring and fall, the weekly measurements were only made at one of the three sites in a treatment, so that 5 of the 16 total sites were measured per week. Adjustments to the measuring scheme were made because of diminished daylight hours and frequent adverse weather conditions. SRR was not measured when it was raining or snowing, or when collars were filled with more than 2.5 cm of snow to minimize the effects of these extreme events on measured SRR. Freshly fallen leaf litter was allowed to stay where it landed, whether inside or outside of a collar.

Soil temperature at 5 cm (T₅) and 10 cm (T₁₀) was measured with a Taylor Switchable Digital Pocket Thermometer (Oak Brook, IL.) within 30 cm of the PVC collar. Gravimetric soil moisture (GM) was measured at each burned site by taking three soil samples to a depth of 5 cm with a 5 cm diameter corer, compositing the samples, weighing the wet soil, and then weighing the soil again after it was oven dried at 65°C for
at least 24 hours. Gravimetric soil moisture was calculated as the water weight (difference between wet and dry weight) divided by the soil weight (dry weight). GM was not measured at the unburned treatment; instead, volumetric soil moisture was measured with a HydroSense water content probe (Decagon Devices, Inc., Pullman, WA.). An adequate conversion between GM and volumetric soil moisture was not successfully derived; hence, no soil moisture data were reported for the unburned treatment.

In the original experimental design, three enclosures made of aluminum sheet metal were used to exclude prescribed fire from site sized areas within the approximately 15 ha 0yr burning unit. Through fire exclusion, freshly burned sites would be instantly paired with almost identical neighboring sites, thus controlling for landscape variability and isolating the influence of fire. Prescribed fire was applied to the swath of land containing the 0yr sites on the afternoon of 4 April 2005; pre-burn data (DOY 78-94) represented sites last burned 3yr ago. Two of the three chambers failed to exclude fire; therefore, required replication was provided by adding alternative sites burned 3 years ago to the study. The single functioning exclusion chamber was the most northern of the 3yr sites (Figure 1) and is henceforth labeled 3yr forest, while the two alternative sites are labeled 3yr prairie. For most analyses 3yr forest and 3yr prairie are discussed separately, firstly because a paired comparison can still be made between 0yr and 3yr forest, and secondly because of large site differences in $T_s$, GM, and SRR that, if combined, lower model fit and increase error terms.

In order to assess the impact of fire on vegetation, tree species composition and diameter at breast height (DBH) were measured at each of the 16 sites in December 2005.
Quercus rubra and Q. velutina were grouped together because hybridization has made the two species difficult to accurately distinguish. Site species composition, tree densities, biomass, and basal area (BA) were calculated from live trees with DBH > 6 cm. Biomass was estimated using species specific allometric equations (Ter-Mikaelian and Korzukhin 1997). Fisheye photographs were also taken in early September in order to estimate leaf area index (LAI). At each site, five photographs were taken: one in the site’s center, then one 7 m north, east, south, and west of center. Photographs were analyzed with Gap Light Analyzer V2.0 (Simon Fraser University, B.C. and Institute of Ecosystem Studies, N.Y.), through which LAI were determined for each photograph.

Crucial both as an indicator of available C and as a determinant of T5 and GM, leaf litter biomass (litter) was estimated for each site. Litter was randomly sampled with a 0.5 m² PVC square by collecting all organic matter above the mineral soil that rested within the square. Shears were used to cut around the edges of the square to most accurately collect materials incompletely located within the square. Samples were oven dried for 24 hours, at 65°C then woody material was removed and the sample weighed.

Four samples of litter were collected near each SR site once a season. Fall samples were collected after the onset of dormancy (i.e. after 95% of tree leaves had already fallen). Litter was collected at 0yr sites twice in spring; the first sampling was taken before application of the 4 April 2007 fire (pre-burn), and the second sampling occurred the day after the fire.

Mineral soil was sampled in spring with a 2.5 cm diameter soil corer. Ten samples 0-5 cm were taken at each site and composited. Soil was collected at 0yr sites twice; the first sampling was taken before application of the 4 April 2007 fire (pre-burn),
and the second sampling occurred the day after the fire. Soil samples were oven dried at 65°C for at least 24 hours and thoroughly ground before further analysis. Soils were analyzed with the CHNS/O Analyzer 2400 Series II (Perkin Elmer, MA.) for total soil carbon and nitrogen. Soil C:N ratios were calculated by site and then averaged by treatment. Soils were also analyzed for cation concentrations of calcium, potassium, magnesium, phosphorus, lead, and sulfur using an inductively coupled plasma optical emission spectroscope (ICP-OES; Thermo Fischer Scientific, U.S.A.). Soil solutions were prepared for ICP analysis by extracting cations with KCl, and titrating with NaOH and HCl.

2.2 Statistical Analyses

Means, standard deviations, and standard errors were calculated by treatment for tree density, BA, biomass, LAI, soil nutrients (C, N, C:N), and soil cations (Ca, K, Mg, P, S). Means, standard deviations, and standard errors were calculated by treatment and season for leaf litter, T_5, T_10, GM, and SRR. SRR was transformed using natural logarithm to better meet the assumption of normality. All analyses were conducted using SAS software (V9.1, SAS Institute Inc., Cary, N.C.) and alpha of 0.05 to determine statistical significance.

Tree density, BA, biomass, and LAI at all burned treatments (0yr, 1yr, 3yr forest, 3yr prairie, 5yr) were averaged and compared to the unburned treatment using Student’s t-test. Analysis of variance (ANOVA) was conducted with general linear model procedures (GLM) to evaluate the effect of fire treatment on litter, T_5, GM, and lnSRR.
over the entire sampling period and during each of the three seasons. GLM ANOVA was also used to evaluate the effect of fire treatment on soil C, N, C:N ratio, and cations. Tukey’s honestly significant difference test was used to determine significant groupings for litter, soil C, N, C:N, and cations, which generated mean separation labels on figures. Mixed models including fire treatment, day of year (DOY), and fire interactions with DOY were used in repeated measures ANOVA by treatment for T₅, GM, and lnSRR [i.e. T₅=f(Fire DOY Fire*DOY)]. The repeated subject was fire treatment, which was nested within site. First order autoregressive covariance structure was chosen to minimize Akaike’s Information Criteria (AIC). The Kenward-Roger (KR) adjustment, which was strongly recommended for repeated measures mixed models by Littell et al. (2006), was also utilized in all repeated measures models. Repeated measures models of lnSRR also included GM as covariates for maximized AIC [lnSRR=f(Fire DOY Fire*DOY GM)]. An analysis of fire’s influences under reduced landscape variability conditions was achieved by comparing annual and seasonal T₅, GM, and SRR between the paired freshly burned site (0a) and its neighboring site (3yr forest) with an un-nested version of the same repeated measures models used to compare among treatments. Student’s t-test was also used to compare 0a and 3yr forest annual T₅, GM, and SRR means. Variation in fire’s effects on T₅, GM, C, N, C:N, litter, and SRR were examined within the 0yr treatment using GLM ANOVA models and Tukey test.

Relationships between the microclimatic factors of T₅ and GM and fire treatment, biomass, and leaf litter were tested using annual and seasonal GLM models. Data was averaged by season because of the relative lack of litter sampling dates compared to high frequency T₅ and GM sampling. Regressions were also examined without 0yr and 1yr
treatments because these treatments had significantly less litter biomass than other treatments, and consequently acted as outliers. Regression without 0yr and 1yr is only presented for GM because the impact of their removal on T5 models was trivial.

The importance of individual predictors to annual lnSRR models was evaluated with iterative GLM. Variables in models are: fire treatment, DOY, T5, GM, litter and biomass. Soil C:N and DOY interactions with fire were also tested and found to be insignificant. Unburned sites were excluded from all GLM models because of lacking GM data.

Stepwise regression models predicting annual and seasonal lnSRR were run for all sites combined and by treatment. Variables entered the model and were left in the model only if they met a 0.15 significance level. Stepwise regression was performed with and without soil moisture. Unburned sites were excluded from annual stepwise models with GM because of lacking data at this treatment. Variables available for input into the models were: fire treatment, season, T5, GM, litter, biomass, and C:N. Season was only included in annual models. Site and BA were excluded from stepwise regression models based on collinearity test results.

Because T5 is typically a crucial predictor of SRR (Lloyd and Taylor 1994), the relationship between T5 and SRR was evaluated with GLM by treatment. The sensitivity of SRR to 10°C changes in T5 was determined using the exponential Q10 model:

$$SRR = R_{ref} * e((\ln Q_{10})/10) * T5$$  \hspace{1cm} (1)

where SRR is the measured soil respiration rate, $R_{ref}$ is base soil respiration normalized to 0°C, $Q_{10}$ is the temperature sensitivity of SRR, and $T5$ is measured soil temperature at 5 cm depth. Both $R_{ref}$ and $Q_{10}$ were calculated with non-linear least squares regression.
Models were computed annually and by season for all treatments combined, and for each treatment. SRR data were excluded from two sampling dates (DOY 144 and 353) because recent rain pulse events made SRR exceptionally high (Yuste et al. 2005). Including these two dates in models either made Q_{10} incalculable, or elevated Q_{10} to unrealistic levels (i.e. Q_{10} > 10).
3.0 Results

3.1 Fire Effects on Vegetation and Leaf Litter Biomass

3.1b Effects on Vegetation

Vegetation, as measured by stand density, biomass, BA, and LAI, were all influenced over the long-term by fire treatment and forest management (Table 1). When averaged together, burned treatments had lower tree density, biomass, BA, and LAI than the unburned treatment. Separated by treatment, 1yr, 3yr forest, and 3yr prairie generally

Table 1: Mean density, biomass, basal area and leaf area index (LAI) by treatment. The n represents the number of sites included in treatment averages. Values in parenthesis show standard error of the mean. The burned category included data from all burned treatments (0yr, 1yr, 3yr forest, 3yr prairie, 5yr) and was compared to the unburned treatment with Student’s t-test. Superscript letters show differences between burned and unburned treatments.

