# THE INFLUENCE OF PRESCRIBED FIRE AND MECHANICAL FUELS MASTICATION ON SOIL CO2 EFFLUX RATES IN TWO SOUTHEASTERN U.S. PINE ECOSYSTEMS

By

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| | |
|---|---|
| FRI | Fire return interval ($yr^{-1}$) |
| $M_s$ | Soil volumetric moisture content ($m^3$ x $m^3$) |
| $R_a$ | Autotrophic soil respiration (μmol $CO_2$ $m^{-2}$ $sec^{-1}$) |
| $R_h$ | Heterotrophic soil respiration (μmol $CO_2$ $m^{-2}$ $sec^{-1}$) |
| $R_s$ | Soil respiration (μmol $CO_2$ $m^{-2}$ $sec^{-1}$) |
| $T_s$ | Soil temperature (°C) |

Abstract of Dissertation Presented to the Graduate School
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Soil $CO_2$ efflux ($R_s$) is a significant flux of carbon dioxide from ecosystem soils to the atmosphere and is a critical component of the total ecosystem carbon budget. $R_s$ fluxes are comprised of autotrophic ($R_a$) sources of $CO_2$ produced by plant roots and associated rhizosphere fungi and heterotrophic ($R_h$) sources of $CO_2$ produced by aerobic soil microbes. A variety of forest management activities, including prescribed fire and mechanical fuels mastication treatments have been shown to significantly influence $R_s$ rates in forests of the Western United States (US), yet these relationships are not well known for southeastern US forests. Prescribed fire is one of the most prevalent forest management tools employed in the southeastern US, and mechanical fuels treatments are becoming more common in the region as efforts to mitigate potential wildfire behavior in the wildland urban interface grow. Given that many of these forests provide habitat for endangered species, understanding the implications of management activities on ecosystem carbon dynamics may allow landowners to capitalize on future alternative revenue streams for carbon sequestration services while maintaining their properties in conserved states.

This study investigated the influence of prescribed fire and mechanical fuels mastication treatments on $R_s$ rates in longleaf / slash pine flatwoods forests and loblolly / shortleaf pine old-field forests in North Florida, USA. In the old-field forests, sites managed with over 60-years of annual and biennial dormant season prescribed fire had significantly lower monthly mean $R_s$ rates and estimated annual soil carbon fluxes than sites on which fire was excluded during that same period. Experimental litter manipulations in the old-field forests found that $R_s$ rates in frequently burned sites increased significantly following litter additions, while sites excluded from fire for over 60-years did not respond to litter additions. In the flatwoods forests, neither mechanical fuels treatments nor prescribed fire significantly altered monthly mean $R_s$ rates.

These results highlight some of the ways that forest management practices can influence $R_s$ rates. Our results suggest that future methods to model soil carbon emissions in the region should incorporate not only current vegetative conditions, but also land management activities and tenure.

# CHAPTER 1
# INTRODUCTION

Managing forests to increase carbon sequestration and decrease carbon emissions has been suggested as a method for reducing global atmospheric $CO_2$ concentrations that have increased over the last century (IPCC, 1995; Lal, 2005; Woodbury et al., 2007). As the southeastern United States (US) has over 81 million ha of forested land there exists significant potential for public and private forest landowner compensation for carbon sequestration services ("Cap and Trade" programs) (USFS/FIA 2006; Maier et al., 2012). Furthermore, given that many of the forested lands in the southeastern US provide valuable habitat for various threatened and endangered and sport-hunting species, alternative revenue streams for carbon sequestration services may facilitate some landowners maintaining their properties in conserved states (Engstrom and Palmer, 2005).

It has been suggested that understanding soil carbon pools and fluxes are the weakest links in assessing carbon in southeastern US forests (Raich and Schlesinger, 1992; Johnson et al., 2001). This is important as much of the carbon sequestered in temperate forested systems is found within the soils (50-60%), with soil $CO_2$ efflux comprising a significant portion (50-60%) of temperate forest total ecosystem carbon budgets (Post et al., 1982; Raich and Schlesinger, 1992; Lal, 2005; Noormets et al. 2010). At landscape scales, given that soils contribute such large fluxes to atmospheric $CO_2$, even small changes in soil $CO_2$ efflux rates over broad regions could have significant impacts on overall atmospheric $CO_2$ concentrations (Raich and Schlesinger, 1992; Bond-Lamberty and Thomson, 2010). Because of the importance of soil $CO_2$

efflux rates in local, regional, and global carbon cycles it is important to understand how forest management practices influence soil $CO_2$ efflux rates.

Soil $CO_2$ efflux ($R_s$) is a combination of $CO_2$ respired by plant roots and associated rhizosphere fungi ($R_a$) and heterotrophic soil microorganisms ($R_h$) (Luo and Zhou, 2006; Subke et al., 2010). Soil $CO_2$ efflux is the product of a multitude of interrelated biogeochemical factors that govern the production of $CO_2$ by plant roots (and associated mycorrhizal fungi) and soil micro and macro biota, including: soil temperature, soil moisture content, aboveground vegetative composition and belowground carbon allocation, phenology, soil carbon and nutrient content, and disturbance processes (Raich and Tufekciogul, 2000; Ryan and Law, 2005; Luo and Zhou, 2006). In addition a suite of physical factors including soil porosity, $CO_2$ pressure gradients, surface wind speed, and surface air turbulence influence the evolution of $CO_2$ to the soil surface (Luo and Zhou, 2006).

Prescribed fire is one of the most prevalent forest management tools employed in the management of conserved lands in the southeastern US, with over 2.4 million ha burned in 2011 (Waldrop and Goodrick, 2012). Prescribed fire is frequently used to maintain open, low-density pine forests that favor game and non-game wildlife species and fire dependent plant species, as well as to reduce wildfire risk by consuming litter, understory, and midstory vegetative fuels (Outcalt and Wade, 2004; Mitchell et al., 2006; Waldrop and Goodrick, 2012). While prescribed fire in the southeastern US is an obvious source of atmospheric carbon in the short-term, investigations of the rapid response of vegetation following prescribed fires suggest that the ecosystem recovery and sequestration of carbon lost via emissions is relatively fast (1-2 years), especially in comparison to other regions of the US (Wiedinmyer and Neff, 2007; Lavoie et al., 2010). It is known that variations in the frequency or season of prescribed fire management regimes can result in significant changes in forest vegetation structure and composition in the southeastern US (White et al., 1990; Waldrop et al., 1992; Knapp et al., 2009; Glitzenstein et al., 2012). What are not so well known are the effects of such management regime variations on the biotic and abiotic factors that drive forest soil carbon fluxes.

Mechanical fuels mastication treatments are becoming more common in the southeastern US as wildfire prone forests and urban areas intermix (Mitchell et al., 2006; Menges and Gordon, 2010). Mechanical fuels mastication is used to reduce understory fuel heights which has been shown to reduce wildfire behavior in many systems (Agee and Skinner, 2005; Glitzenstein et al., 2006; Kobziar et al., 2009; Kreye, 2012). In many wildland urban interface areas in the southeastern US, prescribed fire has become difficult for land managers to implement due to concerns from adjacent and nearby landowners over smoke and wildfire risk and as such, many land managers and agencies are opting to use mechanical fuels treatments in place of prescribed fire (Miller and Wade, 2003; Long et al., 2004; Menges and Gordon, 2010). As the implementation of mechanical fuel treatments has increased, it is important to understand the influence of such practices on forest carbon dynamics. Previous studies of mechanical fuels mastication in Western US systems have shown that treatments can significantly alter soil $CO_2$ efflux rates (Kobziar and Stephens, 2006; Ryu et al., 2009) as well as soil environmental factors known to influence long-term soil carbon dynamics (Concilio et al., 2005; Kobziar and Stephens, 2006; Xu et al., 2011). Given the increased use of mechanical fuels mastication treatments in place of or in combination with prescribed fire in the southeastern US, it is important to understand the effects of such activities on forest soil carbon fluxes and soil abiotic and biotic conditions.

Soil $CO_2$ efflux has been significantly positively correlated with soil temperature in many ecosystems and it has been suggested that increases in soil temperature due to global climate change may drive landscape level elevated soil $CO_2$ efflux rates and soil carbon losses (Raich and Schlesinger, 1992; Ryan and Law, 2005; Bond-Lamberty and Thomson, 2010). Experimental manipulations simulating future climate change scenarios have also found that soil $CO_2$ efflux rates can increase following exposure to elevated atmospheric $CO_2$ concentrations (Schlesinger and Andrews, 2000; Butnor et al., 2003; Carney et al., 2007). While much remains to be understood regarding the interactions of climate change and ecosystem carbon cycles (Bonan, 2008), the results of these studies further reinforce the importance of understanding the implications of forest management practices on soil $CO_2$ efflux rates.

As mentioned previously a variety of forest management activities, including prescribed fire, and mechanical fuels mastication treatments have been shown to significantly influence soil $CO_2$ efflux rates in the Western US, yet these relationships are not well known for southeastern US forests (Concilio et al., 2005; Tang et al., 2005; Kobziar and Stephens, 2006; Ryu et al., 2009; Xu et al., 2011). To address this knowledge gap, the following studies in this document sought to improve the understanding of forest management practices on soil $CO_2$ efflux rates in two forest types managed for conservation in Florida, USA. The objectives of these studies were to 1) assess the implications of prescribed fire management regimes on monthly mean and annual soil $CO_2$ efflux rates in old-field forests; 2) assess the importance of aboveground litter inputs in influencing soil $CO_2$ efflux rates for a range of old-field forest prescribed fire management regimes; and 3) evaluate the effects of mechanical fuels mastication treatments, prescribed fire, and mechanical fuels mastication treatments followed by prescribed fire on soil $CO_2$ efflux rates and soil abiotic conditions in pine flatwoods forests.

# CHAPTER 2
# FORTY YEARS OF PRESCRIBED FIRE ALTERS SOIL CO2 EFFLUX RATES AT THE STODDARD FIRE PLOTS IN NORTH FLORIDA

## Background

Soil $CO_2$ efflux ($R_s$) is a significant flux of carbon dioxide from ecosystem soils to the greater atmosphere and is a critical component in determining total ecosystem carbon budgets (Raich and Schlesinger, 1992; Schlesinger and Andrews, 2000; Ryan and Law, 2005). It has been estimated that soil $CO_2$ efflux represents one of the largest global terrestrial fluxes of carbon to the atmosphere, with the total annual $R_s$ flux (75 Pg C $yr^{-1}$) an order of magnitude greater than current annual anthropogenic C emissions from fossil fuel combustion (6 Pg C $yr^{-1}$) (Luo and Zhou, 2006). Soil $CO_2$ efflux is comprised of autotrophic ($R_a$) and heterotrophic ($R_h$) sources of $CO_2$ (Luo and Zhou, 2006; Subke et al., 2010). Total $R_s$ is a function of a multitude of interrelated biogeochemical factors that govern the production of autotrophic soil $CO_2$ efflux by plant roots (and associated mycorrhizal fungi) and heterotrophic soil $CO_2$ efflux by soil micro and macro biota, including: soil temperature, soil moisture content, aboveground vegetative composition and carbon allocation, phenology, soil carbon content, and disturbance processes (Raich and Tufekciogul, 2000; Ryan and Law, 2005). Beyond the biological factors associated with soil $CO_2$ efflux, a suite of physical factors including soil porosity, $CO_2$ pressure gradients, surface wind speed, and surface air turbulence govern the $R_s$ rate at the soil surface (Luo and Zhou, 2006).