<table>
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<tr>
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<th>n</th>
<th>Density (trees ha⁻¹)</th>
<th>Biomass (Mg C ha⁻¹)</th>
<th>Basal Area (m² ha⁻¹)</th>
<th>LAI</th>
</tr>
</thead>
<tbody>
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<td>0yr</td>
<td>3</td>
<td>563 (87)</td>
<td>92 (21)</td>
<td>12.5 (2.2)</td>
<td>2.14 (0.04)</td>
</tr>
<tr>
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<td>108 (22)</td>
<td>37 (9)</td>
<td>5.2 (1.0)</td>
<td>1.93 (0.04)</td>
</tr>
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<td>325 ( - )</td>
<td>37 ( - )</td>
<td>5.1 ( - )</td>
<td>2.37 (0.04)</td>
</tr>
<tr>
<td>3yr prairie</td>
<td>2</td>
<td>260 (65)</td>
<td>45 (37)</td>
<td>6.3 (4.3)</td>
<td>1.35 (0.03)</td>
</tr>
<tr>
<td>5yr</td>
<td>3</td>
<td>606 (152)</td>
<td>65 (11)</td>
<td>10.0 (1.9)</td>
<td>2.39 (0.04)</td>
</tr>
<tr>
<td>Burned</td>
<td>12</td>
<td>390 (73)</td>
<td>59 (10)</td>
<td>8.4 (1.2)</td>
<td>2.03 (0.06)</td>
</tr>
<tr>
<td>Unburned</td>
<td>4</td>
<td>633 (55)</td>
<td>139 (17)</td>
<td>25.5 (2.3)</td>
<td>2.48 (0.08)</td>
</tr>
</tbody>
</table>
Figure 2: Species composition for trees based on stem density (DBH > 5cm) by treatment: (A) 0yr (B) 1yr (C) 3yr forest (D) 3yr prairie (E) 5yr (F) unburned. Values surrounding the pies show number of trees counted by species and treatment.

had low density, biomass, BA and LAI, while 0yr and 5yr had middle range values. All treatments were dominated by oak species (>50%) with mixed red maple, sassafras, and black cherry understories, though all five tree species were only found together in 0yr and unburned treatments (Figure 2). Of all trees, 73% are *Quercus* species, which cumulatively accounted for 93% of tree biomass.

Red/black oak alone accounted for 84% of biomass, though they represented only 53% of the total number of trees. The dominance of red/black oak is less pronounced at
the unburned treatment where it represented 31% of trees, than at burned treatments
where it represented 62% of trees. Finally, the unburned treatment had a higher
percentage of non-oak species (36%) than the burned treatment (13%), which further
suggested that fire history had changed species composition towards oak dominance.

DBH distribution by size class was skewed toward smaller trees at all treatments
except 1yr, where every tree was >30 cm DBH. Trees above 50 cm DBH were not found
at 3yr forest, 3yr prairie, or 5yr treatments. The five largest trees (DBH >45 cm) were
found at 0yr and 1yr treatments. The skewing of DBH by size class changed by species.
Only red/black oak had a normal DBH size class distribution, with 64% of trees 20-40 cm
DBH, and 5% of trees in the largest size class DBH>50 cm. White oak had a slightly
skewed size class distribution toward smaller DBH classes (52% of trees were 10-20 cm),
and had few trees in higher DBH classes (11% >30 cm). Red maple and black cherry
size class distributions were strongly skewed towards low DBH classes with 75% and
93% of trees less than 20 cm, respectively. Sassafras size class distributions were also
slightly skewed toward low DBH classes, but two of the seven trees were large, with
DBH 40-50 cm.

3.1b Effects on Leaf Litter Biomass
The combustion of litter biomass is an immediate and obvious impact from
prescribed burning. Across all seasons, treatments with longer time since burning had
higher leaf litter biomass than more recently burned treatments (Figure 3). Fire treatment
explained variation in leaf litter biomass best in spring (p< 0.0001, R²= 0.66), which was
immediately after the fire that reduced litter at the 0yr treatment by 57%. Significant
treatment differences in litter biomass persisted through summer ($p<0.0001$, $R^2=0.44$), and after leaf fall to a lesser extent ($p=0.0040$, $R^2=0.29$) when 0yr had 25% less litter biomass than the unburned treatment. Fire treatment explained less variation on an annual basis ($p<0.0001$, $R^2=0.33$) than when analyzed within a single season.

**Figure 3**: Leaf litter biomass by treatment measured in spring, before leaf fall, and immediately after leaf fall. An immediate burn effect on litter was seen by comparing pre-burn litter with 0yr. Longer-term litter reduction can be seen across treatments on all three sampling dates, with significantly more leaf litter at burned treatments than unburned. Error bars represent the standard error of the mean and letters distinguish significantly different means across treatments and within a season.
3.2 Fire Effects on Biophysical Variables

3.2a Effects on Soil Temperature (T5)

Mean T5 was not significantly impacted by fire treatment (p=0.9961) when averaged to an annual time scale (Table 2). Only in summer, did mean T5 vary by treatment (p= 0.0004, R²= 0.86) so that T5 at the 0yr treatment averaged 2.5°C higher than at the unburned treatment (Figure 4). When averaged only by DOY, spring and summer T5 were found to be significantly lower at the unburned treatment than all treatments except 3yr forest (Table 3). After leaf fall T5 was equal at all treatments (Table 3). All treatments displayed the same unimodal seasonal pattern and annual T5 ranged from approximately 0 - 25°C (Figure 5).

Table 2: Mean annual soil respiration rate (SRR), soil temperature at 5cm (T5) and 10cm (T10), and gravimetric soil moisture (GM). The n represents the total number of sampling points taken at a treatment. Values in parenthesis represent standard error of the mean. Letter superscripts show differences in treatment means obtained with repeated measures.

<table>
<thead>
<tr>
<th></th>
<th>n</th>
<th>SRR (umol CO₂ m⁻² s⁻¹)</th>
<th>T5 (°C)</th>
<th>T10 (°C)</th>
<th>GM (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0yr</td>
<td>563</td>
<td>3.86 (0.11)cd</td>
<td>14.6 (0.2)ab</td>
<td>13.9 (0.2)ab</td>
<td>0.20 (0.00)abc</td>
</tr>
<tr>
<td>1yr</td>
<td>443</td>
<td>5.32 (0.20)ab</td>
<td>15.9 (0.3)a</td>
<td>15.2 (0.3)a</td>
<td>0.25 (0.01)a</td>
</tr>
<tr>
<td>3yr forest</td>
<td>189</td>
<td>4.85 (0.30)bc</td>
<td>13.9 (0.4)b</td>
<td>13.5 (0.4)b</td>
<td>0.21 (0.01)b</td>
</tr>
<tr>
<td>3yr prairie</td>
<td>273</td>
<td>3.90 (0.16)d</td>
<td>15.4 (0.4)a</td>
<td>14.7 (0.3)ab</td>
<td>0.17 (0.01)c</td>
</tr>
<tr>
<td>5yr</td>
<td>446</td>
<td>5.91 (0.22)a</td>
<td>15.5 (0.3)a</td>
<td>15.0 (0.3)a</td>
<td>0.24 (0.01)a</td>
</tr>
<tr>
<td>Unburned</td>
<td>547</td>
<td>4.59 (0.17)bd</td>
<td>13.2 (0.2)b</td>
<td>13.2 (0.3)c</td>
<td>-</td>
</tr>
</tbody>
</table>
Figure 4: Mean temperature at 5cm ($T_5$) by treatment (0yr, 1yr, 3yr forest, 3yr prairie, 5yr, unburned) and season (spring, summer, fall). Only in summer, did mean $T_5$ vary significantly by treatment ($p=0.0004$, $R^2=0.86$). Error bars represent the standard error of the mean.
Table 3: Pairwise comparisons based on Tukey adjustment to repeated measures ANOVA models by treatment (unburned, 0yr, 1yr, 3yr forest, 3yr prairie, 5yr) and season (annual, spring, summer, fall). 3yr prairie and 3yr forest were abbreviated respectively as 3yr P and 3yr F. The repeated measures comparison between the paired sites 0a and 3yr forest was also included. Analyses of each variable occurred independently. Variables were soil temperature at 5cm ($T_5$), gravimetric moisture (GM), and natural log of soil respiration rate (lnSRR). When available, models of lnSRR included GM as a covariate to minimize AIC. Shaded areas represent missing data. Asterisks denote a statistically significant difference between treatments.

<table>
<thead>
<tr>
<th></th>
<th>Annual</th>
<th>Spring</th>
<th>Summer</th>
<th>Fall</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$T_5$</td>
<td>GM</td>
<td>lnSRR</td>
<td></td>
</tr>
<tr>
<td>Unburned - 0yr</td>
<td></td>
<td></td>
<td>*</td>
<td></td>
</tr>
<tr>
<td>Unburned - 1yr</td>
<td>*</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Unburned - 3yr F</td>
<td>*</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Unburned - 3yr P</td>
<td>*</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Unburned - 5yr</td>
<td>*</td>
<td></td>
<td>*</td>
<td></td>
</tr>
<tr>
<td>0yr - 1yr</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0yr - 3yr F</td>
<td></td>
<td></td>
<td>* * *</td>
<td>*</td>
</tr>
<tr>
<td>0a - 3yr F (paired)</td>
<td></td>
<td></td>
<td>* * *</td>
<td>* *</td>
</tr>
<tr>
<td>0yr - 3yr P</td>
<td></td>
<td></td>
<td>*</td>
<td></td>
</tr>
<tr>
<td>0yr - 5yr</td>
<td></td>
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</tr>
<tr>
<td>1yr - 3yr F</td>
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<td>* *</td>
</tr>
<tr>
<td>1yr - 5yr</td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>3yr F - 3yr P</td>
<td>*</td>
<td></td>
<td>*</td>
<td></td>
</tr>
<tr>
<td>3yr F - 5yr</td>
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<td></td>
</tr>
<tr>
<td>3yr P – 5yr</td>
<td>*</td>
<td></td>
<td>*</td>
<td></td>
</tr>
</tbody>
</table>
Figure 5: Mean temperature at 5cm (T5) by treatment (A) 0yr, (B) 1yr, (C) 3yr forest, (D) 3yr prairie, (E) 5yr, (F) unburned by day of year. Error bars represent standard deviation; where error bars are not visible, standard deviation is smaller than the dot.