Given the magnitude of this source of $CO_2$, research over the past decades has increased to improve the understanding of the drivers and mechanisms influencing $R_s$ (Luo and Zhou, 2006). While many of the significant factors influencing $R_s$ rates have been identified, much remains to be understood regarding the effect of specific land management practices on $R_s$ rates and those driving factors (Schlesinger and Andrews, 2000; Ryan and Law, 2005; Luo and Zhou, 2006). Studies have shown that both fire and forest management can influence soil carbon pools, biogeochemical properties, and $R_s$ rates (Johnson, 2001; Johnson et al., 2002; Certini, 2005; Kobziar and Stephens, 2006, Kobziar, 2007). For example, in a study of an oak forest in Oklahoma, USA, Williams et al. (2012) found that a 20-year management regime of frequent prescribed fire significantly reduced soil organic matter, increased bulk density, and reduced the biomass of certain soil bacteria; all factors that may have led to reduced sources of $R_h$ and subsequently overall $R_s$ rates. Similarly, in a study of a mixed conifer forest in California, USA, Ryu et al. (2009) found that prescribed fire reduced $R_s$ rates while simultaneously altering soil conditions that would otherwise be associated with increased $R_s$ rates. In a contrasting study of forest management and prescribed fire in a mixed conifer forest in California, USA, and an upload oak forest in Missouri, USA, Concilio et al. (2005) found that $R_s$ increased in both sites following forest thinning operations and that prescribed burning significantly altered forest floor conditions, but had no clear effect on $R_s$. Also in California, Kobziar and Stephens (2006) found that prescribed fire within a ponderosa pine plantation reduced $R_s$ rates in stands treated with understory mechanical mastication, while increasing $R_s$ rates in non-masticated stands. The results of these studies describe the complex interactions that can occur between prescribed fires, forests, and soil $CO_2$ efflux rates. Given the frequency of the use of prescribed fire in the upland forests of the southeastern USA, it is notable that few studies have addressed the influence of the management practice on $R_s$ rates in the region.

The effect of fire on $R_s$ depends on the ecosystem, fire history, and fire severity. Fire can influence $R_s$ rates by impacting the $R_h$ and $R_a$ sources of $CO_2$ (Neary et al., 1999; Luo and Zhou, 2006). Short-term autotrophic production of $CO_2$ can be reduced by fire due to aboveground plant mortality and injury. The long-term impacts of fire on $R_a$ are variable, however $R_a$ production often increases with time since fire as vegetation recovers following disturbance. In many cases, the consumption of vegetation and surface fuels by fire reallocates nutrient resources via incomplete combustion and subsequent deposition of ash, char, and other residues (Neary et al., 1999; Medvedeff, 2012). In the period following the deposition of those residues both plants and soil microbes may respond positively to the availability of such resources, subsequently increasing $R_s$ rates. Changes in forest vegetative composition and structure such as those described by Glitzenstein et al. (2012) caused by long-term prescribed fire management regimes may also impact $R_h$ sources of $CO_2$, by influencing litter and duff quality, production, and accumulation rates, as such factors have been shown to influence soil microbial populations and metabolic activity (Sulzman et al., 2012). Fire can also reduce $R_h$ sources through soil microbial population mortality caused by the direct combustion or heating of litter and duff layers and upper soil horizons (Luo and Zhou, 2006).

Prescribed fire is one of the dominant tools for forest management in the old-field forest type in the ‘Red Hills’ region of North Florida and South Georgia and the region is famous for its history of fire ecology research (Stoddard, 1969; Engstrom and Palmer, 2005; Way, 2006). The loblolly pine - shortleaf pine old-field forest type is frequently found on a collection of large privately owned plantation properties managed to promote

Northern Bobwhite quail (*Colinus virginianus* (L.)) populations for recreational hunting and selective timber harvesting (Figure 2-1) (Moser, 2002; Engstrom and Palmer, 2005). Many of these properties contain a mixture of old-field forests and patches of remnant upland longleaf pine forests that together provide habitat for many threatened and endangered species such as the Red-cockaded Woodpecker (*Picoides borealis*). Collectively, these private properties represent a significant regional holding of conserved lands, totaling over 121,000 ha found north of the Cody Scarp and stretching from the Ochlocknee River to the Aucilla River in Florida and Georgia (Paisley, 1989; Engstrom and Palmer, 2005). Regional suburban development, economic incentives for alternative uses, and changes in property ownership over the past several decades have resulted in the decline in total area managed for conservation purposes (Engstrom and Palmer, 2005). Beyond the Red Hills region, across much of the southeastern United States, many former agricultural lands are now covered in similar old-field forests comprised of loblolly pine, shortleaf pine, and mixed hardwoods representing an area estimated to cover up to 21 million ha (Frost, 1993)

Future and anticipated alternative revenue streams for carbon sequestration services may provide incentives for old and new landowners in the region to maintain their properties in conserved states providing critical habitat for threatened and endangered species. Previous and ongoing research in old-field plots at the Tall Timbers Research Station in Leon County, Florida, USA has quantified aboveground carbon pools across multiple prescribed fire management regimes, with the intent of understanding the implications of specific prescribed fire return intervals on forest carbon allocation and dynamics (K Robertson, 2009 pers. comm.).

Given the effects of fire on the autotrophic and heterotrophic sources of soil respiration documented in studies of other ecosystems, this study sought to address the following hypothesis for loblolly-pine old-field forests: a prolonged management regime of frequent prescribed fire results in reduced soil $CO_2$ efflux rates relative to a management regime of fire exclusion. In addition, this study sought to understand the influence of biotic and abiotic factors including soil temperature, soil moisture, monthly precipitation, and stand characteristics on soil $CO_2$ efflux rates. Given that previous research in the literature has found those factors to influence soil respiration rates, it was hypothesized that variations in those factors would explain any observed differences in soil respiration rates among the prescribed fire treatments.

The intent of this research is to support broader efforts in the region to quantify the effects of prescribed fire on Southeastern forest carbon dynamics and carbon sequestration. Studies such as this also provide insight into the response of ecosystem carbon dynamics to forecasted changes in temperature and moisture regimes due to global climate change.

## Methods

### Study Site

The study sites were located within the Tall Timbers Fire Ecology Research Plots (Stoddard Fire Research Plots) at the Tall Timbers Research Station (TTRS) in Leon County, Florida, USA, approximately 30 km from the cities of Tallahassee, Florida (to the south) and Thomasville, Georgia (to the north) (30° 39'N, -084° 12'W)(Figure 2-1)(Clewell and Komarek, 1975; Glitzenstein et al., 2012). The Stoddard Plots, established in 1960 as a long-term study of fire frequency on old-field forest vegetation and soils, have been consistently managed with a sequence of differing prescribed fire return intervals for over fifty-years (Clewell and Komarek, 1975; Glitzenstein et al., 2012). For this study, sampling took place within the annually burned (1YR), biennially burned (2YR) and fire excluded (40YR) Stoddard Plots (Figure 2-2). Prior to establishment of the plots in 1960 and 1966, the areas had been burned annually since agricultural abandonment in the late 1800s and 1920s (K Robertson, 2012 pers. comm.). The study sites were located approximately 59 m a.s.l. Average annual precipitation was 137 cm with the majority falling during the summer months of June, July and August (National Climate Data Center 2009, Thomasville, Georgia). Mean maximum and minimum temperatures for January and July for the area from long-term records (1971-2000) were 16.8°C and 4.6°C for January and 33°C and 21.8°C for July (National Climate Data Center 2009, Thomasville, Georgia). Soils within the sites were heavily cultivated for corn and cotton from the 1820s-1920s and occasionally as recent as the 1950s, with subsequent understory and overstory vegetation assemblages highly influenced by past agricultural practices (Clewell and Komarek, 1975). Soils were generally classified as fine-loamy, kaolinitic, thermic Typic Kandiudults of the Orangeburg and Faceville series (Natural Resource Conservation Service (NRC) Soil Survey Geographic Database (SSURGO)).

Vegetation across the 1YR and 2YR burned sites consisted of an overstory mixture of naturally regenerated shortleaf pine (*Pinus echinata* P. Mill), loblolly pine (*P. taeda* L.) and longleaf pine *(P. palustris* P. Mill) and an understory composed of annual grasses and hardwood resprouts (Clewell and Komarek, 1975; Myers and Ewel, 1990; Engstrom and Palmer, 2005; Glitzenstein et al., 2012). Vegetation within the unburned sites consisted of an overstory of shortleaf pine, loblolly pine and with lesser counts of longleaf pine and slash pine (*P. elliottii* Engelm.)(Clewell and Komarek, 1975). Due to the prolonged absence of fire, the unburned plots contained a much greater component of shade-tolerant midstory and overstory hardwood species including but not limited to: sweetgum (*Liquidambar styraciflua* L.), mockernut hickory (*Carya alba* (L.) Nutt. ex Ell.), live oak (*Quercus virginiana* P. Mill.) and water oak (*Q. nigra* L.) (Clewell and Komarek, 1975; Myers and Ewel, 1990).

**Sampling**

A total of nine plots were arranged in three blocks, with one representative plot per block of three prescribed fire return intervals (FRI): annual burn (1YR), biennial burn (2YR) and long unburned (40YR). To account for variability within the individual plot, each plot was comprised of nine 20 cm diameter x 10 cm height PVC sample collars (Figure 2-3) arranged in a 3 x 3 grid with 5 m separation following Kobziar and Stephens (2006). PVC sampling collars were constructed of Schedule 30 white 20 cm diameter pipe cut to 10 cm lengths and beveled along one edge. Collars were inserted beveled edge down into the soil or duff to a depth of approximately 8 cm using a rubber mallet. During the course of study, any vegetative growth within the sample collars was clipped and removed prior to $R_s$ measurement. The soil collar sample sites were excluded from the annual and biennial prescribed burning in the Stoddard Plot during the months of March 2010 and March 2011. Sampling of $R_s$ (μmol $CO_2$ $m^{-2}$ $sec^{-1}$) for all plots occurred on a monthly interval over the course of two days using a LI-COR Biosciences LI-8100 automated soil $CO_2$ sampling instrument with a 20 cm survey chamber (LI-COR Biosciences Inc., Lincoln, NE, USA).

Sampling consisted of a 120 second measurement initiated by a 15 second dead-band. Concurrently with $R_s$ measurements, soil temperature ($T_s$) (°C) and moisture content ($M_s$) ($m^3$ / $m^3$) at 10 cm and 5 cm depths respectively, were recorded onboard the LI-8100 using an Omega 8831 type E T-Handle temperature probe and a Decagon Systems EC-5 soil moisture probe (Omega Inc., Stamford, CT; Decagon Systems Inc., Pullman, WA), respectively. The $R_s$ study was established in the summer of 2009 with collars installed in June and July and sampling initiated in August. To account for diurnal variability, from August of 2009 until February 2010, $R_s$, $T_s$, and $M_s$ were sampled eight times per day, once per month. An assessment of the preliminary results found that fewer daily measurements would sufficiently capture the diurnal variability in $R_s$, $T_s$, and $M_s$. Because of this, daily plot measurements were scaled back to three times per day (morning, mid-day, and late afternoon-early evening) from March 2010 until the end of the study in May 2011. Measurements were taken on a consistent monthly interval with interruptions only due to equipment problems, heavy rain, lightning, or hazardous conditions within the plot. The resulting dataset for the entire twenty-one-month study totaled 7566 $R_s$ measurements. Collected data were assessed for quality prior to analyses with strong outliers in $R_s$, $T_s$, and $M_s$ attributed to measurement or equipment error excluded from the analysis. Recorded soil moisture content values less than 0.00, and soil temperature measurements greater than 40°C were excluded from the analyses as they resulted from equipment malfunction.

Plot characteristics and vegetative sampling were assessed in the winter and spring of 2011. Overstory vegetation was sampled using a 15 m radius circular plot (0.07 ha) centered on the middle $R_s$ sample collar. In addition to $R_s$, $T_s$, and $M_s$, the following field parameters with abbreviation and unit were recorded per $R_s$ sample collar: linear distance (m) from the sample collar to the nearest tree with a diameter at

1.3 m height (DBH) > 10 cm (Dnearest), diameter (cm) at breast height of the nearest tree to the sample collar (DBH), mean litter depth (cm) from three measurements within 30 cm of the sample collar (Litter), mean duff depth (cm) from three measurements taken within 30 cm of the sample collar (Duff), and total mean duff and litter depth (cm) from three measurements taken within 30 cm of the sample collar (DL) (Table 2-1). The following stand condition parameters with abbreviation and units were recorded one-time per sample plot: total basal area (BA) ($m^2$ $ha^{-1}$), pine basal area (P BA) ($m^2$ $ha^{-1}$), hardwood basal area (HW BA) ($m^2$ $ha^{-1}$), and stand density (TPH) (trees $ha^{-1}$) (Table 2-2). In addition, the following meteorological and climatic conditions for the entire study area were recorded monthly from external sources: monthly total precipitation from the Florida Automated Weather Network Station (FAWNS) at Quincy, Florida approximately 30 km from the study site (Precip) (cm), monthly mean ambient air temperature (°C) from the FAWNS site (Temp), and monthly regional Palmer Drought Severity Index (PDSI) score from the National Oceanic and Atmospheric Administration (NOAA) National Climatic Data Center.

**Analysis**

Treatments were analyzed as a randomized complete block design with FRI as the main treatment. For each month, daily measurements per soil collar were averaged, and the nine soil collar means were then averaged to produce a plot-level mean value for each month. This resulted in a sample size of three for each FRI treatment (total n = 9). Repeated measures analysis of variance (ANOVA) was used to test for differences in these monthly means among FRI treatments for $R_s$, $T_s$, and $M_s$, over the twenty-one monthly sampling periods between August 2009 and May 2011. Significant treatment effects were identified at p-value < 0.05. To assess differences among field parameters by FRI, one-way ANOVA tests were used. Where significant differences were identified, differences among treatments were analyzed using Tukey's HSD test. With treatments ignored, Pearson's correlation coefficients and linear regression were used to assess for relationships between overall study period mean plot $R_s$ rates and $T_s$, $M_s$, and field parameters following Gough et al. (2004). Additional linear (Equation 2-1) and nonlinear (Equation 2-2) regression models were developed using monthly plot means per treatment and measurement season for $T_s$, $M_s$, and field parameters listed in Table 2-1. The non-linear models of the relationship between $R_s$ rates and $T_s$ and M Temp were explored using an exponential equation (Equation 2-2) frequently used to describe the response of $R_s$ rates to soil temperature (Lundegardh, 1927; Samuelson et al., 2004; Concilio et al., 2005; Kobziar and Stephens, 2006). Following Samuelson et al. (2004) and Ryu et al. (2009) multiple regression using a forward step-wise procedure was used to develop models per FRI of monthly mean $R_s$ rates using Equation 2-3, utilizing the field and meteorological parameters that best explained the observed variability in $R_s$ rates (using $R^2$ and p-value), while minimizing multicollinearity and BIC scores.

$$R_s = \beta_0 + \beta_1(parameter) \tag{2-1}$$

$$R_s = \beta_0 e^{\beta_1(Ts)} \quad \text{or} \quad R_s = \beta_0 e^{\beta_1(M\,Temp)} \tag{2-2}$$

$$R_s = \beta_0 + \beta_1(parameter_1) + \beta_2(parameter_2) + \beta_i(parameter_i) \tag{2-3}$$

Where $\beta_0$, $\beta_1$, $\beta_2$, and $\beta_i$ were coefficients estimated through regression analysis. Residuals of regressions were checked for normality and heteroscedasticity, and where necessary model terms were transformed to meet assumptions.

The $\beta_1$ estimates developed using Equation 2-2 were used to estimate the $Q_{10}$ value per treatment using Equation 2-4 following Kobziar and Stephens (2006) (Lundegardh, 1927). The $Q_{10}$ value is often reported in studies of $R_s$ to describe the response of $R_s$ to a 10°C change in soil temperature (Luo and Zhou, 2006).

$$Q_{10} = e^{10\beta_1} \tag{2-4}$$

All statistical analyses were performed using JMP 9.0 (SAS Institute, Cary, NC, USA).

## Results

Vegetation and groundcover among the three prescribed fire treatment types varied significantly, with the highest basal area (37.72 $m^2$ $ha^{-1}$), stand density (1716.41 trees $ha^{-1}$), duff depth (1.58 cm), and litter depth (2.81 cm) in the 40YR treatment (Table 2-2). Both the hardwood and pine components of total plot basal area increased with decreasing fire frequency (Table 2-2). Throughout the study period, across all fire return intervals, the observed soil temperature ($T_s$) ranged from 5.2 - 37.39 °C (Figure 2-4). Trends in $T_s$ generally followed seasonal and monthly ambient temperature patterns with monthly mean $T_s$ in all treatments highly correlated ($R^2$ = 0.81 – 0.90 $p <$ 0.0001) with monthly mean 2 m temperature (M Temp) recorded at the Quincy, Florida FAWNS station. The effect of treatment on $T_s$ varied with time (treatment x time $p <$ 0.0001), with the greatest difference between treatments generally observed in the summer months and the least in the winter months (Table 2-3). Although soil temperature did not differ significantly among FRI treatments ($p$ = 0.1007), the lowest temperatures were generally in the 40YR treatment and the highest generally in the 1YR treatment (Table 2-3 and 2-4) (Figure 2-5). A distinct seasonal $T_s$ trend among the

FRI treatments was observed, with the 1YR treatment recording the highest mean $T_s$ in the warmer spring through fall seasons and the 40YR treatment recording the highest mean $T_s$ in the cooler winter seasons (Table 2-4) (Figure 2-4).

Soil moisture content ($M_s$) ($m^3/m^3$) ranged from 0 - 0.45 $m^3/m^3$ during the study period, with $M_s$ generally highest during the winter and early spring months of the year (Table 2-5) (Figure 2-6). The effect of FRI on soil moisture content varied monthly (treatment x time $p = 0.02$), with the smallest treatment effect observed during periods of very low soil moisture (Table 2-3). Although fire return interval was not found to significantly affect $M_s$ ($p = 0.11$), the lowest soil moisture content was generally observed in the 40YR treatment and the highest generally observed in the 1YR treatment (Table 2-3 and 2-5). Overall mean soil moisture content was highest in the 1YR treatment (0.17 $m^3/m^3$), lowest in the 40YR treatment (0.12 $m^3/m^3$), and between the two in the 2YR (0.15 $m^3/m^3$) (Figure 2-5). Monthly mean soil moisture content was significantly negatively correlated with both monthly mean soil temperature (1YR $R^2 = 0.37$ $p < 0.0001$, 2YR $R^2 = 0.32$ $p < 0.0001$, and 40YR $R^2 = 0.26$ $p < 0.0001$) and monthly mean temperature (M Temp) (1YR $R^2 = 0.40$ $p < 0.0001$, 2YR $R^2 = 0.42$ $p < 0.0001$, and 40YR $R^2 = 0.36$ $p < 0.0001$). Starting around April of 2010, the region experienced a moderate-extreme drought due to a precipitation deficit that grew in intensity until the end of the study period (Figure 2-7). The soil moisture data supported a link with the regional drought as soil moisture content had a positive linear relationship with the monthly precipitation totals in all treatments: 1YR ($R^2 = 0.17$ $p = 0.001$), 2YR ($R^2 = 0.15$ $p = 0.002$), and 40YR ($R^2 = 0.20$ $p = 0.0002$). In addition, monthly mean $M_s$ and PDSI were moderately positively correlated: 1YR ($R^2 = 0.22$ $p =0.0001$), 2YR ($R^2 =$

0.21 $p = 0.0002$), and 40YR ($R^2 = 0.29$ $p < 0.0001$). The monthly precipitation data were also only moderately linearly correlated with the regional monthly PDSI values ($R^2 = 0.34$ $p < 0.0001$).

Soil $CO_2$ efflux rates ($R_s$) ranged from 0 - 11.98 μmol $CO_2$ $m^{-2}$ $sec^{-1}$ during the study period, with the highest $R_s$ rates during the warmer months and the lowest rates during the cooler months (Table 2-6) (Figure 2-8). $R_s$ rates varied significantly among treatments ($p = 0.0007$), with the highest $R_s$ rates typically in the 40YR treatment and the lowest typically in the 1YR treatment (Table 2-3 and 2-6). The average overall 40YR mean $R_s$ rate 4.28 μmol $CO_2$ $m^{-2}$ $sec^{-1}$) was 37% higher than the 1YR mean rate (2.68 μmol $CO_2$ $m^{-2}$ $sec^{-1}$) and 25% higher than the 2YR rate (3.20 μmol $CO_2$ $m^{-2}$ $sec^{-1}$) (Figure 2-5). The treatment effect of FRI varied monthly (treatment x time $p < 0.0001$), with the greatest difference between treatments observed during the summer months and the least during the winter months (Table 2-3).

When treatments were ignored and monthly mean plot values pooled and analyzed as a group, relationships between $R_s$, $T_s$, $M_s$, and plot vegetative and meteorological characteristics were explored using Pearsons's correlation coefficients and linear regression. Pearson's correlations indicated positive relationships between $R_s$ and $T_s$ (0.68) and $R_s$ and Mean Temp (0.77) (Table 2-7). $R_s$ also exhibited a surprisingly negative relationship with $M_s$ (-0.34) while exhibiting a weak positive correlation with monthly precipitation (0.11) (Table 2-7). In the same test $R_s$ also exhibited correlations with the following plot level vegetative characteristics: basal area (0.34), stand density (0.33), distance to nearest tree (-0.31), duff depth (0.36), litter depth (0.29) and total duff+litter depth (0.36). Soil temperature was only weakly correlated with the same plot level vegetative characteristics (Table 2-7) indicating that while $T_s$ explained much of the temporal variation in $R_s$, it did not explain the differences in $R_s$ observed between the treatment types. In the linear regressions, overall mean $R_s$ rates were significantly positively correlated with stand basal area ($R^2 = 0.75$ $p = 0.003$), and stand density ($R^2 = 0.76$ $p = 0.002$) and significantly negatively correlated with the distance to the nearest tree ($R^2 = 0.68$ $p = 0.006$), although the diameter of the nearest tree was not significant (Figure 2-9). In addition, litter depth ($R^2 = 0.64$ $p = 0.001$), duff depth ($R^2 = 0.87$ $p = 0.0003$), and litter+duff depth ($R^2 = 0.91$ $p < 0.0001$) were significantly correlated with overall mean $R_s$ rates (Figure 2-10).

To assess the influence of vegetative and meteorological parameters on monthly mean $R_s$ rates within treatments, simple linear regression models (Equation 2-1) were developed for each parameter and FRI (Table 2-8). Linear regression indicated that a strong positive relationship between monthly mean $R_s$ rates and $T_s$ existed for the 1YR ($R^2 = 0.62$, $p < 0.0001$), 2YR ($R^2 = 0.78$, $p < 0.0001$), and 40YR ($R^2 = 0.65$, $p < 0.0001$) fire return intervals (Table 2-8) (Figure 2-11). Nonlinear exponential models (Equation 2-2) used to explore the relationship between monthly mean $R_s$ and $T_s$ by treatment reported similar fit to linear models (Table 2-9) (Figure 2-12) (Lundegardh, 1927). Model coefficients $\beta_0$ and $\beta_1$ from the nonlinear models were similar to estimates reported by Samuelson et al. (2004) and Kobziar and Stephens (2006). Similar to $T_s$, monthly mean ambient air temperature (M Temp) as recorded by the FAWNS station, also had a strong positive linear ($R^2 = 0.61 - 0.77$) and nonlinear relationship with $R_s$ ($R^2 = 0.63$ and 0.79, respectively) (Figure 2-13) (Figure 2-14). Soil moisture content ($M_s$) had a very weak negative linear relationship with monthly mean $R_s$ for the 1YR ($R^2 =$

0.14, p = 0.004), 2YR ($R^2$ = 0.14, p = 0.003), and 40YR ($R^2$ = 0.03, p = 0.22) treatments (Table 2-8) (Figure 2-15). Monthly total precipitation did not have a notable ($R^2$ > 0.10) relationship with monthly mean $R_s$.

For the following variables analyzed within each treatment there was either no significant simple linear regression relationship with monthly mean $R_s$ or the relationship was $R^2 < 0.10$: distance to nearest tree, diameter at breast height of the nearest tree, litter depth, duff depth, total duff +litter depth, plot basal area, pine species plot basal area, hardwood species plot basal area, plot tree density, or monthly total precipitation. While the plot level variables did not correlate with monthly mean $R_s$ rates, they did vary significantly among the treatments (Table 2-2).

To assess seasonal variations in the relationship between $R_s$ and $T_s$, and $R_s$ and $M_s$, simple linear ($T_s$ and $M_s$) and nonlinear ($T_s$) regression models were developed per treatment and season (fall, winter, spring, and summer) (Table 2-10, 2-11, and 2-12). In the $T_s$ linear models, for all treatments, monthly mean $R_s$ was most closely correlated with $T_s$ during the fall and winter months ($R^2$ = 0.69 - 0.90) and weakly correlated during the spring and summer months ($R^2$ = 0.11 - 0.63). Similarly in the nonlinear $T_s$ models, for all treatments, monthly mean $R_s$ was most closely correlated with $T_s$ during the fall and winter months ($R^2$ = 0.66 - 0.96) and least correlated during the spring and summer months ($R^2$ = 0.10 - 0.62). In the soil moisture content linear models, monthly mean $R_s$ was most closely correlated with $M_s$ during the summer and fall seasons ($R^2$ = 0.13 - 0.82), but the relationship was only significant ($p < 0.05$) in the 40YR treatment.