3.2b Effects on Soil Moisture (GM)

Annual mean GM (Table 2) varied only slightly by fire treatment (p< 0.0001, R²= 0.07). Fire treatment was also a significant, but weak, predictor of seasonal GM: spring (p< 0.0001, R² = 0.29), summer (p< 0.0001, R² = 0.12), and fall (p< 0.0001, R² = 0.10) (Figure 6). Fire’s effects were confounded by landscape variability so that location east of the river (1yr and 5yr) or west of the river (0yr, 3yr forest, and 3yr prairie), acted
similarly to treatment as a weak predictor of annual GM (p< 0.0001, R²= 0.06). Annual GM was at a minimum of 17% at the westerly 3yr prairie, while maximum GM of 25% was at the easterly 1yr treatment (Table 2). Further suggesting the importance of location to GM, the two treatments with highest overall GM (1yr and 5yr) were both eastern in location. Treatment differences and seasonal means also corresponded more to location than to a fire chronology (Table 3; Figure 6). Regardless of location or treatment, all treatments displayed the same seasonal pattern of dry summers and wet springs (Figure 7).

Figure 6: Mean gravimetric moisture 0-5cm by treatment (0yr, 1yr, 3yr forest, 3yr prairie, 5yr) and season (spring, summer, fall). Fire treatment was weakly related to seasonal GM: spring (p< 0.0001, R²= 0.29), summer (p< 0.0001, R²= 0.12), and fall (p< 0.0001, R²= 0.10). The 3yr prairie was consistently the driest treatment throughout all seasons. Error bars represent the standard error of the mean.
3.2c Effect on Soil Cations and Nutrients

Frequent, low-intensity fires did not significantly change soil cation concentrations (calcium, potassium, magnesium, phosphorus, sulfur) either immediately post-burn or across the fire chronosequence. A few pairwise differences were found, especially between 3yr prairie and 5yr treatments, but differences were unlikely to be biologically significant or directly related to burning chronology (Table 4). Western treatments (0yr, 3yr forest) had relatively high N, P, K, and Mg, but lower Ca and S,
Table 4: Cation concentrations in parts per million for major soil elements: calcium, potassium, magnesium, phosphorus, and sulfur. Values in parenthesis represent standard error of the mean. Letters distinguish significantly different means across treatments for a given element. Pre-burn refers to conditions before burning at 0yr. 3yr forest and 3yr prairie are abbreviated as 3yr F and 3yr P, respectively.

<table>
<thead>
<tr>
<th></th>
<th>Ca (ppm)</th>
<th>K (ppm)</th>
<th>Mg (ppm)</th>
<th>P (ppm)</th>
<th>S (ppm)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Pre-burn</strong></td>
<td>110.18 (23.21)$^{ab}$</td>
<td>8.27 (0.49)$^{b}$</td>
<td>6.35 (0.15)$^{b}$</td>
<td>0.25 (0.05)$^{ab}$</td>
<td>31.41 (9.21)$^{a}$</td>
</tr>
<tr>
<td><strong>0yr</strong></td>
<td>106.67 (20.31)$^{ab}$</td>
<td>9.21 (0.35)$^{b}$</td>
<td>7.65 (0.95)$^{c}$</td>
<td>0.34 (0.11)$^{ab}$</td>
<td>16.20 (1.27)$^{a}$</td>
</tr>
<tr>
<td><strong>1yr</strong></td>
<td>150.91 (12.55)$^{ab}$</td>
<td>5.65 (0.07)$^{a}$</td>
<td>5.87 (0.25)$^{abc}$</td>
<td>0.14 (0.02)$^{ab}$</td>
<td>20.85 (0.75)$^{a}$</td>
</tr>
<tr>
<td><strong>3yr F</strong></td>
<td>97.08 (0.42)$^{ab}$</td>
<td>5.60 (0.02)$^{a}$</td>
<td>6.43 (0.04)$^{bc}$</td>
<td>0.20 (0.01)$^{ab}$</td>
<td>16.32 (0.04)$^{a}$</td>
</tr>
<tr>
<td><strong>3yr P</strong></td>
<td>172.48 (32.95)$^{b}$</td>
<td>4.48 (0.49)$^{a}$</td>
<td>3.60 (0.62)$^{a}$</td>
<td>0.08 (0.01)$^{a}$</td>
<td>18.28 (0.10)$^{a}$</td>
</tr>
<tr>
<td><strong>5yr</strong></td>
<td>71.19 (13.54)$^{a}$</td>
<td>7.55 (0.49)$^{b}$</td>
<td>5.58 (0.22)$^{abc}$</td>
<td>0.12 (0.03)$^{ab}$</td>
<td>14.55 (1.66)$^{a}$</td>
</tr>
<tr>
<td><strong>Unburned</strong></td>
<td>124.11 (7.14)$^{ab}$</td>
<td>4.94 (0.05)$^{a}$</td>
<td>4.89 (0.22)$^{ab}$</td>
<td>0.43 (0.06)$^{b}$</td>
<td>20.35 (0.67)$^{a}$</td>
</tr>
</tbody>
</table>

while eastern treatments (1yr, 3yr prairie) had relatively low N, P, K, and Mg, but higher Ca and S, which possibly suggested dynamics beyond those connected to recent fires.

Cool fires altered mean soil carbon and nitrogen content 0-5cm, which increased immediately after spring burning in 0yr by 31% and 28%, respectively (Figure 8). C:N did not change immediately after burning, but C:N was significantly lower at unburned treatments than all burned treatments except 3yr prairie. Differences in C:N ratios were not evident across the chronosequence.
Figure 8: Mean soil carbon content 0-5 cm (A), soil nitrogen content 0-5 cm (B), soil carbon to nitrogen ration 0-5 cm (C) for each treatment (pre-burn, 0yr, 1yr, 3yr, 5yr, unburned). Carbon and nitrogen increased immediately after burning, but their ratio did not change. Error bars represent the standard error of the mean and different letter distinguish significantly different means across treatments.

3.2d Variation in Soil Nutrients among Fresh Burn Sites (0yr)

Though mean C and N increased after burning, the site response within the 0yr treatment was not consistent (Figure 9). Unlike the increase in C and N seen at 0a and 0c,
Figure 9: Mean soil carbon content 0-5 cm (A), soil nitrogen content 0-5 cm (B), soil carbon to nitrogen ration 0-5 cm (C) comparing the three 0yr treatment replicates (0a 0b 0c) pre-burn and post-burn. At two of the sites, carbon and nitrogen increased immediately after fire, while at the third site carbon and nitrogen decreased. At none of the three sites did the carbon to nitrogen ration change significantly after fire. Error bars represent the standard error of the mean. Capital letters distinguish significantly different means between pre-burn and post-burn at one location, while lowercase letters compare locations at one time.
C and N significantly decreased at 0b, possibly because of varying fire intensity. C:N was unchanged at all three replicates after burning. Additional differences between the three replicates included higher overall biomass and SRR at 0b, and higher GM at 0a (Figure 10). Annual mean $T_5$ (not shown) and pre- and post-burn leaf litter did not vary between 0yr sites.

**Figure 10:** Soil respiration rate (A), biomass (B), gravimetric soil moisture (C), pre-burn leaf litter and post-burn (0yr) litter comparing the three replicates of the 0yr treatment (0a 0b 0c). Mean soil moisture is lower at 0b than 0a and 0c, while biomass and soil respiration are higher. Prefire and postfire leaf litter does not vary significantly between replicates. Error bars represent the standard error of the mean. Capital letters distinguish significantly different means between pre-burn and post-burn at one location, while lowercase letters compare locations at one time.
3.3 Relationships between Microclimate and Litter

3.3a Predicting Soil Temperature (T₅)

Including factors beyond fire treatment into predictive models of T₅ did not greatly improve predictive ability, but did make annual models statistically significant, when they previously were not. Mean site litter and fire treatment were found to be the best predictors of T₅ both annually (p= 0.0019, R²= 0.46) and by season: spring (NS), summer (p= 0.0063, R²= 0.88), and fall (NS). When fire treatment was removed from the model, average seasonal leaf litter was still negatively related to T₅ (p= 0.0204, R²= -0.33) across the entire sampling period. Similarly, the direct relationship between litter and T₅ was strongest in summer when temperatures peaked and burned sites were warmer than unburned sites (p= 0.0330, R²= -0.53; Figure 11A). Biomass followed a similar pattern with high values at the unburned treatment and low values at 1yr (Table 1), and might be expected to relate to litter and T₅ dynamics, but annual and seasonal regressions between biomass and T₅ were not significant.

3.3b Predicting Soil Moisture (GM)

The inclusion of factors beyond fire treatment into models did not greatly improve predictive ability of GM. Annual GM prediction based on treatment, biomass, and litter remained poor (p<0.0001, R²= 0.11). Significant model components, goodness of fit, and the amount of improvement generated with increasing model complexity changed with season. In spring, all three predictors of GM were significant (p<0.0001, R²=0.32), while in summer only biomass and treatment were significant (p<0.0001, R²=0.13), and in fall,
Figure 11: Regression between mean leaf litter and soil temperature at 5cm by site and season (A), leaf litter and mean gravimetric moisture by site and season (B), and mean leaf litter and soil respiration by site and season (C). Summer leaf litter and soil temperature are negatively related (p= 0.0330, R² = -0.53443) so that burned sites are warmer than unburned sites.
the season with the best fitting model, only treatment was significant (p<0.0001, R\(^2\)= 0.41). Only in fall, when R\(^2\) increased by 0.31, did the inclusion of factors beyond fire treatment lead to substantial improvement in model fit. Figure 11B shows the insignificant relationship between mean seasonal GM and litter. If 0yr and 1yr treatment outliers with low litter and high GM were excluded from regression models, the relationship between GM and its predictors increased in strength overall (p<0.0001, R\(^2\)= 0.13), in spring (p<0.0001, R\(^2\)= 0.51), and in summer (p<0.0001, R\(^2\)= 0.19), but not in fall (p<0.0001, R\(^2\)= 0.35) when predictive ability was already relatively good.