To assess the drivers of $R_s$ and to determine if the drivers varied per treatment, all variables (Table 2-1) were tested for their effect on monthly means of $R_s$ for each treatment in three separate forward step-wise multiple linear regression procedures (Equation 2-4) (Table 2-13). In each of the developed models, either $T_s$ or M-Temp were the first terms added, explaining > 50% of the variability of $R_s$. Soil $M_s$ was the second term added for all treatments, which was then followed by distance to the nearest tree (D Nearest) in the 1YR and 40YR models, and pine basal areas (P BA) in the 2YR model. A negative correlation with D Nearest was observed in both the 1YR and 40YR models. Overall the multiple linear regression models by treatment fit the data ($R^2$ = 0.82-0.89) only slightly more than the best fitting linear and nonlinear regression models.

The β1 model estimates from Equation 2-2 were used in the $Q_{10}$ model (Equation 2-4) to describe the incremental response of $R_s$ to a change of 10 degrees C in soil temperature (Table 2-9) (Table 2-11) (Lundegardh, 1927). The annual $Q_{10}$ values (1YR = 1.65, 2YR = 1.96, and 40YR = 2.16) were similar to those reported by Kobziar and Stephens (2006) for a Sierra Nevada pine plantation and Xu et al. (2011) for an oak forest in Missouri, USA, but lower than those reported by Maier and Kress (2000) for a loblolly pine plantation in North Carolina, USA.

Total monthly and annual soil carbon emissions per prescribed fire interval were estimated using the linear regression models of $R_s$ responses to changes in ambient temperature (Table 2-6) following Samuelson et al. (2004). Twenty-four hour 2 m elevation ambient temperature measurements recorded hourly from August 1, 2009-July 31, 2010 at the Quincy, FL FAWNS site located approximately 30 km from the study sites and offering the most consistent data available were used as inputs to predict hourly $R_s$ rates. The predicted $R_s$ rates (µmol $CO_2$ $m^{-2}$ $sec^{-1}$) were then converted to hourly soil carbon fluxes (g C $m^{-2}$ $hr^{-1}$) which were then summed to estimate monthly and annual soil carbon fluxes. Estimated total monthly soil carbon emissions (Figure 2-16) were consistently higher in the unburned 40YR treatment than the frequently burned 1YR and 2YR treatments. Similarly, estimated total annual soil carbon emissions per treatment showed the highest soil carbon efflux in the 40YR treatment (1688 g $m^{-2}$ $y^{-1}$) and the lowest in the 1YR (1069 g $m^{-2}$ $y^{-1}$) and 2YR (1268 g $m^{-2}$ $y^{-1}$) treatments.

## Discussion

The plot level monthly mean $R_s$ rates observed in our study (0.56 - 9.16 µmol $CO_2$ $m^{-2}$ $sec^{-1}$) were similar on average, but ranged much higher than those reported in a Georgia, USA loblolly pine plantation (1.27 - 5.59 µmol $CO_2$ $m^{-2}$ $sec^{-1}$) (Samuelson et al., 2004), a North Carolina, USA loblolly pine plantation (0.5 - 6.0 µmol $CO_2$ $m^{-2}$ $sec^{-1}$) (Maier and Kress, 2000), and a Sierra Nevada, California, USA CA ponderosa pine - Jeffrey pine plantation (2.37 - 4.55 µmol $CO_2$ $m^{-2}$ $sec^{-1}$) (Kobziar and Stephens, 2006), although each of those particular study locations had management tenures, soils, climates, and ecosystems different from those investigated here. The higher range of $R_s$ rates observed in our sites relative to those mentioned previously were likely related to the length of the growing seasons, warm annual temperatures, annual precipitation, and high stand biomass associated with the long-unburned treatment at the Tall Timbers Research Station which may have driven higher autotrophic and heterotrophic respiration rates. The results of our study indicate that the old-field forest conditions that were shaped by over 50 - years of frequent prescribed fire (or a lack of burning during the same period) can cause significant differences in overall mean and monthly mean soil $CO_2$ efflux rates.

Across all treatments on a monthly basis, soil temperature and monthly mean 2 m temperature (M Temp) explained more of the temporal variability of $R_s$ rates than any other recorded vegetative or meteorological parameter. In our simple linear and nonlinear regression models of monthly mean $R_s$ rates, $T_s$ and M Temp explained the majority of the variation in $R_s$ compared to the other parameters and in the forward step-wise multiple linear regression procedures $T_s$ or M-Temp were the first terms to be entered into any of the models. These results are consistent with others who have investigated the drivers of $R_s$ rates in Southeastern forest systems and found strong correlations with soil temperature (Fang et al., 1998; Gough and Seiler, 2004; Samuelson et al., 2004, 2009; Gough et al., 2005). The $R_s$ correlation with $T_s$ reported in this study ($R^2$ = 0.62 - 0.78 in linear models and $R^2$ = 0.60 - 0.80 in nonlinear models) was higher than those reported ($R^2$ = 0.38 - 0.56) by Samuelson et al. (2004) for a Georgia, USA loblolly pine plantation, much higher than those ($R^2$ = 0.26) reported by Gough and Seiler (2004) for a loblolly pine plantation in South Carolina, USA, and similar to those ($R^2$ = 0.70) reported for a loblolly pine plantation in North Carolina, USA by Maier and Kress (2000). While $T_s$ explained the majority of the temporal variability in $R_s$ rates, a lack of significant differences for $T_s$ among treatments suggests that other factors such as vegetation explained the differences in $R_s$ rates between the treatments.

Soil moisture content ($M_s$) also explained some of the temporal variability in $R_s$ rates even though significant differences in soil moisture content were not observed among treatments. In the Pearson's correlation assessment $M_s$ was moderately negatively correlated with $R_s$ (-0.34) when treatments were ignored, and in the treatment specific regression models a weak negative linear relationship was in the

1YR, 2YR, and 40YR treatments ($R^2$ = 0.14, 0.14, and 0.03, respectively). In contrast, the forward step-wise multiple linear regression models by treatment identified a positive relationship with $M_s$ as the second most significant term behind $T_s$ or M Temp in explaining monthly mean $R_s$ rates. The fact that soil moisture content explained some but relatively little of the variability in $R_s$ rates is consistent with the results of other studies of $R_s$ in the Southeast as soil moisture is rarely limited in these systems (Fang et al., 1998; Gough and Seiler, 2004; Samuelson et al., 2009). The positive and negative relationships identified between $R_s$ and $M_s$ may have been the result of interactions between temporal patterns of precipitation, seasonal plant soil water use, seasonal changes in $R_s$ rates due to temperature and plant growth patterns, and the effects of drought on soil water content and vegetation. The widespread regional drought during much of our study likely resulted in near-term reduced plant photosynthetic activity and belowground carbon allocation and root respiration ($R_a$), as well as reduced heterotrophic microbial activity and respiration due to limited moisture availability ($R_h$) (Ryan and Law, 2005; Cisneros-Dozal et al., 2007). This is supported by the results of a recent multi-year eddy-covariance study of north Florida slash pine plantation carbon dynamics which revealed that during periods of drought stress above ground carbon assimilation and total ecosystem respiration, including $R_s$, were reduced relative to non-drought periods (Bracho et al., 2012). Future and longer term studies of $R_s$ rates in this system during drought and non-drought periods may better elucidate the impacts of prescribed fire management regime on the connectivity of soil water content, $R_s$ rates, and forest carbon assimilation.

While soil temperature explained the majority of the temporal variation in $R_s$ rates in our study, it did not explain the observed differences among the prescribed fire treatments. we suggest that the observed differences in mean $R_s$ rates among treatments were related to the amount of total aboveground carbon in living biomass in the treatments (1YR ≈ 50 tons $ha^{-1}$, 2YR ≈ 80 tons $ha^{-1}$, and 40YR ≈ 150 tons $ha^{-1}$) (Kevin Robertson unpublished data.). In support of this, previous research has found no significant differences in soil carbon, nitrogen, or phosphorus content among treatments suggesting that soil carbon and nutrient content were not responsible for the observed differences in $R_s$ between treatments (Kevin Robertson unpublished data). Other studies investigating $R_s$ rates across stand age and biomass gradients have found mean $R_s$ rates to be higher in older stands with greater aboveground biomass (Ewel et al., 1987a; Amiro et al., 2010). In a trenching and exclusion experiment along a chronosequence of temperate forests in China, Luan et al. (2011) found that $R_s$ rates were significantly ($R^2$ = 0.59 $p < 0.05$) correlated with site basal area. While our research did not investigate belowground living root biomass among the treatments, we suspect that total belowground biomass would follow similar trends among the treatments as aboveground biomass. Previous research has shown that $R_s$ rates tend to be positively correlated with root biomass (Lou and Zhou, 2006). In our study both Pearson's correlations (Table 2-7) and linear regression identified relationships between overall mean $R_s$ rates and plot basal area ($R^2$ = 0.75 $p$ = 0.003) and stand density ($R^2$ = 0.76 $p$ = 0.002) when treatments were ignored and the data pooled. In a review of the controls and correlates of $R_s$ across multiple ecosystems Raich and Tufekciogul (2000) found evidence supporting positive correlations between $R_s$ rates and aboveground productivity in grasslands ($R^2 = 0.80$ $p < 0.01$) and $R_s$ rates and litterfall production in forests ($R^2 = 0.90$ $p < 0.001$). In this study we suggest that the weak within-treatment relationships between $R_s$ rates and plot basal area and stand density were due to the relatively low range of within treatment variability of those characteristics.

The differences in $R_s$ rates among treatment types in our study may have also been associated with variations in forest composition, as the long unburned sites had a much greater component of deciduous tree species than the frequently burned sites. Soil $CO_2$ efflux rates have been shown in other studies to differ between forest types, with lower rates often reported in coniferous forests than in broad-leafed forests of the same soil type (Raich and Tufekciogul, 2000). In a study of $R_s$ rates in a mixed coniferous - deciduous forest in Belgium, Yuste et al. (2005) found that mean $R_s$ rates were lower under conifer tree canopies than under deciduous canopies, with total estimated annual carbon flux approximately 50% greater in the deciduous sites (8.8 ± 2.2 Mg C $ha^{-1}$ $yr^{-1}$) than in the coniferous sites (4.8 ± 0.7 Mg C $ha^{-1}$ $yr^{-1}$). In their review Raich and Tufekciogul (2000) suggested that the observed differences in $R_s$ between coniferous and deciduous forests may have been driven by forest litter production and quality, carbon allocation, and autotrophic contributions to total $R_s$. It is important to note however, in nearly all of the cases mentioned previously experimental partitioning of the relative contributions of autotrophic and heterotrophic sources of $R_s$ had not been assessed.

Litter has been shown to be a significant source of labile carbon for heterotrophic respiration (Sayer, 2006). In a study of a chronosequence of deciduous forests in China, Luan et al. (2011) suggested that labile carbon quantity and quality from leaf litter primarily drove the observed spatial variation in $R_h$ rates. Furthermore, experimental manipulations in litter addition and exclusion have shown to both positively and negatively (respectively) influence $R_h$ rates in multiple ecosystems (Bowden et al., 1993; Sayer, 2006; Chemidlin Prevost-Boure et al., 2010; Sulzman et al., 2012). In our study the ratio of hardwood basal area to pine basal area (Table 2-2), litter and duff depths (Table 2-2), and mean annual litter and duff loads (1YR = 4.62, 2YR = 5.42, and 40YR = 5.47 t $ha^{-1}$ $yr^{-1}$, respectively) were highest in the 40YR treatment, suggesting that those factors contributed to the differences in $R_s$ rates among treatments. Though not quantified in our study, observations in the plots suggest that the litter in the 40YR treatment and lesser so in the 2YR treatment was dominated by deciduous leaf litter with a mixture of pine needles and few understory forbs and grasses. On the other hand, similar to the findings of Robertson and Ostertag (2007), observations in the 1YR treatments suggested that the leaf litter was dominated by pine needles, and annual understory forbs and grasses, and contained relatively little deciduous leaf litter. Differences in the composition of the leaf litter by treatment type may have been associated with variations in the quality of the leaf litter with regards to the litter as microbial substrate. In our study we did not assess the carbon and nutrient content of the litter samples, however in an old-field loblolly-shortleaf pine successional study, Hinesley and Nelson (1991) reported that the quality of the litter increased with seral stage, as N, P, K, Ca, and Mg increased 15%, 20%, 75%, 202%, and 72% respectively, between early sere mature pine forests and late sere mixed hardwood forests. Given this, the observed differences in $R_s$ rates between treatments may have been due to variations in the relative contributions of $R_h$ caused by litter composition, quality, depth, and loading.

The results of our study also suggest that forest structure may have had some influence on the spatial variability of $R_s$ rates, likely through the variable contributions of root and mycorrhizal respiration to $R_s$. In our within treatment multiple regression models, in addition to temperature and soil moisture, $R_s$ rates were negatively associated with distance to nearest tree in the 1YR and 40YR treatments and positively associated with pine basal area in the 2YR treatment. In addition, in the overall simple linear regression models when treatments were ignored and all plots grouped, $R_s$ rates were significantly negatively correlated with distance to the nearest tree ($R^2$ = 0.68 p = 0.006) but not at all correlated with the diameter of the nearest tree. These results contrast with the findings of a study in a tropical rainforest in Borneo that found $R_s$ to be highly correlated ($R^2$ = 0.60 $p < 0.001$) with the diameter of trees within 6 m of the sampling point (Katayama et al., 2009). It is likely that the difference between our results and those of the Borneo study may have been due to biome related differences in forest composition and species, as Katayama et al. attributed much of the spatial variation in $R_s$ to the influence of very large (DBH > 60 cm) *Dipterocarpaceae* trees. A similar study by Samuelson et al. (2004) found a small but significant difference in $R_s$ rates based on the horizontal sampling position within a loblolly pine plantation, with higher $R_s$ rates closer to the base of trees (Samuelson et al., 2004). This is not surprising given the very spatially explicit linear arrangement of pine plantations which contrast greatly to the naturally regenerated stands at Tall Timbers where the arrangement of trees and their root growth is more variable. Further study explicitly designed to address the linear effect of distance to nearest trees on $R_s$ rates (similar to Clinton et al. (2011)) may identify statistically stronger effects than we were able to identify in our study design.

Prescribed fire may have affected the heterotrophic soil microbial populations and thus $R_h$ rates in the 1YR and 2YR treatments.  Given that the annual litterfall rates were similar among treatments, while litter and duff depths differed significantly among treatments (Table 2-2), we attribute much of the difference in litter and duff depths to the direct combustion of surface fuels by the fast-moving, low-intensity prescribed fires in the frequently burned sites.  The combustion of soil surface litter and duff material could result in an immediate reduction in forest floor and duff inhabiting heterotrophic organisms through direct consumption and temperature related mortality (DeBano, 1998, Neary, 1999, Choromanska and DeLuca, 2002; Certini, 2005).  While a temporary post-fire decline in surface dwelling heterotrophic populations is expected as fires of this type have been shown to increase soil temperatures at 5 cm depth to near 150°C, we suspect that prescribed fire resulted in little direct temperature related mortality of the deeper subsurface soil microbial communities (Debano, 2000; Certini, 2005).

Following fire, depending on fire intensity and soil characteristics, there is generally both a direct loss of surface organic material due to combustion and also a deposition of organic carbon, nitrogen, and phosphorus in the form of ash and partially combusted material (Neary, 1999; Choromanska and DeLuca, 2002; Certini, 2005). The loss of surface litter and duff can reduce labile carbon available for microbial decomposition, while the post-fire pulse of available carbon, nitrogen, and phosphorus can result in increased soil microbial activity in the post-fire period due to the release of previously bound nutrients (Neary, 1999; Certini, 2005). As no sample collars were designated as unburned controls in the 1YR and 2YR treatments, we were unable to test for the specific effect of an individual prescribed burn on monthly $R_s$ rates. The results of an experiment in a frequently burned loblolly pine forest in South Carolina, USA, however found no significant impact on forest soil microbial enzyme activity following a low intensity prescribed fire (Boerner et al., 2006).

The estimated $Q_{10}$ values that describe the response of $R_s$ to a change in temperature, suggested that the relative contributions of heterotrophic ($R_h$) and autotrophic ($R_a$) respiration to total $R_s$ may have existed among the treatment types. The annual $Q_{10}$ values in our study 1.65 (1YR), 1.96 (2YR), and 2.16 (40YR) suggest that higher contributions of soil microbial sources ($R_h$) drove higher $R_s$ rates in the 40YR treatment and lesser so in the 2YR and 1YR treatments. This is because others have reported that the $Q_{10}$ temperature response of autotrophic and heterotrophic sources of $R_s$ differ, with heterotrophic soil microorganisms more sensitive to changes in soil temperature than plant associated autotrophic sources (Bhupinderpal-Singh et al., 2003; Zhou and Zhou, 2012). Bhupinderpal-Singh et al. (2003) reported following a girdling experiment in a boreal Scots pine forest, that $R_s$ from heterotrophic sources dropped significantly following a 6°C decline in soil temperature, while autotrophic sources of $R_s$ were unchanged during that same period. Similarly, Zhou and Zhou (2012) reported in a review of several studies that average $Q_{10}$ values were less for roots (2.07) than litter (2.68) or bulk soil organic matter (2.54). Likewise, in a trenching and exclusion experiment along a chronosequence of temperate forest sites in China, Luan et al. (2011) reported that $Q_{10}$ values for heterotrophic sources of $R_s$ were higher than for autotrophic sources, regardless of stand age.

We suggest however that using $Q_{10}$ values as a proxy for experimental partitioning methods should be considered with caution, as our results and those mentioned previously, contrast with others that have found $Q_{10}$ values for plant roots to be higher than the heterotrophic $R_s$ sources in the bulk soil (Boone et al., 1998; Saiz et al., 2006). The relative partitioning of $R_s$ suggested by our $Q_{10}$ values also contradicts the results of a review of global $R_s$ studies that found the ratio of $R_h$ contributions to total $R_s$ declined with both increasing $R_s$ and ecosystem productivity (Subke et al., 2006). Both Subke et al. (2006) and Kuzyakov and Gavrichkova (2010) suggested that the proportional decline in $R_h$ contributions to total $R_s$ might be due to an increase in total belowground C allocation on sites with greater aboveground biomass. While we didn't quantify productivity across the treatments in our study, the increase in total $R_s$, basal area, stand density, and estimated total aboveground biomass in the 40YR sites relative to the 1YR and 2YR sites, may have led to higher $R_a$ contributions relative to $R_h$ in the 40YR sites, contrasting the results of our $Q_{10}$ values.

In our study it was observed that the relationship between $R_s$ and soil temperature ($T_s$) and soil moisture content ($M_s$) varied seasonally. We suggest that the changes were indicative of phenological shifts in the relative contributions of $R_a$ and $R_h$ to $R_s$. Previous research in partitioning studies has shown that during periods of aboveground vegetative growth, $R_a$ contributions to $R_s$ can increase relative to $R_h$, as plants allocate recent C photosynthate belowground, driving higher root maintenance, root growth, and mycorrihizal fungal respiration rates (Subke et al., 2006; Kuzyakov and Gavrichkova, 2010). Consequently, it has been shown that during periods of aboveground vegetative growth, the $T_s$ and $R_s$ relationship weakens as other variables such as soil moisture ($M_s$) and available photosynthetically active radiation become more important in governing belowground C allocation by plants (Ekblad and Hogberg, 2001; Davidson et al., 2006; Wertin and Teskey, 2008). Fenn et al. (2010) reported similar results for a multi-season study of $R_s$ rates in a woodland in Oxfordshire, UK, with soil temperature explaining less of the variation in $R_s$ during the summer months than during the spring. Our data tend to support these previous observations as the seasonal relationships between $R_s$ and $T_s$ were strongest during the fall and winter seasons in all treatments and the seasonal relationship between $R_s$ and $M_s$ were strongest during the summer season in the 2YR and 40YR treatments. While spatial-temporal correlations between $T_s$ and $R_s$ have been well documented in the literature for many ecosystems, soil temperature has also been identified as a potentially confounding variable in $R_s$ studies by masking other phenological and meteorological variables that more directly govern the physiological mechanisms of autotrophic soil $CO_2$ production (Hogberg et al., 2009).

It was interesting to observe the seasonal reverse of soil temperature trends between the 1YR and 40YR treatments wherein the warmest soils were found in the summer in the 1YR plots and in the winter in the 40YR plots. These temperature variations were likely the result of the differences in canopy cover between the treatments and the effect of canopy cover on the balance of incoming shortwave radiation and outgoing longwave radiation. These seasonal soil temperature fluctuations were similar to results reported by Samuelson et al. (2004) in a study of loblolly pine plantation management types. In their study, instead of prescribed fire, herbicidal weed control resulted in a similar seasonal soil temperature reversal (Samuelson et al., 2004). Herbicidal weed control in some cases can alter forest structure similar to frequent low intensity prescribed fire, suggesting that long-term management induced changes in vegetative cover may have caused the seasonal temperature shift among treatment types (Brose and Wade, 2002). A linear transect study of forest cover effects on soil temperature from New York, USA, found that forest cover increased soil temperature in the winter and decreased it in the warmer months relative to an open field (Michelsen-Correa and Scull, 2005). Even though a positive correlation was observed between $R_s$ and $T_s$, a similar seasonal change in the hierarchal order of $R_s$ rates among treatments was not observed in our study. This is comparable to a disconnect between soil temperature and $R_s$ following prescribed burning reported by Ryu et al. (2009) in a mixed conifer forest in California, USA. In their study, the authors reported that prescribed fire reduced $R_s$ while simultaneously increasing soil temperature and moisture content (Ryu et al., 2009). The seasonal disengagement between $R_s$ rates and $T_s$ observed in our study further suggest that mechanisms other than soil temperatures were driving soil $CO_2$ efflux rates.

The $R_s$ rates observed in this study resulted in reduced estimated total annual soil carbon emissions in the 1YR (37%) and 2YR (25%) treatments relative to the long unburned stands. The estimated monthly carbon emissions for all treatments were similar to those reported by Samuelson et al. (2004) for an unburned loblolly pine plantation in southwestern Georgia, USA, while the estimated total annual soil carbon emissions reported in our study, 1069 g $m^{-2}$ $y^{-1}$ (1YR), 1268 g $m^{-2}$ $y^{-1}$ (2YR), and 1688 g $m^{-2}$ $y^{-1}$ (40YR), were similar to those (1410 g $m^{-2}$ $y^{-1}$) reported by Maier and Kress

(2000) for an unburned loblolly pine plantation, but less than those (778-966 g $m^{-2}$ $y^{-1}$) reported by the Samuelson et al. (2004) study.

## Conclusion

A forest management regime employing frequent prescribed fire can fundamentally alter forest structure and composition relative to a fire exclusion regime, resulting in reduced soil carbon fluxes in burned vs. fire excluded treatments. It was reported that average $R_s$ rates in the annually burned forests were approximately 37% lower than those of the long unburned forests, while total estimated annual soil carbon fluxes were also lower in the annually (1069 g $m^{-2}$ $y^{-1}$) and biennially (1268 g $m^{-2}$ $y^{-1}$) burned forests than in the long unburned forest (1688 g $m^{-2}$ $y^{-1}$). Our results indicate that the differences in $R_s$ rates between treatments were driven by variations in the amount and composition of forest vegetation and litter and duff depths between treatments sites. Similar to the results of others (Raich and Tufekciogul, 2000) we found that mean $R_s$ rates were higher at sites with greater aboveground biomass and litter and duff depths. We suggest that these conditions were responsible for the variations in $R_s$ rates due to increased total belowground carbon allocation by plants and labile carbon for heterotrophic soil microbes, respectively.

To assess the full effect of prescribed fire management on total ecosystem carbon dynamics, future research is needed that also quantifies aboveground carbon gains and losses including losses due to combustion. Additional research is also needed to understand the implications of prescribed fire season on $R_s$ rates, as some forest lands managed for conservation or ecosystem restoration in the region apply prescribed fire during the growing season while still others burn during the dormant season. Given that the season in which prescribed fire is applied can have significant impacts on forest species composition and structure, it is not known whether corresponding changes in $R_s$ rates occur (Waldrop et al., 1992).