### 3.4 Fire Effects on Soil Respiration Rates

#### 3.4a Effects on Soil Respiration Rate (SRR)

Though fire treatment influenced litter, T\(_5\), and GM, fire treatment alone was only a very weak predictor of lnSRR both annually (p<0.0001, R\(^2\)= 0.03) and by season: spring (p<0.0001 R\(^2\)= 0.07), summer (p<0.0001, R\(^2\)= 0.09), and fall (p<0.0001, R\(^2\)= 0.08). Annual mean SRR (Table 2) was highest at the 5yr treatment (5.91 umol CO\(_2\) m\(^{-2}\) s\(^{-1}\)) and lowest at 0yr (3.86 umol CO\(_2\) m\(^{-2}\) s\(^{-1}\)). Annual SRR was not ordered by treatment chronology; for example, 0yr had lower SRR than 1yr, though 0yr SRR was equal to unburned, and unburned SRR was less than 5yr (Table 2).

Differences in treatment lnSRR were noticeable in spring, and more so in summer when plants were most active and T\(_5\) and GM varied most between treatments (Figure 12; Table 3). Immediately after burning (DOY 99-129), lnSRR at 0yr was slightly elevated, then during summer (DOY 180-234) 0yr lnSRR was reduced when GM dropped, T\(_5\) was
high, and SRR peaked overall (Figure 14; Table 3). Seasonal variation in SRR was highest in summer when SRR peaked, but at the 0yr treatment summer SRR variation was relatively small (SD= 2.66 umol CO₂ m⁻² s⁻¹) compared to unburned (SD=4.12 umol CO₂ m⁻² s⁻¹; Figure 13). In fall, variation in lnSRR was minimal, and only 3yr prairie had significantly lower than lnSRR than any other treatment (Table 3).

**Figure 12:** Mean soil respiration rate (SRR) by treatment (0yr, 1yr, 3yr forest, 3yr prairie, 5yr, unburned) and season. Across the chronology, fire treatment was only a very weak predictor of lnSRR by season: spring (p<0.0001 R² = 0.07), summer (p<0.0001, R² = 0.09), and fall (p<0.0001, R² = 0.08). When comparing only 0yr and unburned, spring SRR was higher at 0yr than unburned, while summer SRR was lower at 0yr than unburned. SRR at the 3yr prairie was consistently lower than all other treatments excluding 0yr, to which it behaved similarly.
Figure 13: Mean soil respiration rate (SRR) by treatment (A) 0yr, (B) 1yr, (C) 3yr forest, (D) 3yr prairie, (E) 5yr, (F) unburned and day of year (DOY). In summer, 0yr SRR is lower than the unburned treatment. Error bars represent standard deviation.
Figure 14: Mean soil respiration rate (SRR) by treatment (0yr, 1yr, 3yr forest, 3yr prairie, 5yr, unburned) and day of year (DOY). In summer (DOY 180-234), 0yr SRR was lower than the unburned treatment; however, shortly after spring prescribed fire application, SRR at 0yr was higher than all other sites (DOY 99-129). An arrow marks the date of prescribed burning.
Figure 15: Mean soil temperature at 5cm (T₅) (A), gravimetric soil moisture 0-5cm (GM) (B), and soil respiration rate (SRR) (C) by day of year (DOY) and between a paired freshly burned replicate (0a) and a neighboring site from which fire was excluded (3yr forest). An arrow marks the date of burning. Annual mean T₅ was 6% higher (NS) at 0a than at 3yr forest, GM was 23% higher (p<0.0001), while SRR was 25% lower (p=0.0004). Stars represent significantly different seasonal means between sites; analysis excluded pre-fire data. Error bars represent standard error of the mean.
A comparison of the three freshly burned 0yr sites with the single paired unburned site (3yr forest) was revealing. Between these treatments, annual T₅, GM, and lnSRR were not statistically impacted by fire, while in summer T₅ was higher at 0yr, GM was lower at 0yr, and lnSRR is still not different (Table 3). Narrowing the focus still more by comparing only the neighboring freshly burned 0yr site (0a) and 3yr forest limited within-treatment variation, and yielded different results than the broader comparison including all three 0yr sites. Annual mean SRR at 0a was 25% lower than at 3yr forest (p=0.0004), while GM was 23% higher (p<0.0001) and T₅ was 6% higher (NS); however, according to repeated measures ANOVA, annual trends were not statistically different over time (Figure 15; Table 3). Broken down by season, significant differences between 0a and 3a were found in spring T₅, GM, and lnSRR, and in summer lnSRR and T₅, while in fall no differences were found (Table 3). After burning, mean spring lnSRR was 18% higher at 0a (3.04 umol CO₂ m⁻² s⁻¹) compared to 3yr forest (2.48 umol CO₂ m⁻² s⁻¹), but by summer a reversal occurred and mean lnSRR was 36% lower at 0a (4.91 umol CO₂ m⁻² s⁻¹) than 3yr forest (7.72 umol CO₂ m⁻² s⁻¹). Thus, through this narrow comparison of 0a and 3yr forest, the influence of fire was related to increased T₅, increased GM, and increased and decreased SRR.

### 3.4b Predicting Soil Respiration Rate (SRR)

The mechanisms controlling SRR can be suggested by examining model components and model fit. Using only T₅ to predict annual lnSRR resulted in $R^2 = 0.70$ (Table 5). Adding fire treatment into the annual GLM increased predictive ability of lnSRR, but relatively little compared to the essential factor of T₅. C:N was insignificant
Table 5: General linear model results predicting the natural log of soil respiration rates (lnSRR) across the entire sampling period. Variables in models are: years since burning (fire), day of year (DOY), soil temperature at 5cm (T5), gravimetric moisture 0-5cm (GM), leaf litter biomass (litter), and tree biomass (biomass). Soil carbon to nitrogen ratio to 5cm (C:N), and DOY and fire interactions were also tested and found insignificant. Adding fire into the annual model increased predictive ability, but relatively little compared to the essential factors of T5 and GM. C:N was insignificant, and litter became insignificant when biomass was included in the model. All factors listed for each model were significant. The unburned treatment was excluded from all GLM models because of lacking GM data.

<table>
<thead>
<tr>
<th>General Linear Models</th>
<th>F</th>
<th>p</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>lnSRR f(T5)</td>
<td>4259</td>
<td>&lt; 0.0001</td>
<td>0.699</td>
</tr>
<tr>
<td>lnSRR f(T5 Fire)</td>
<td>952</td>
<td>&lt; 0.0001</td>
<td>0.723</td>
</tr>
<tr>
<td>lnSRR f(T5 Fire DOY)</td>
<td>796</td>
<td>&lt; 0.0001</td>
<td>0.724</td>
</tr>
<tr>
<td>lnSRR f(T5 Fire DOY GM)</td>
<td>672</td>
<td>&lt; 0.0001</td>
<td>0.742</td>
</tr>
<tr>
<td>lnSRR f(T5 DOY GM)</td>
<td>1413</td>
<td>&lt; 0.0001</td>
<td>0.720</td>
</tr>
<tr>
<td>lnSRR f(T5 Fire DOY GM Litter)</td>
<td>590</td>
<td>&lt; 0.0001</td>
<td>0.747</td>
</tr>
<tr>
<td>lnSRR f(T5 Fire DOY GM Biomass)</td>
<td>607</td>
<td>&lt; 0.0001</td>
<td>0.747</td>
</tr>
</tbody>
</table>

when added to models already incorporating T5 and GM. Litter and biomass functioned similarly in models, but litter became insignificant when the superior factor, biomass, was also included. Thus, the best model for predicting annual lnSRR consisted of five factors: T5, fire treatment, DOY, GM, and biomass, yielding $R^2 = 0.75$, which was only 0.05 higher than the $R^2$ generated by T5 alone.

Stepwise regression was used to evaluate how predictors of lnSRR changed by season and by treatment. Within all seasons and treatments, T5 was consistently the best predictor of lnSRR (Table 6; Figure 16). Fire treatment also explained a significant,
Table 6: Stepwise regression results overall and by treatment predicting the natural logarithm of soil respiration rates (lnSRR) across the entire sampling period (annual) and within each season. Variables available for modeling were: years since burning (fire), time of year (season), soil temperature at 5cm (T5), gravimetric moisture 0-5cm (GM), leaf litter biomass (litter), tree biomass (bio), and soil carbon to nitrogen ratio to 5cm (C:N). Partial R² values are listed for each significant variable, and cumulative model R² values are shown below the dotted lines. T5 was consistently the best predictor of lnSRR, and fire was significant overall and within each season. The unburned treatment was excluded from the overall model because of lacking GM data at this treatment.