Regardless of prescribed fire management regime and consistent with previous studies, soil temperature explained well over half of the variability in $R_s$ rates in old-field forests. Interestingly, the strength of temperature models of $R_s$ rates varied seasonally, with the least predictive power occurring in models of the warmer spring and summer months during the growing season. Future efforts to model carbon dynamics under elevated temperatures should address this seasonal variability in the relationship between soil temperature and $R_s$ rates. Furthermore, research is needed to understand the specific response of autotrophic and heterotrophic sources of $R_s$ to changes in factors other than temperature, such as aboveground litter inputs and forest management practices.

Table 2-1. Parameters for use in regression analysis of each variable's influence on soil $CO_2$ efflux rates at the Tall Timbers Research Station, FL

| Parameter category | Plot variable | Abbreviation | Measured | Measurement location |
|---|---|---|---|---|
| Microclimate | Soil temperature | $T_s$ (°C) | 3x daily | 5 - 15 cm of collar |
| | Soil moisture content | $M_s$ ($m^3/m^3$) | 3x daily | 5 - 15 cm of collar |
| Vegetation | Basal area | BA ($m^2$ $ha^{-1}$) | Winter 2011 | 15 m radius circular plot from center collar |
| | Pine basal area | PBA ($m^2$ $ha^{-1}$) | Winter 2011 | 15 m radius circular plot from center collar |
| | Hardwood basal area | HWBA ($m^2$ $ha^{-1}$) | Winter 2011 | 15 m radius circular plot from center collar |
| | Stand density | TPH (trees $ha^{-1}$) | Winter 2011 | 15 m radius circular plot from center collar |
| | Distance to the nearest tree | Dnearest (m) | Spring 2011 | Linear distance from soil collar to nearest tree (DBH > 10 cm) |
| | Diameter of the nearest tree | DBH (cm) | Spring 2011 | DBH of the nearest tree measured in Dnearest |
| Forest floor | Duff depth | Duff (cm) | Spring 2011 | Avg. of three measurements within 30 cm of collar |
| | Litter depth | Litter (cm) | Spring 2011 | Avg. of three measurements within 30 cm of collar |
| | Total duff and litter depth | DL (cm) | Spring 2011 | Avg. of three measurements within 30 cm of collar |
| Weather | Total precipitation | Precip (cm) | Monthly | Quincy, FL FAWNS station |
| | Mean air temperature (2 m) | Temp (°C) | Monthly | Quincy, FL FAWNS station |
| | Palmer drought severity index | PDSI | Monthly | Northwest Florida regional estimate from NOAA-NCDC |

Table 2-2. Mean forest characteristics per prescribed fire treatment type at the Tall Timbers Research Station, FL

| FRI | Year | Trees (ha) | Hardwood basal area ($m^2$ $ha^{-1}$) | Pine basal area ($m^2$ $ha^{-1}$) | Total basal area ($m^2$ $ha^{-1}$) | Mean diameter at breast height (DBH) (cm) | Distance to nearest tree (m) | DBH of nearest tree (cm) | Duff depth (cm) | Litter depth (cm) | Annual litterfall (t $ha^{-1}yr^{-1}$) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1YR | 2011 | 282.93 (64.83) b | 3.87 (6.28) b | 7.92 (3.68) a | 11.79 (7.22) b | 16.48 (5.50) a | 3.26 (0.90) a | 10.38 (3.81) c | 0.08 (0.06) c | 1.77 (0.91) c | 4.63 (1.53) a |
| 2YR | 2011 | 400.81 (344.87) b | 6.30 (4.28) ab | 9.16 (6.14) a | 15.45 (2.15) b | 22.26 (8.14) a | 3.18 (1.40) a | 27.73 (7.82) a | 0.46 (0.41) b | 2.17 (0.79) b | 5.42 (0.69) a |
| 40YR | 2011 | 1716.41 (681.42) a | 15.73 (3.59) a | 21.99 (11.22) a | 37.72 (8.36) a | 12.77 (5.82) a | 1.48 (0.16) b | 14.22 (2.40) b | 1.58 (0.55) a | 2.81 (0.58) a | 5.47 (1.37) a |

Data presented are means of three sample plots per FRI treatment. Data in parentheses are standard deviation. FRI is fire return interval. Letters per column show significant differences between fire return intervals (Tukey's HSD test; Tukey 1953). Distance to nearest tree is the average distance from each soil respiration sampling point to the nearest tree (DBH > 10 cm). DBH of the nearest tree is the average DBH of the nearest tree to each soil respiration sampling point. Litter and duff depth are the average of 18 measurements taken one-time per sample plot. Litterfall rates provided by K. Robertson (unpublished data).

Table 2-3. Results of the repeated measures ANOVA for soil $CO_2$ efflux ($R_s$), soil temperature ($T_s$), and soil moisture content ($M_s$) means at the Tall Timbers Research Station, FL

| | | $R_s$ | | | $T_s$ | | | $M_s$ | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Analysis period | Source | df | F | P > F | df | F | P > F | df | F | P > F |
| Total | Month | 20 | 105.19 | < 0.0001 | 18 | 306.76 | < 0.0001 | 19 | 97.51 | < 0.0001 |
| | Treatment*Month | 40 | 3.25 | < 0.0001 | 36 | 4.04 | < 0.0001 | 38 | 1.68 | 0.0190 |
| | Treatment | 2 | 20.72 | 0.0007 | 2 | 3.09 | 0.1007 | 2 | 2.95 | 0.1130 |
| Fall | Month | 5 | 114.16 | < 0.0001 | 5 | 241.78 | < 0.0001 | 5 | 66.73 | < 0.0001 |
| | Treatment*Month | 10 | 4.12 | 0.0012 | 10 | 1.31 | 0.2684 | 10 | 2.06 | 0.0611 |
| | Treatment | 2 | 17.65 | 0.0031 | 2 | 2.70 | 0.1457 | 2 | 4.26 | 0.0705 |
| Winter | Month | 5 | 25.16 | < 0.0001 | 3 | 61.75 | < 0.0001 | 5 | 25.45 | < 0.0001 |
| | Treatment*Month | 10 | 1.96 | 0.0761 | 6 | 0.40 | 0.8650 | 10 | 1.96 | 0.0753 |
| | Treatment | 2 | 13.40 | 0.0061 | 2 | 10.48 | 0.0036 | 2 | 6.30 | 0.0335 |
| Spring | Month | 5 | 25.61 | < 0.0001 | 5 | 243.07 | < 0.0001 | 5 | 75.96 | < 0.0001 |
| | Treatment*Month | 10 | 2.73 | 0.0168 | 10 | 5.50 | 0.0001 | 10 | 1.03 | 0.4454 |
| | Treatment | 2 | 11.24 | 0.0054 | 2 | 4.11 | 0.0646 | 2 | 1.41 | 0.3003 |
| Summer | Month | 2 | 16.70 | 0.0003 | 2 | 38.05 | < 0.0001 | 1 | 139.44 | < 0.0001 |
| | Treatment*Month | 4 | 3.78 | 0.0327 | 4 | 4.70 | 0.0163 | 2 | 3.02 | 0.1235 |
| | Treatment | 2 | 16.03 | 0.0039 | 2 | 9.91 | 0.0126 | 2 | 1.32 | 0.3340 |

For each month, daily measurements per soil collar were averaged, and the nine soil collar means were then averaged to produce a plot-level mean value for each month. This resulted in a sample size of three for each FRI treatment (total n=9). The effect of month, treatment, and treatment*month on plot-level means were tested for significance ($p < 0.05$).

Table 2-4. Mean seasonal and total study period soil temperature per prescribed fire treatment type at the Tall Timbers Research Station, FL

| FRI | Fall mean $T_s$ (°C) | Winter mean soil $T_s$ (°C) | Spring mean $T_s$ (°C) | Summer mean $T_s$ (°C) | Study mean $T_s$ (°C) |
|---|---|---|---|---|---|
| 1YR | 21.74 (4.79) a | 11.86 (3.81) b | 22.04 (6.21) a | 28.84 (2.90) a | 20.45 (7.16) a |
| 2YR | 21.44 (4.35) a | 12.20 (3.59) ab | 20.67 (4.74) a | 27.81 (1.64) ab | 19.98 (6.37) a |
| 40YR | 21.10 (3.50) a | 12.93 (3.13) a | 18.90 (3.26) a | 25.90 (0.82) b | 19.42 (5.19) a |

Values are means with standard deviations in parentheses. Letters per column show significant differences between fire return intervals (Tukey's HSD test; Tukey 1953).

Table 2-5. Mean seasonal and total study period soil moisture content per prescribed fire treatment type at the Tall Timbers Research Station, FL

| FRI | Fall mean $M_s$ ($m^3/m^3$) | Winter mean $M_s$ ($m^3/m^3$) | Spring mean $M_s$ ($m^3/m^3$) | Summer mean $M_s$ ($m^3/m^3$) | Study mean $M_s$ ($m^3/m^3$) |
|---|---|---|---|---|---|
| 1YR | 0.16 (0.06) a | 0.25 (0.06) a | 0.15 (0.09) a | 0.15 (0.09) a | 0.20 (0.08) a |
| 2YR | 0.14 (0.07) a | 0.22 (0.08) ab | 0.14 (0.09) a | 0.12 (0.09) a | 0.17 (0.09) a |
| 40YR | 0.11 (0.06) a | 0.20 (0.08) b | 0.12 (0.08) a | 0.10 (0.07) a | 0.15 (0.09) a |

Values are means with standard deviations in parentheses. Letters per column show significant differences between fire return intervals (Tukey's HSD test; Tukey 1953).

Table 2-6. Mean seasonal and total study period soil $CO_2$ efflux per prescribed fire treatment type at the Tall Timbers Research Station, FL

| FRI | Fall mean $R_s$ (μmol $CO_2$ $m^{-2}$ $sec^{-1}$) | Winter mean $R_s$ (μmol $CO_2$ $m^{-2}$ $sec^{-1}$) | Spring mean $R_s$ (μmol $CO_2$ $m^{-2}$ $sec^{-1}$) | Summer mean $R_s$ (μmol $CO_2$ $m^{-2}$ $sec^{-1}$) | Study mean $R_s$ (μmol $CO_2$ $m^{-2}$ $sec^{-1}$) |
|---|---|---|---|---|---|
| 1YR | 3.36 (1.71) b | 1.24 (0.87) b | 2.56 (1.21) b | 4.93 (1.95) b | 2.67 (1.87) b |
| 2YR | 3.75 (2.02) b | 1.60 (1.24) b | 3.09 (1.39) b | 5.49 (2.11) b | 3.09 (2.12) b |
| 40YR | 4.93 (2.36) a | 2.61 (1.49) a | 3.98 (1.94) a | 7.59 (2.25) a | 4.22 (2.52) a |

Values are means with standard deviations in parentheses. Letters per column show significant differences between fire return intervals (Tukey's HSD test; Tukey 1953).

Table 2-7. Pearson's Correlations between soil $CO_2$ efflux ($R_s$), soil temperature ($T_s$), soil moisture content ($M_s$) and plot vegetative and meteorological characteristics

| Variable | $R_s$ (µmol $CO_2$ $m^{-2}$ $sec^{-1}$) | $T_s$ (°C) | $M_s$ ($m^3/m^3$) |
|---|---|---|---|
| $R_s$ (µmol $CO_2$ $m^{-2}$ $sec^{-1}$) | 1.00 | 0.68 | -0.34 |
| $T_s$ (°C) | 0.68 | 1.00 | -0.53 |
| $M_s$ ($m^3/m^3$) | -0.34 | -0.53 | 1.00 |
| Dist nearest (m) | -0.31 | 0.10 | 0.09 |
| DBH nearest (cm) | 0.01 | 0.00 | -0.07 |
| Stand density (tree $ha^{-1}$) | 0.33 | -0.09 | -0.17 |
| Basal area ($m^2$ $ha^{-1}$) | 0.34 | -0.12 | -0.23 |
| Hardwood basal area ($m^2$ $ha^{-1}$) | 0.30 | -0.12 | -0.19 |
| Pine basal area ($m^2$ $ha^{-1}$) | 0.26 | -0.08 | -0.18 |
| Duff depth (cm) | 0.36 | -0.10 | -0.23 |
| Litter depth (cm) | 0.29 | -0.12 | -0.14 |
| Duff+litter depth (cm) | 0.36 | -0.12 | -0.20 |
| Monthly temp (°C) | 0.77 | 0.91 | -0.61 |
| Monthly precip (cm) | 0.11 | 0.03 | 0.40 |

Correlations are of monthly mean plot measurements with treatments ignored and all treatment x plot x month means pooled. $R_s$ is soil $CO_2$ efflux rate (µmol $CO_2$ $m^{-2}$ $sec^{-1}$), $T_s$ is soil temperature (°C), $M_s$ is soil volumetric moisture content ($m^3/m^3$). Plot vegetative and meteorological characteristics described further in Table 2-1.

Table 2-8. Linear regression relationships between soil $CO_2$ efflux rates and field conditions by fire return interval

| FRI | Variable | Model and estimates | $R^2$ | p |
|---|---|---|---|---|
| 1YR | $T_s$ | $R_s = -0.5101 + 0.16029*T_s$ | 0.62 | < 0.001 |
| 1YR | $M_s$ | $R_s = 3.6182 - 6.3661* M_s$ | 0.14 | 0.004 |
| 1YR | Mean Temp | $R_s$ = -0.4641 + 0.1799*M Temp | 0.76 | < 0.001 |
| 2YR | $T_s$ | $R_s = -1.1736 + 0.2218*T_s$ | 0.78 | < 0.001 |
| 2YR | $M_s$ | $R_s = 4.1907 - 7.6204* M_s$ | 0.14 | 0.003 |
| 2YR | Mean Temp | $R_s$ = -0.1556 + 0.1918*M Temp | 0.77 | < 0.001 |
| 40YR | $T_s$ | $R_s = -2.0303 + 0.3337 *T_s$ | 0.65 | < 0.001 |
| 40YR | $M_s$ | $R_s = 4.6763 - 4.6868* M_s$ | 0.03 | 0.215 |
| 40YR | Mean Temp | $R_s$ = 0.2708 + 0.2291*M Temp | 0.61 | < 0.001 |

Model data are mean monthly measurements from August 2009 – May 2011 taken at the Tall Timbers Research Station near Tallahassee, Florida, USA. $R_s$ is soil $CO_2$ efflux rate (μmol $CO_2$ $m^{-2}$ $sec^{-1}$), $T_s$ is soil temperature (°C), $M_s$ is soil volumetric moisture content ($m^3/m^3$), Mean Temp is the mean monthly air temperature (°C), Models other than $M_s$ that had fit less than $R^2 = 0.10$ were not reported.

Table 2-9. Results of nonlinear models of soil $CO_2$ efflux rates using soil temperature as a predictor

| FRI | Model | $Q_{10}$ | $R^2$ | p |
|---|---|---|---|---|
| 1YR | $R_s = 0.9727\ e^{0.0502*Ts}$ | 1.65 | 0.60 | < 0.001 |
| 2YR | $R_s = 0.7973\ e^{0.0673*Ts}$ | 1.96 | 0.80 | < 0.001 |
| 40YR | $R_s = 0.9712\ e^{0.0770*Ts}$ | 2.16 | 0.76 | < 0.001 |

Models are of monthly mean soil $CO_2$ efflux rate ($R_s$) (μmol $CO_2$ $m^{-2}$ $sec^{-1}$) responses to soil temperature ($T_s$). Data are presented by prescribed fire return interval (FRI). Coefficients were estimated using statistical software JMP 9.0. $Q_{10}$ was calculated using the exponential equation $Q_{10} = e^{10\beta 1}$ (Lundegardh, 1927) where β1 was the coefficient estimated in the initial model. $R^2$ is the linear regression fit of the exponentially predicted $R_s$ values against the observed $R_s$ values and *p* is the significance of the model fit of predicted to observed values.

Table 2-10. Linear regression relationship between soil $CO_2$ efflux rates and soil temperature by fire return interval and season

| FRI | Season | Model and estimates | $R^2$ | p |
|---|---|---|---|---|
| 1YR | Spring | $R_s$ = 1.0261 + 0.0700*$T_s$ | 0.29 | 0.021 |
| | Summer | $R_s$ = 12.83.11 - 0.2799*$T_s$ | 0.40 | 0.068 |
| | Fall | $R_s$ = -1.4494 + 0.2159*$T_s$ | 0.71 | < 0.001 |
| | Winter | $R_s$ = -0.4895 + 0.14355*$T_s$ | 0.69 | 0.002 |
| 2YR | Spring | $R_s$ = 1.0808 + 0.09766*$T_s$ | 0.48 | 0.002 |
| | Summer | $R_s$ = 15.7301 - 0.3751*$T_s$ | 0.28 | 0.144 |
| | Fall | $R_s$ = -3.1609 + 0.3197*$T_s$ | 0.90 | < 0.001 |
| | Winter | $R_s$ = -0.4894 + 0.1661*$T_s$ | 0.71 | 0.002 |
| 40YR | Spring | $R_s$ = 1.5400 + 0.1302*$T_s$ | 0.11 | 0.170 |
| | Summer | $R_s$ = 49.5720 - 1.6300*$T_s$ | 0.63 | 0.011 |
| | Fall | $R_s$ = -4.3665 + 0.4270*$T_s$ | 0.71 | < 0.001 |
| | Winter | $R_s$ = -2.0244 + 0.3544*$T_s$ | 0.90 | < 0.001 |

Spring (March - May), summer (June - August), fall (September - November), and winter (December - February). $R_s$ is soil $CO_2$ efflux rate (μmol $CO_2$ $m^{-2}$ $sec^{-1}$), $T_s$ is soil temperature (°C).

Table 2-11. Seasonal nonlinear models of soil $CO_2$ efflux rates using soil temperature as a predictor

| FRI | Season | Equation | $Q_{10}$ | $R^2$ | p |
|---|---|---|---|---|---|
| 1YR | Spring | $R_s = 1.5095\ e^{0.0238*Ts}$ | 1.27 | 0.26 | 0.031 |
| | Summer | $R_s = 37.6590\ e^{-0.0721*Ts}$ | 0.49 | 0.45 | 0.049 |
| | Fall | $R_s = 0.8564\ e^{0.0598*Ts}$ | 1.82 | 0.66 | < 0.001 |
| | Winter | $R_s = 0.2704\ e^{0.1200*Ts}$ | 3.32 | 0.77 | 0.000 |
| 2YR | Spring | $R_s = 0.2778\ e^{0.1250*Ts}$ | 3.49 | 0.33 | 0.012 |
| | Summer | $R_s = 36.2629\ e^{-0.0692*Ts}$ | 0.50 | 0.27 | 0.149 |
| | Fall | $R_s = 0.5967\ e^{0.0823*Ts}$ | 2.28 | 0.89 | < 0.001 |
| | Winter | $R_s = 0.3701\ e^{0.1114*Ts}$ | 3.05 | 0.78 | 0.001 |
| 40YR | Spring | $R_s = 2.2967\ e^{0.0292*Ts}$ | 1.34 | 0.10 | 0.195 |
| | Summer | $R_s = 259.9167\ e^{-0.1388*Ts}$ | 0.25 | 0.62 | 0.012 |
| | Fall | $R_s = 0.6935\ e^{0.0883*Ts}$ | 2.42 | 0.69 | < 0.001 |
| | Winter | $R_s = 0.3990\ e^{0.1383*Ts}$ | 3.99 | 0.96 | < 0.001 |

Models are of monthly mean soil $CO_2$ efflux rate ($R_s$) (µmol $CO_2$ $m^{-2}$ $sec^{-1}$) responses to soil temperature ($T_s$). Data are presented by prescribed fire return interval (FRI). Coefficients were estimated using statistical software JMP 9.0. $Q_{10}$ was calculated using the exponential equation $Q_{10} = e^{10\beta1}$ (Lundegardh, 1927) where β1 was the coefficient estimated in the initial model.

Table 2-12. Seasonal linear models of soil $CO_2$ efflux rates using soil moisture content as a predictor

| FRI | Season | Equation | $R^2$ | p |
|---|---|---|---|---|
| 1YR | Spring | $R_s = 2.7146 - 1.0286*M_s$ | 0.01 | 0.675 |
| | Summer | $R_s = 3.8796 + 4.5559*M_s$ | 0.13 | 0.475 |
| | Fall | $R_s = 2.2962 + 7.8960*M_s$ | 0.15 | 0.109 |
| | Winter | $R_s = 1.0143 + 0.5351*M_s$ | 0.00 | 0.904 |
| 2YR | Spring | $R_s = 3.4316 - 2.5191*M_s$ | 0.08 | 0.264 |
| | Summer | $R_s = 4.2300 + 7.2134*M_s$ | 0.44 | 0.152 |
| | Fall | $R_s = 2.5987 + 10.2822*M_s$ | 0.14 | 0.129 |
| | Winter | $R_s = 2.4157 - 3.7664*M_s$ | 0.05 | 0.366 |
| 40YR | Spring | $R_s = 3.9373 + 0.6649*M_s$ | 0.00 | 0.887 |
| | Summer | $R_s = 4.3603 + 28.4285*M_s$ | 0.82 | 0.013 |
| | Fall | $R_s = 2.1477 + 28.9752*M_s$ | 0.49 | 0.001 |
| | Winter | $R_s = 2.8535 - 2.0522*M_s$ | 0.02 | 0.627 |

Spring (March-May), summer (June-August). fall (September-November), winter (December-February). $R_s$ is soil $CO_2$ efflux rate (µmol $CO_2$ $m^{-2}$ $sec^{-1}$), $M_s$ is soil moisture content ($m^3/m^3$).

Table 2-13. Step-wise multiple regression models to explain soil $CO_2$ efflux rates using field parameters

| FRI | Model | $R^2$ | RMSE | p |
|---|---|---|---|---|
| All FRI | $R_s$ = -2.982 + 0.243*M Temp + 8.416*$M_s$ + 1.178*Duff Depth | 0.80 | 0.78 | < 0.001 |
| 1YR | $R_s$ = -0.766 + 0.209*M Temp + 5.103* $M_s$ - 0.334*Dist Nearest | 0.86 | 0.52 | < 0.001 |
| 2YR | $R_s$ = -3.312 + 0.255* $T_s$ + 6.990* $M_s$ + 0.049*P BA | 0.89 | 0.50 | < 0.001 |
| 40YR | $R_s$ = -2.292 + 0.421* $T_s$ + 16.805* $M_s$ - 2.512*Dist Nearest | 0.82 | 0.86 | < 0.001 |

$R_s$ is soil $CO_2$ efflux rate (μmol $CO_2$ $m^{-2}$ $sec^{-}1$), FRI is prescribed fire return interval treatment type. For model term details see Table 2-1. Terms were selected for inclusion using a forward step-wise procedure in SAS JMP 9.0 (SAS Institute Inc., Cary, North Carolina, USA) based on input parameter significance ($p < 0.05$) and minimum model BIC.

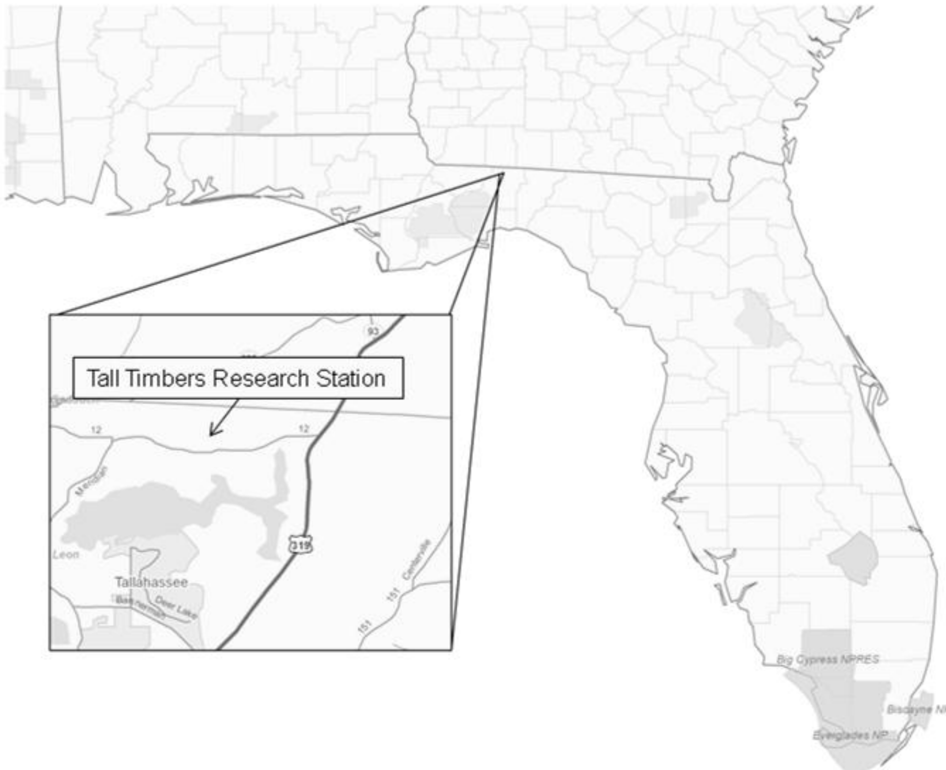


Figure 2-1. The research site, Tall Timbers Research Station, was located in Leon County, Florida, USA. The site is approximately 30 km north of the city of Tallahassee, Florida, USA. Map produced by David Godwin.