<table>
<thead>
<tr>
<th>Season</th>
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<th>1yr</th>
<th>3yr</th>
<th>5yr</th>
<th>Unburned</th>
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<tr>
<td>Annual</td>
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<td>T5</td>
<td>0.7180</td>
<td>T5</td>
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<tr>
<td></td>
<td>Litter</td>
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<td>C:N</td>
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<td>Season</td>
<td>0.0118</td>
</tr>
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<td>GM</td>
<td>0.0158</td>
<td>Bio</td>
<td>0.0115</td>
</tr>
<tr>
<td></td>
<td>GM</td>
<td>0.0021</td>
<td>Bio</td>
<td>0.0033</td>
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</tr>
<tr>
<td></td>
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<td></td>
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<tr>
<td></td>
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<td></td>
<td></td>
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<td></td>
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<td>T5</td>
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<td></td>
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<td>GM</td>
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<td></td>
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<td>0.3810</td>
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<td>Summer</td>
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<tr>
<td></td>
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<td>Litter</td>
<td>0.0161</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>C:N</td>
<td>0.0129</td>
<td></td>
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<td></td>
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</tr>
<tr>
<td></td>
<td>Bio</td>
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<td></td>
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<td>0.2373</td>
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<td>Fall</td>
<td>T5</td>
<td>0.3676</td>
<td>T5</td>
<td>0.4895</td>
<td>T5</td>
<td>0.6920</td>
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<tr>
<td></td>
<td>Fire</td>
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<td>GM</td>
<td>0.0363</td>
<td>C:N</td>
<td>0.0192</td>
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<tr>
<td></td>
<td></td>
<td>0.3846</td>
<td>0.4895</td>
<td>0.7620</td>
<td>0.4165</td>
<td>0.2960</td>
</tr>
</tbody>
</table>
albeit small, amount of annual and seasonal variation. The best fitting annual model included all seven available variables and resulted in an $R^2$ of 0.74, which was actually a 0.01 lower fit than the best annual GLM model (Table 6). Seasonality highly influenced model fit and significant components. Predictive ability was lowest in summer when variation in lnSRR was highest, plants were active, $T_5$ was highest, and GM was lowest.

**Figure 16:** Mean soil temperature at 5cm ($T_5$) and mean soil respiration rate (SRR) calculated by treatment. Seasons are distinguished by shape: spring (hollow diamond), summer (square), fall (triangle). The relationship between $T_5$ and SRR was more variable during the growing season than in spring or fall.
In summer, GM was the second best predictor of lnSRR, which was supported by the positive relationship between summer GM and SRR (p<0.0001, $R^2 = 0.58$). However, removal of GM from models most impacted spring lnSRR prediction, despite the $R^2$ between GM and fire treatment being lowest at this time. Beyond $T_5$ and GM, other components appeared erratically in seasonal models. C:N was significant in summer predictive models with combined treatments, but was not significant in spring and fall, though the regression between spring mean site C:N and lnSRR represented the only significant relationship (p<0.0039, $R^2 = 0.30$). Biomass was important in most models, 

Figure 17: Mean site biomass and soil respiration rate (SRR) by season distinguished by shape: spring (triangle), summer (circle), fall (square). Fall biomass was positively related to lnSRR ($p= 0.0032$, $R^2 = 0.69$).
especially in spring and summer; however, a positive relationship between mean site 
biomass and lnSRR was only found in fall (p = 0.0032, R^2 = 0.69) (Figure 17). Similarly, 
litter was included in stepwise spring and summer models, but seasonal relationships with 
mean site lnSRR were not significant (Figure 11C). Fall showed the least variation in 
model components, with only two factors significant in combined treatment models, as 
opposed to five significant factors in spring and six in summer.

Separating stepwise models by treatment provided additional information. Season 
was consistently important in every treatment’s annual model, except 0yr. Biomass was 
also frequently significant within treatment models, even though these models only 
included three sites, and therefore three biomass measurements. The inclusion of 
individual components in seasonal treatment models was not obviously related to 
treatment, and instead appeared rather random. Predictive ability showed a limited 
connection with treatment. Unburned and 5yr treatments had lower R^2 values than more 
recently burned treatments, but all annual treatment models showed an R^2 of at least 0.70. 
Seasonal divisions in treatment models showed further unexplained irregularities in 
goodness of fit. Spring model fit was exceptionally high at 0yr immediately after burning 
(R^2 = 0.72) compared to average model fit at other treatments (R^2 = 0.36); likewise, fall 
model fit was inflated at 1yr treatments (R^2 = 0.76) compared to average (R^2 = 0.39).
3.4c Temperature Sensitivity of Soil Respiration Rate ($Q_{10}$)

$T_5$ was a crucial predictor of lnSRR, as shown in the general liner models and stepwise models. Goodness of fit of these models changed by treatment, but fit was not ordered according to burning chronology: 0yr ($p<0.0001$, $R^2 = 0.71$), 1yr ($p<0.0001$, $R^2 = 0.79$), 3yr forest ($p<0.0001$, $R^2 = 0.60$), 3yr prairie ($p<0.0001$, $R^2 = 0.77$), 5 yr ($p<0.0001$, $R^2 = 0.67$), unburned ($p<0.0001$, $R^2 = 0.67$) (Figure 18).

Figure 18: Mean soil temperature at 5cm ($T_5$) and mean soil respiration rate (SRR) calculated by treatment. Treatments are distinguished with shapes. Mean $T_5$ is a good predictor of SRR across the sampling period for all treatments: 0yr ($p<0.0001$, $R^2 = 0.71$), 1yr ($p<0.0001$, $R^2 = 0.79$), 3yr forest ($p<0.0001$, $R^2 = 0.60$), 3yr prairie ($p<0.0001$, $R^2 = 0.77$), 5 yr ($p<0.0001$, $R^2 = 0.67$), unburned ($p<0.0001$, $R^2 = 0.67$).
The sensitivity of SRR to $T_5$ ($Q_{10}$) suggested one aspect of ecosystem functioning and was hypothesized not to change by fire treatment; however, annual $Q_{10}$ was related to burning chronology, with highest $Q_{10}$ values in unburned and 5yr treatments, and lower $Q_{10}$ values in more recently burned treatments (Table 7). This pattern was reversed in spring where $Q_{10}$ values were higher in recently burned treatments as compared to 5yr and unburned treatments. The elevation of spring SRR temperature sensitivity was reflected in the $Q_{10}$ curves of 0yr and unburned where 0yr had higher $Q_{10}$ below 9°C, and unburned had higher $Q_{10}$ above 9°C (Figure 19). Summer and fall seasons were not obviously related to burning chronology, but seasonal patterns by treatment were ambiguous because of erratic values with high standard error. Overall, seasonal dynamics showed $Q_{10}$ values to be lowest in summer (2.05) and highest in fall (2.66), but this pattern was not constant within each treatment (3yr forest, 3yr prairie, 5yr, unburned differ). Depressed summer $Q_{10}$, as seen most dramatically at 3yr prairie, is likely

Table 7: Temperature sensitivity of soil respiration rate ($Q_{10}$) to changes in soil temperature at 5cm. $Q_{10}$ values were calculated by treatment (overall, 0yr, 1yr, 3yr forest, 3yr prairie, 5yr, unburned) and season (annual, spring, summer, fall). Values in parenthesis are standard error of the mean.

<table>
<thead>
<tr>
<th></th>
<th>$Q_{10}$ Annual</th>
<th>$Q_{10}$ Spring</th>
<th>$Q_{10}$ Summer</th>
<th>$Q_{10}$ Fall</th>
</tr>
</thead>
<tbody>
<tr>
<td>Overall</td>
<td>2.85 (0.07)</td>
<td>2.36 (0.15)</td>
<td>2.05 (0.12)</td>
<td>2.66 (0.26)</td>
</tr>
<tr>
<td>0yr</td>
<td>2.44 (0.11)</td>
<td>2.45 (0.23)</td>
<td>2.29 (0.33)</td>
<td>2.65 (0.45)</td>
</tr>
<tr>
<td>1yr</td>
<td>2.98 (0.18)</td>
<td>2.68 (0.74)</td>
<td>2.05 (0.27)</td>
<td>2.95 (0.35)</td>
</tr>
<tr>
<td>3yr forest</td>
<td>2.39 (0.14)</td>
<td>2.28 (0.13)</td>
<td>3.37 (1.08)</td>
<td>1.47 (0.57)</td>
</tr>
<tr>
<td>3yr prairie</td>
<td>2.02 (0.11)</td>
<td>3.31 (0.65)</td>
<td>1.44 (0.15)</td>
<td>3.00 (0.68)</td>
</tr>
<tr>
<td>5yr</td>
<td>3.25 (0.23)</td>
<td>1.27 (0.21)</td>
<td>2.37 (0.38)</td>
<td>2.43 (0.41)</td>
</tr>
<tr>
<td>Unburned</td>
<td>3.74 (0.19)</td>
<td>1.89 (0.20)</td>
<td>3.37 (0.32)</td>
<td>2.64 (0.46)</td>
</tr>
</tbody>
</table>
Figure 19: Predicted soil respiration rate (SRR) based on $Q_{10}$ model for 0yr and unburned treatments. Below 9°C the 0yr treatment has higher SRR, while above 9°C the unburned treatment has higher SRR.

related to summer moisture limitations, as also suggested by the positive relationship ($p<0.0001, R^2=0.58$) between summer GM and SRR (Figure 20). Finally, no direction connection emerged between SRR temperature sensitivity and predictive ability of SRR; for example, 3yr prairie had the lowest $Q_{10}$ and the highest $R^2$ between $T_5$ and SRR, while 3yr forest had low $Q_{10}$ and also low $R^2$, and unburned treatment had the highest $Q_{10}$ and a mid-range $R^2$. 
Figure 20: Mean gravimetric soil moisture to 5cm (GM) versus mean soil respiration rate (SRR) by treatment and day of year. Seasons are shown by shape spring (triangle), summer (circle), fall (square). Summer GM and SRR were positively related ($p < 0.0001$, $R^2 = 0.58$), while in fall they were negatively related ($p = 0.0022$, $R^2 = -0.47$), likely because of temperature limitations on SRR.
4.0 Discussion

4.1 Fire effects on Vegetation and Leaf Litter Biomass

Repeated burning is known to determine forest structure (density, BA, LAI) and species composition over a long scale by increasing sapling mortality and changing germination patterns (Huddle and Pallardy 1999; Peterson and Reich 2001; Reich et al. 2001; Hutchinson et al. 2005; Glasgow and Matlack 2007); thus, differences within the five year chronosequence cannot entirely be attributed to the most recently occurring fire. Disregarding a site’s specific burn history by cumulatively comparing all burned treatments to the unburned treatment provided a coarser, yet more accurate analysis that revealed decreased density, biomass, BA, and LAI at burned sites, as well as increased dominance of oak species in the burned treatment. Previous observations at the 40 ha Mary's savanna sites within Oak Opening’s Metropark showed a reduction in sassafras, black cherry, white oak, and black oak saplings after burning (Brewer and Grigore 1993; Abella et al. 2004). In the current study, all tree species had individuals in small DBH size classes (<20 cm), and all species but red/black oak had DBH classes skewed toward smaller classes, regardless of burning treatment. The abundance of small trees at burned and unburned treatments suggested that in this study area, fire had not been so frequent and intense as to completely prevent regrowth of young trees; however, fire was
sufficient to alter survival rates and change species composition, density, BA, and biomass between burned and unburned treatments.

These findings tentatively supported the ideas of Hutchinson et al. (2005) who suggested that fire can influence species composition and structure, even in successional woodland. Contrary to this conclusion, overstory trees in Oak Openings Metropark were not found to be impacted prescribed fires over a 15 year interval (Abella et al. 2004). Unknown supplementary management (i.e. thinning, and herbicide application) may also have been preformed by the Metroparks within the study area, which could have contributed to long-term overstory species composition. Because of these two caveats, the possibility remains that Franklin et al. (2003) were correct in asserting that burning alone will not return successional forests to oak savanna. Without knowing further site history, mechanisms cannot be suggested in detail, and it can only be concluded that managed burn treatments currently have significantly different structure and species composition than unburned treatments.

Litter biomass was obviously related to burning treatment, as litter was reduced by 57% immediately after burning at the 0yr treatment. The amount of litter consumed was very similar between 0yr sites (58%, 55%, 58%), which suggested equal burn intensity across the burn unit. Leaf fall increased litter biomass, but did not return 0yr or 1yr treatments to unburned levels. Previous research in Mary’s Savanna also found decreased depth of the O1 and O2 layers due to repeated burning between 1988 and 1990 (Brewer and Grigore 1993). In the current study, without repeated application of fire, recovery time of litter biomass was less than 3 years after burning, as shown by equal litter biomass at the 3yr treatment and the unburned treatment in spring.
H1 stated that fire will impact biotic variables through combustion; therefore burned treatments will have lower biomass, a higher percentage of oaks, and lower litter biomass than unburned treatments. All components of H1 were supported by collected data. Changes in forest structure were the result of long-term burning history unaccounted for in this study, while changes in litter biomass were the result of the short-term burning history seen in this study.

4.2 Fire Effects on Biophysical Variables

The degree to which fire combusts litter and heats soil, and thereby impacts biophysical variables and ecosystem processes, is highly dependent on fire severity and duration (Wan et al. 2001). Though no direct measurements of fire intensity were made in this study, based on partial consumption of the litter layer, the 4 April 2005 prescribed burn was classified as a low intensity cool burn where litter temperature would reach 250°C, soil temperatures 0 to 2.5 cm would reach 100°C, and soil temperatures 2.5 to 5.0 cm would reach <50°C (DeBano et al. 1998; Overby et al. 2002). Under such a relatively cool fire, it was suggested that roots would be killed to a depth of 2.5 cm, microorganisms would be unaffected in the mineral soil, N would be volatized in the forest floor, and nutrients would be unaffected in the mineral soil (Overby et al. 2002).

The incomplete removal of leaf litter through cool burning raised spring and summer T5 an average of 1°C (0a site compared to the paired 3yr forest). A recent study in Ohio oak forest found no change in T5 after prescribed burning (McCarthy and Brown 2006), but this finding is rare. The slight increase in T5 seen in the current study was
comparable to the 0.5°C increase seen at a depth of 2 cm at another cool prescribed burn in an Ohio oak-hickory forest; however, elevated T₅ in the current study persisted for approximately 200 days compared to the more fleeting effect of 75 days found by Iverson and Hutchinson (2002). A larger difference in summer T₅ (2.5°C) was observed between the 0yr and unburned treatment than between the paired sites. Such differences in T₅ across the chronosequence were not fully explained by fire treatment and litter combustion ($R^2=0.88$) because confounding variation in forest structure would also contribute to microclimate at these two treatments (Chen et al. 1999). Though biomass measurements were unable to account for additional differences in T₅ between treatments, forest structure’s influence on T₅ was further suggested by 2.0°C higher summer T₅ at 5yr than the unburned treatment. Variation in T₅ between 5yr and unburned would not be a consequence of litter removal because annual litter inputs would have replaced combusted litter approximately three years after burning, thereby already returning 5yr litter biomass to pre-burn levels (Figure 3). Thus, the 1°C differences in spring and summer T₅ could be reasonably attributed to immediate changes in litter biomass, while differences of 2.5°C across the entire chronosequence were more likely attributable to interactions between short-term fire effects that reduced litter biomass, and long-term fire effects that influenced forest structure.

While many studies found a clear decrease in soil moisture after cool burning reduced litter biomass (Knapp 1984; Knapp and Seastedt 1986; Bremer and Ham 1999; Iverson and Hutchinson 2002; Hubbard et al. 2004; Sulzman et al. 2005), or no change in soil moisture after burning (McCarthy and Brown 2006), in this study, GM values were 24% higher immediately after burning (0a site compared to the paired 3yr forest). After
spring canopy closure, GM trends were no longer different between the paired sites. The same temporal variation in GM was found by Iverson and Hutchinson (2002) after an OH prescribed burn, but they found the common result of decreased spring GM (0-10 cm) after burning. Perhaps short-term GM increases (0-5 cm) in the current study were related to fine root mortality from burning (Dress and Boerner 2001; Overby et al. 2002) that limited plants’ ability to access water in the upper soil layers where GM was measured. A biotic dimension to GM variation was also suggested by the significant relationship between spring, summer, and annual biomass and GM, though this could be a result of reduced evaporation because of shading and not related to plant activity. Regardless of mechanism, in this study, the immediate effect of burning was a significant, but very short-lived, increase in GM.

Across seasons and treatments, predictive ability of GM based on biomass, fire treatment, and litter biomass was poor for many reasons. Seasonally, the connection between litter, treatment, and GM was surprisingly strongest in fall ($R^2 = 0.41$) when losses to evaporation would be low, and therefore least regulated by litter biomass. GM was also unexpectedly influenced by landscape position, with eastern sites having higher GM than western sites, regardless of burn treatment. However, incorporating landscape position into models did not appreciably improve model fit. Variation in annual GM within the 0yr treatment was also substantial ($0a = 0.26\%$; $0b = 0.16\%$; $0c = 0.18\%$) and unexplained by available correlates, despite small differences in litter biomass and consistent westerly position in the landscape (Figure 10). Thus, in this study, predictive models of GM were, at best, moderately connected in fall, or if recently burned treatments were excluded from analyses. The weak connection between GM and litter in
this study may be related to summer drought, which could have made litter’s role in
determining GM irrelevant (Shay et al. 2001). Another possibility is that the amount of
litter left behind after the cool fire may still have been sufficient to prevent the increased
evaporation seen in other post-fire studies (Knapp 1984; Knapp and Seastedt 1986;
Bremer and Ham 1999). Overall, conclusions regarding the effect of fire on GM were
highly confounded, and whether because of biotic variation, high landscape variability,
drought, or incomplete combustion of litter, GM prediction was poor, and fire was not
found to substantially influence GM dynamics across the chronosequence.

In addition to combustion of litter, fire also impacted the 0yr treatment through
soil heating, thereby providing a spring pulse of nutrients as total C and total N both
increased immediately after burning (Figure 8). Total C decreased by 31% immediately
after fire in tropical forest (Ewel et al. 1981) and by 46% in California shrublands (Ma et
al. 2004), but in North Carolina oak-pine, Knoepp et al. (2004) found no change in total
C after a single burn, and in Minnesota oak savanna Tilman et al. (2000) found no change
in total soil C (0-20cm) after 35 years of repeated burns. Differences in total soil C
responses to fire were attributed to variation in burn intensity and soil properties across
the landscape. Changes in N are important to nutrient cycling because N is often the
limiting nutrient in forests. Decreases in available N (NH$_4$ and NO$_3$) have been measured
after fire (Seastead 1984), but increased in available N are typically seen immediately
after prescribed burning due to increased mineralization (Dijkstra 2006; Wan et al. 2001).
The increase in total N measured immediately after burning in this study is rare, at least
in part because many studies sample soil to a depth of 20 cm and not to 5 cm (Wan et al.
2001). Measurements isolating available N were not made in this study, but given overall
trends in the literature showing increases in available N immediately after fires, it is likely that the abrupt increase in total N observed after burning represented an increase in available forms of the nutrient. The observed increase in soil nutrients also supported previous findings in this study area, where a post-burn doubling of *Carex pennsylvanica* and *Pteridium aquilinum* cover led the authors to speculate that available nutrients increased because of cool fires (Brewer and Grigore 1993).

Though the average impact of fire at 0yr was to increase N and C, within the 0yr treatment the immediate effect of fire on total C and N was found to be inconsistent (Figure 9) and may be explained by varying burn intensity. Looking at prescribed fire in an oak-hickory forest, Boerner et al. (2000b) found that more intense fires decreased total inorganic N, while less intense fires increased total inorganic N. In the present study, burn intensity was not measured and other collected data did not corroborate the idea that a more intense fire at 0b lowered total C and N. The amount of litter combusted by fire was similar at all 0yr sites, while moisture differences would suggest parallel burn intensity between 0b and 0c, not between 0a and 0c. More data would be required to establish the contradictory effects of fire on total C and N as resulting from variable fire intensity.

Changes in total C and N were not evident across the chronosequence, though the C:N ratio was significantly lower at the unburned treatment. This result is contrary to meta-analysis showing that both total C and total N decrease with repeated prescribed fires on a decadal scale (Johnson and Curtis 2001). Though is impossible to quantify a burn effect on overall soil carbon storage with this limited data set, variation in soil C across the chronosequence did not suggest a long-term trend toward increased soil C
storage, as was seen immediately after burning. Instead, the largest change in C storage caused by prescribed burning likely occurred aboveground, in the prevention of increased C uptake in new plant biomass (Tilman et al. 2000). Long-term decreases in total N are common, both because N volatizes with minimal soil heating, > 65°C, (Dijkstra 2006; Knapp et al. 1988), and because repeated fires shift vegetation composition by reducing trees and increasing grasses, which reduces ecosystem productivity and leads to slower N cycling (Reich et al. 2001; Dijkstra 2006). High fire frequency is also known to increase the rate of N losses (Dijkstra 2006; Knapp et al. 1988). Therefore, differences in forest structure and unknown fire history may have confounded data across the chronosequence; however, total N might still be expected to be higher at the unburned treatment than the grouped burned treatments. Instead, only 3yr prairie had significantly lower N than unburned, suggesting the greater importance of vegetation than fire history in determining soil N at these cool and infrequently burned sites. Manipulative studies focusing on C:N ratios are rare (Attiwill and Adams 1993), but in tropical forest Ewel et al. (1981) saw soil C:N (0-3 cm) decrease after burning. No study was found that related long-term changes in C:N ratios to burning, which leaves the possible mechanism and significance of C:N variation across treatments unknown.

Though many other studies found differences in soil cations after a fire, no differences were found immediately after prescribed burning in this study. In both oak forests and pine forests, elevated levels of Ca, P, Mg, and K have been found to persist approximately one year after prescribed burning (Shay et al. 2001; Franklin et al. 2003; Elliot et al. 2004) with increased Ca persisting 3-5 years (Ahlgren and Ahlgren 1965; Knoepp et al. 2004). One reason a difference in cations may have been absent from the
present study is that 0yr soil samples were collected the day after burning, which was before a rain could send ash into the soil column (Elliot et al. 2004). The element known to be altered for many years after burning, Ca, did not change over the chronosequence, also presenting the possibility that prescribed fires in this system were of low enough intensity to not significantly change soil cations either immediately, or over multiple years (Vose et al. 1999; Overby et al. 2002).

In summary, H2 stated that fire will impact biophysical variables both through litter removal, which will increase T₅ and lower GM, and through soul heating, which will be minimal so soil nutrients and cations will be unchanged after burning. The study showed that burning temporarily increased both T₅ and GM. Observed increases in T₅ were definitively linked to changes in litter biomass, while increased GM was posited to be a result of fine root mortality and diminished water use (0-5 cm). Therefore, hypothesized impacts of litter removal increasing T₅ were supported, while predicted decreases in GM from litter removal were not seen, so that both the direction and possible mechanism of observed GM change were contradictory to H2. As was hypothesized, soil heating led to the unexpected short-term elevation of total soil C and N, though soil cations remained unchanged immediately after burning.

4.3 Fire Effects on Soil Respiration Rate (SRR)

The effect of burning on SRR changed over time, and different mechanisms were likely involved in each season. Spring SRR was inflated at the 0yr treatment (18% higher than the paired site), perhaps because accelerated decomposition was enabled by the
sudden release of nutrients, especially N, thereby increasing heterotrophic respiration. Post-burn increases in spring GM and T₃ at 0yr may also have contributed to elevated SRR, but the increase in SRR was unlikely to only be due to the relatively small changes in microclimate. Furthermore, increased microbial respiration the day after prescribed burning was seen in a sweet chestnut forest after prescribed fire, which was relatively hot due to the application of double litter before burning (Wuthrich et al. 2002). At these double litter sites, SRR remained elevated for 6 months after burning, but at sites with normal litter biomass, SRR was unchanged after burning. Elevated SRR only persisted for 1 month in the current study, suggesting that either different mechanisms influenced SRR at the chestnut stand, or more likely, that the fire in the current study was less intense than the double litter fire, yet more intense than the normal litter fire. Immediate inflation of SRR after burning suggests that the fire released nutrients without significantly impacting the microbial community, which also suggests quick recovery of ecosystem functioning after a fire (Wuthrich et al. 2002; Michelsen et al. 2004). Notably, the 1yr treatment had equal SRR to the unburned treatment during spring, when plant activity (and therefore autotrophic respiration) was relatively low, which indicated that heterotrophic respiration at the 1yr treatment had recovered from prescribed burning within one year after fire application. In spring across the chronosequence, only 3yr prairie had lower SRR than at the unburned treatment, which was a difference unlikely to be due to lasting burn effects, and instead was more likely a consequence of low GM and soil nutrients at the 3yr prairie.

By summer, SRR was reduced at 0yr (statistically lower than unburned, 1yr, 5yr, and the paired site), perhaps because decreased litter biomass made less C available for
decomposition, and thereby reduced heterotrophic respiration. The magnitude of annual SRR decrease was 25% (0a compared to 3yr forest), which was a small enough reduction to be completely a consequence of combusted litter, since 19-37% of annual SRR is attributed litter respiration (Rout and Gupta 1989; Bowden et al. 1993; Sulzman et al. 2005). Though not all litter was physically removed by fire, other studies suggested that, for unexplained reasons, the litter remaining after a fire was no longer a significant source of C efflux (Wuthrich et al. 2002; McCarthy and Brown 2006). This suggests that SRR measured at 0yr was only the product of root respiration and microbial respiration within the soil, signifying the dominance of biotic controls on summer respiration after prescribed fire. The importance of plants to post-fire summer SRR was also suggested within the 0yr treatment, where site level SRR mirrored biomass patterns and not GM, T5, litter biomass, or soil N content (Figure 10). During this season, 0yr acted similarly to 3yr prairie, though probably because of different mechanisms—3yr prairie was most likely limited by low GM, not C, during summer.

In fall, 0yr SRR was not different than any other treatment, likely because the availability of C after leaf fall led to the recovery of heterotrophic respiration at burned treatments. Total SRR variability across the chronosequence was minimized in fall as autotrophic contributions to total SRR variability were made inconsequential by plants entering dormancy; thus, as in spring, heterotrophic respiration represented a large proportion of total SRR and allowed the connection between fire treatment, litter, and SRR to emerge across the chronosequence (R² = 0.41). Landscape variability also decreased as GM limitations on SRR shifted to T5 limitations, except at 3yr prairie where SRR remained lower than other treatments, likely because GM at this treatment was still
33% lower than the average at other treatments. When landscape variability was minimized in fall one year after burning, SRR was seen to be recovered from fire, notwithstanding lower litter biomass at burned sites. The recovery of SRR in fall further suggests the fleeting impact of fire on SRR.

In summary, H3 stated that SRR would be higher in unburned treatments and recovered treatments (>1yr) than in recently burned treatments (0yr) because the impacts of reduced organic matter and decreased GM would outweigh the impact of increased T5. Furthermore, H4 predicted that after leaf fall, C would again be available; therefore, no significant difference in SRR would be observed between controls and treatments burned more than one year ago. The study found significant effects of burning that were probably attributed to seasonal changes in heterotrophic SRR. In support of H3 and H4, SRR was higher at unburned sites and treatments burned > 1yr ago, likely because reductions in litter led to temporary reductions in SRR that disappeared after leaf fall. If the small increases in T5 and GM caused by fire did elevate SRR, their influence was masked by the larger effect of litter removal reducing SRR.

4.4 Predicting the Effects of Fire on Soil Respiration Rate (SRR)

According to stepwise regression, which incorporated fire treatment, season, T5, GM, litter biomass, tree biomass, and soil C:N ratio, by far, the best predictor of annual and seasonal SRR was T5. Where other variables had annual R² < 0.08, the relationship between T5 and SRR had an annual R² of 0.71, with a range of 0.67 to 0.80 across burning treatments. Ma et al. (2004) found an increase in SRR variability and a reduction
of fit between T5 and SRR after burning. In contrast, the current study found that 0yr model fit ($R^2 = 0.76$) was higher than the paired 3yr forest ($R^2 = 0.63$), and almost equal to unburned ($R^2 = 0.75$), which revealed an increase in T5 and SRR fit immediately after burning. The high fit of SRR and T5 at the 0yr treatment may be explained by smaller standard deviation of SRR at 0yr, which was likely a result of fire homogenizing C resources and reducing the contribution of litter to SRR variability within the burned treatment (Boerner et al. 2000a). The high temperature sensitivity of root respiration (Boone et al. 1998) may also have increased the fit of T5 and SRR at burned treatments where, without litter, the root component of SRR would be expected to dominate summer SRR. The fit of T5 and SRR has also been shown to interact with water dynamics, as suggested by Hibbard et al. (2005) who found lower T5 and SRR $R^2$ in water limited systems; however, the current study found the highest $R^2$ at the driest treatment, 3yr prairie. Further experimentation would be needed to clarify the mechanisms behind the shifting fit of T5 and SRR after burning.

In contrast to increased fit of T5 and SRR at 0yr, the annual temperature sensitivity of SRR ($Q_{10}$) was lower at 0yr than the unburned treatment. This finding has precedence in Boone et al. (1998) where $Q_{10}$ was lower at treatments with litter removed than at control treatments. The reduction of $Q_{10}$ may not reflect true temperature sensitivity of SRR in sites with reduced litter, and instead may simply be a reaction to reduced C availability that masks true temperature sensitivity. In spring, $Q_{10}$ was elevated at 0yr, possibly because of the nutrient release caused by fire, but since $Q_{10}$ is itself known to be temperature dependent (Lloyd and Taylor 1994; Davidson et al. 1998), and burned treatments beyond 0yr had higher spring $Q_{10}$ than the unburned treatment,
elevated spring $Q_{10}$ is most likely a symptom of increased spring $T_5$ at burned treatments and is not due to a single fire. $Q_{10}$ is also known to depend on the seasonal dynamics of litter, which often leads to the underestimation of summer $Q_{10}$ and overestimation of fall $Q_{10}$ (Gu et al. 2004). Increased maintenance respiration in fall could also contribute to the overestimation of $Q_{10}$ in dormancy (Ryan 1991). Such seasonal changes in $Q_{10}$ were visible in this study, with low values in summer and high values in fall. Seasonal patterns in $Q_{10}$ were not consistent within each treatment and, unlike decreased annual $Q_{10}$ at 0yr, seasonal patterns in $Q_{10}$ were not related to year since burning.

Through stepwise models, GM was shown to be a significant predictor of annual and seasonal SRR, but the contribution of GM to SRR model fit was not as large as might be expected given both the high variation in GM across the landscape, and previous research that showed an increase in GM and SRR correlations after burning (Ma et al. 2004). In annual stepwise models, GM was most important in summer when GM limitations were strongest, with annual $R^2 = 0.08$. When averaged by season, GM showed a better relationship to SRR than when viewed on a weekly scale. The correlation between mean seasonal GM and SRR was strongest, and positive ($R^2 = 0.58$) in summer. In fall, the relationship between mean seasonal SRR and GM was also strong, but became negative as increases in GM and C were accompanied by simultaneous decreases in $T_5$ (Davidson et al. 1998; Qi and Xu 2001). Throughout all seasons, moisture limitations were especially important at 3yr prairie, which seemed consistently limited by GM. Soil moisture may have yielded better connections to SRR and litter biomass if quantified with a different metric (Hibbard et al. 2005), especially if pulse dynamics, which have been shown to be important during drought in oak forests (Yuste et al. 2005), were
integrated into models. Overall, the relative importance of GM to SRR prediction was small, and did not change according to fire treatment either annually or seasonally.

Despite a significant relationship between mean site C:N and lnSRR in spring ($R^2 = 0.30$), soil C:N was not important in predicting SRR across treatments. Martin and Bolstad (2005) found soil C:N values to be a central predictor of SRR in Wisconsin forest, but in the current study area C:N was only sporadically included in stepwise models, and its inclusion only minimally changed overall predictive ability. The range of C:N in the Oak Openings study area (15.6 to 23.7) is higher and more clustered than found in WI (12.2 to 19.7) and may have thus obscured the impact of C:N across this landscape. At the 0yr treatment C:N played a slightly more important role and was the second best predictor of annual SRR. This suggests that burning may have temporarily increased the role of nutrients in determining spring SRR.

Plant controls (i.e. new photosynthates, root respiration, productivity) on summer SRR are widely known to be important (Hogberg 2001; Litton et al. 2003; Yuste et al. 2004; Campbell et al. 2004; Davidson et al. 2006). Given low litter levels at burned treatments, autotrophic respiration represented an even higher proportion of summer SRR, so correlates to tree biomass, though not litter biomass, might correspondingly be expected to best describe SRR at low litter sites. Indeed, biomass was incorporated into stepwise models predicting annual SRR at 0yr, 1yr, and 3yr burned treatments; whereas, both litter and biomass were included as predictors in 5yr and unburned treatments. Similarly, Ma et al. (2004) found that litter depth became unimportant in SRR prediction after burning. An increase in model fit after burning, as already noted in $T_s$ and SRR models, was also seen in complex stepwise models where average model fit at the burned,
low litter treatments 0yr, 1yr, and 3yr (R² = 0.79) was higher than at the high litter
treatments 5yr and unburned (R² = 0.71). Only in fall, was biomass a significant
predictor of SRR across treatments, suggesting that biomass measurements were still a
relatively poor correlate to autotrophic respiration in this study area.

The relationship between mean litter and SRR was insignificant across treatments,
likely because a relatively small portion of summer SRR was attributable to litter, and the
effect of changing levels of litter biomass on SRR were consequently obscured. When
root respiration was reduced during summer drought in California, a litter effect became
visible and litter depth was found to be an important predictor of SRR across sites (Ma et
al. 2005). Euskirchen et al. (2003) also found litter depth to be a better predictor of SRR
across forest types than either soil temperature or moisture. As was the case in the
current study, most other researchers failed to find strong relationships between site SRR
and the abiotic factors of litter inputs, forest floor, and soil C (Reichstein et al. 2003;
Campbell et al. 2004). Better relationships have been found connecting SRR to the biotic
factors of biomass, fine root biomass, LAI, and foliar mass (Reichstein et al. 2003; Litton
et al. 2003; Yuste et al. 2004; Campbell et al. 2004; Hibbard et al. 2005) than found in
this study. Increased resolution of litter biomass measurements, and more specific data
regarding substrate availability would likely have helped quantify fire impacts, especially
in summer (Hibbard et al. 2005).

In summary, H5 stated that the relationships between SRR and its predictors,
including the temperature sensitivity of SRR (Q₁₀), would not change because of burning
treatment. The study showed that the annual fit of T₅ and SRR, as well as stepwise
models, were higher at burned treatments, while model components did not substantially
shift because of burning. Using stepwise regression that incorporated fire treatment, season, $T_5$, GM, litter biomass, tree biomass, and soil C:N ratio, $T_5$ was shown to be the best predictor of SRR across treatments and seasons. Mean summer GM was positively related to SRR ($R^2 = 0.58$), but the contribution of GM to stepwise model fit was low ($R^2 = 0.08$). Additionally, in stepwise models, the predictive roles of spring C:N and summer biomass were relatively more powerful at the 0yr treatment, while litter biomass became less important at 0yr and 1yr treatments. Though annual $Q_{10}$ was higher at 0yr than unburned for $T_5 < 9^\circ C$, and lower than unburned for $T_5 > 9^\circ C$, these differences were likely due to higher spring $T_5$ at burned treatments and summer C limitations at 0yr, and did not seem to signal long term changes in ecosystem function.
5.0 Summary and Conclusions

The goals of this study were to determine the effects of fire on: (1) biotic variables (forest structure, species composition, litter biomass), (2) biophysical variables (T5, GM, soil nutrients, and soil cations), (3) SRR, (4) recovery time of SRR, and (5) predictive ability of SRR. Briefly, this study suggested that repeated fires had persistent impacts on forest structure and species composition, and transitory impacts on litter biomass, T5, GM, SRR, soil nutrients, and Q10. Therefore, the effects of a single fire on this successional woodland are seen to be weak and short-lived, but the effects of repeated fires might be sufficient to contribute to oak woodland restoration over the long-term.

The mechanisms through which fire impacted biotic and biophysical variables were diverse. Changes in forest structure were the result of long-term burning history unaccounted for in this study, while changes in litter biomass were the result of combustion from observed, short-term burning history. Short-term increases in T5 after burning were definitively linked to changes in litter biomass, while increased spring GM was posited to be a result of fine root mortality and diminished water use (0-5 cm). Total soil C and N were elevated from soil heating, though soil cations remained unchanged immediately after cool prescribed fires.

Alterations in biotic and biophysical variables due to burning variably influenced seasonal heterotrophic SRR. Spring SRR was inflated at the freshly burned 0yr treatment
(18% higher than the paired site), likely because accelerated decomposition was enabled by the sudden release of nitrogen, thereby increasing heterotrophic respiration after burning. By summer, SRR was reduced at 0yr (36% lower than the paired site), perhaps because decreased litter biomass made less C available for decomposition, thereby reducing heterotrophic respiration after burning. In fall, 0yr SRR was not different than any other treatment, as increased availability of C after leaf fall led to the recovery of heterotrophic respiration after burning.

Relationships between SRR and its predictors only changed slightly because of burning. T₅ remained the dominant predictor across all treatments and seasons, whereas fire treatment, season, T₅, GM, litter biomass, tree biomass, and soil C:N ratio were shown to have minimal impact on stepwise R². At the 0yr treatment, the fit of T₅ and SRR was especially high because variation in SRR was reduced by fire homogenizing C resources, which limited the contribution of litter to heterotrophic SRR variability. Annual Q₁₀ was reduced after burning, but this difference is likely a reaction to reduced C availability masking the true temperature sensitivity of SRR. Likewise, elevated spring Q₁₀ at burned treatments is probably symptomatic of high spring T₅ and not a direct consequence of a single fire influencing Q₁₀. Beyond T₅, SRR predictors changed somewhat by treatment, and more obviously by season. Immediately after burning at the 0yr treatment, the roles of C:N in spring, and biomass in summer, were relatively more powerful in stepwise models, while litter biomass became less important. Across treatments, mean spring C:N was related to SRR (R²= 0.30), mean summer GM was related to SRR (R²= 0.58), and both mean fall biomass (R²= 0.69) and GM were related to SRR (R²= -0.47). However, considering the consistently important role of T₅ across
treatments and seasons, model fit and the predictors of SRR among treatments were quite similar, regardless of burn history.

In this study area, the chronosequence approach had only limited benefits both because SRR was seen to recover within a year, and because landscape variability in biomass and GM may have obscured more persistent and subtle fire effects on T5, GM, and soil nutrients. Considering the deeper management history of sites by incorporating long-term data regarding fire frequency and supplementary management like thinning would be necessary to make further conclusions regarding the long-term effects of fire. Otherwise, using better designed burn exclusion chambers replicated in low and high moisture areas, and low and high biomass areas, may help to further tease apart the immediate, and variable, impacts of prescribed burning across the landscape. Models could be used to test if the fit of annual SRR continues to be higher at burned treatments, or if this pattern was limited to this specific year, at these specific treatments. The potential of fire to change model predictors could be further explored with a paired burn exclusion design that also measured pre-burn data. Increased resolution of litter biomass measurements, and more specific data regarding substrate availability would likely help relate fire impacts to summer biotic controls (Hibbard et al. 2005), which would be vital to definitively describing mechanistic changes after burning. Overall, further studies at this site might help address the poorly understood variation in SRR between neighboring stands where climate, nutrients, species composition, and topography are similar (Garnett and Cox 1973; Martin and Bolstad 2005).
5.0 References


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