Figure 2-2. Ground (left) and aerial (right) images of three of the soil $CO_2$ efflux sampling plots located within the Tall Timbers Research Station in Leon County, Florida, USA. The top images show an annual burn frequency site (1YR), the middle images a two-year burn frequency site (2YR), and the bottom image a site unburned since 1966. Ground images original to the author. Ground photographs courtesy of David Godwin. Aerial images courtesy of Microsoft Bing Maps.

Figure 2-3. PVC soil $CO_2$ efflux rate ($R_s$) sampling collar (20 cm diameter) installed at a frequently burned plot at the Tall Timbers Research Station near Tallahassee, Florida, USA. Photograph courtesy of David Godwin.

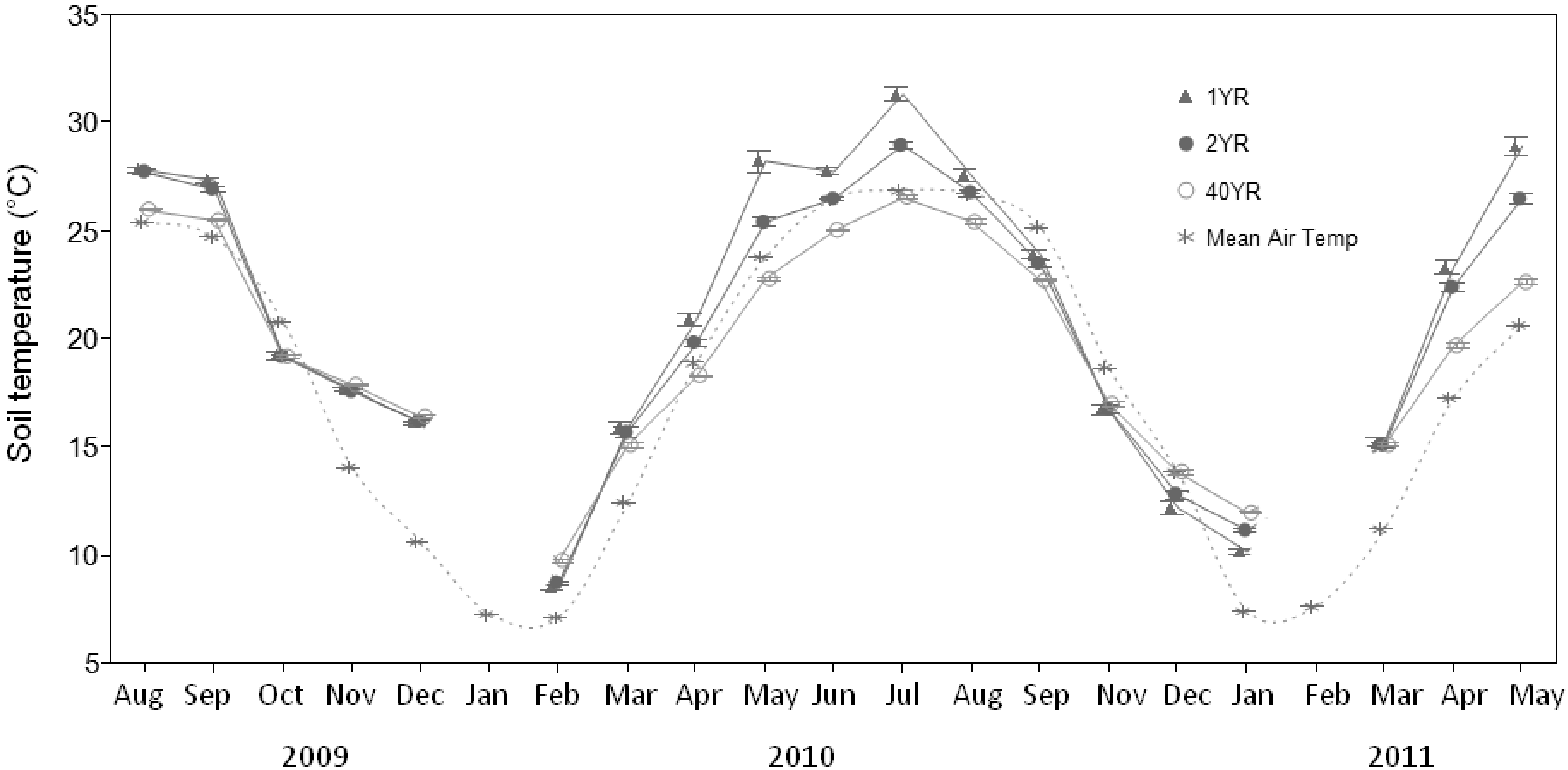


Figure 2-4. Monthly mean soil temperature (°C) and monthly mean regional 2 m air temperature (Mean Air Temp) for three prescribed fire treatment types at the Tall Timbers Research Station near Tallahassee, Florida, USA. Soil temperature data were from 27 sample points per treatment type, measured three-times daily once per month. Mechanical difficulty resulted in erroneous data collected in January 2009 and February 2011. Data were not recorded in the month of October 2010. Monthly mean air temperature were recorded hourly at the Florida Automated Weather Network (FAWN) station approximately 30 km away in Quincy, Florida.

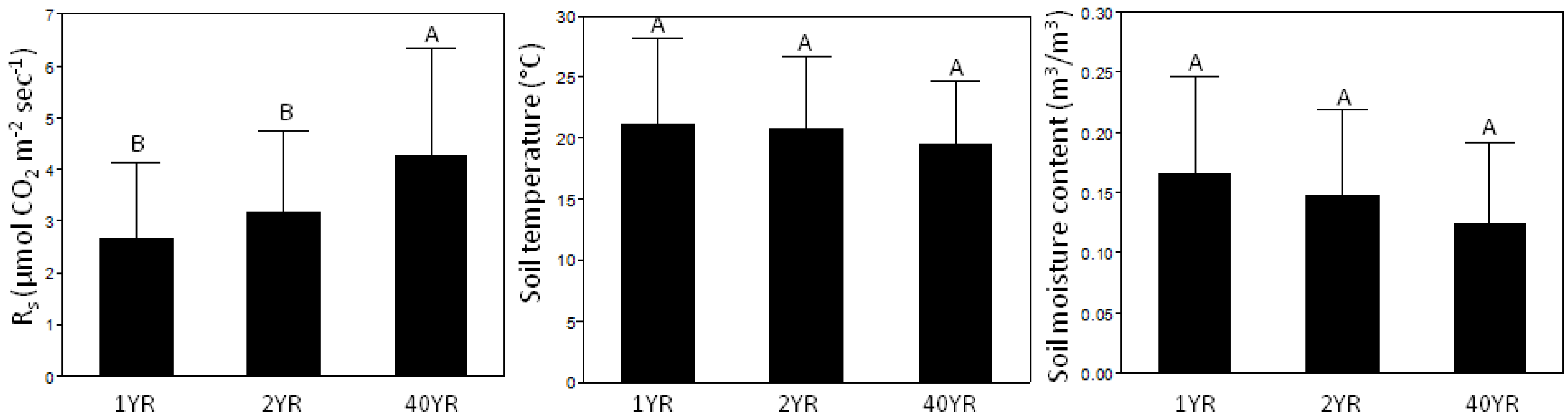


Figure 2-5. Mean soil $CO_2$ efflux rate (µmol $CO_2$ m$^{-2}$ sec$^{-1}$), soil temperature (°C), and soil moisture content (m$^3$/m$^3$) per prescribed fire treatment type at Tall Timbers Research Station near Tallahassee, Florida, USA. Data represent overall study area means of monthly measurements from August 2009 until May 2011. Letters indicate significant differences between treatment types assessed using repeated measures ANOVA and Tukey's HSD test (α = 0.05).

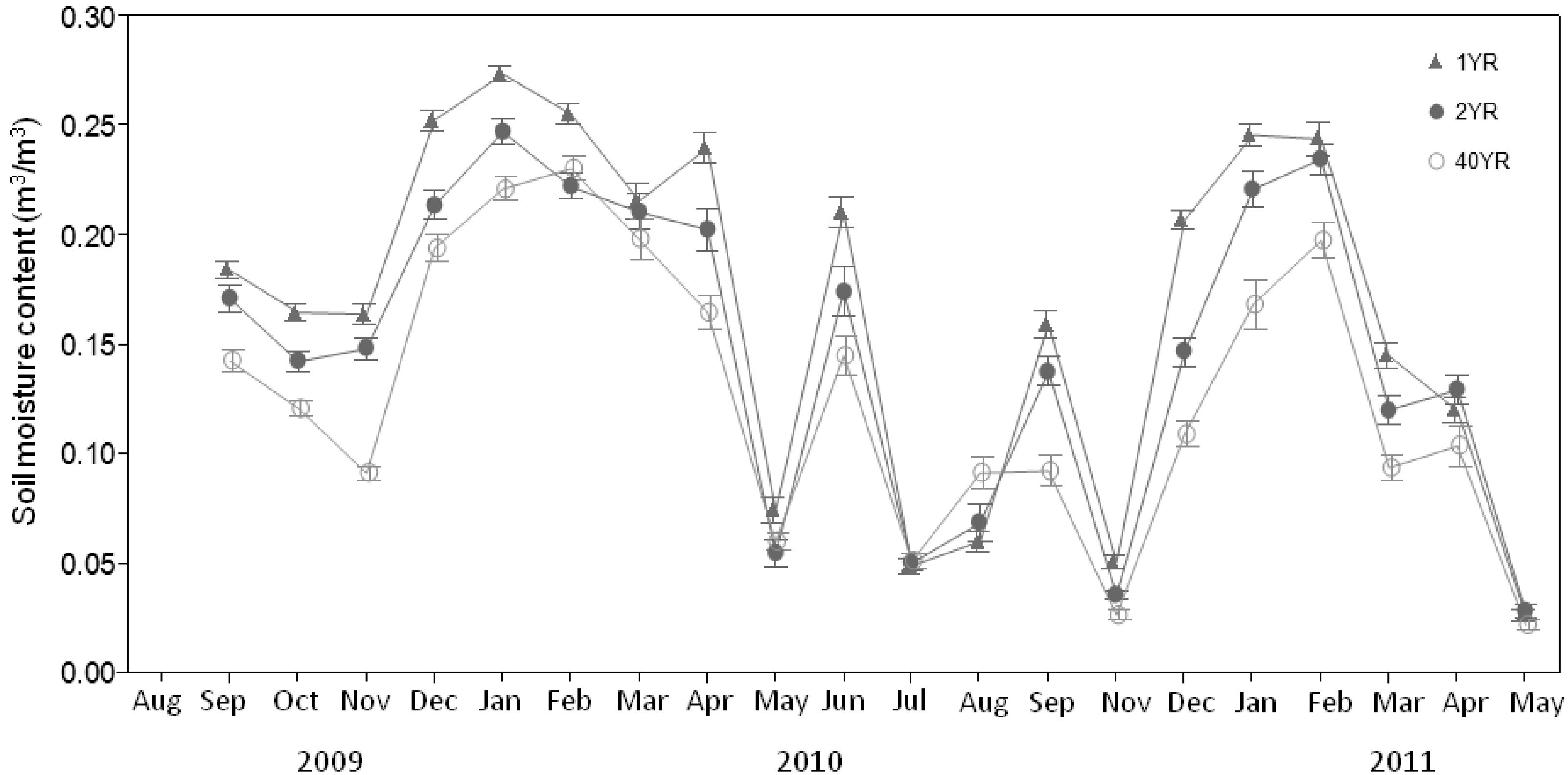


Figure 2-6. Monthly mean soil moisture content ($m^3/m^3$) for three prescribed fire treatment types at the Tall Timbers Research Station near Tallahassee, Florida, USA. Mechanical difficulty resulted in erroneous data collected in August 2009. Data were not recorded in the month of October 2010.

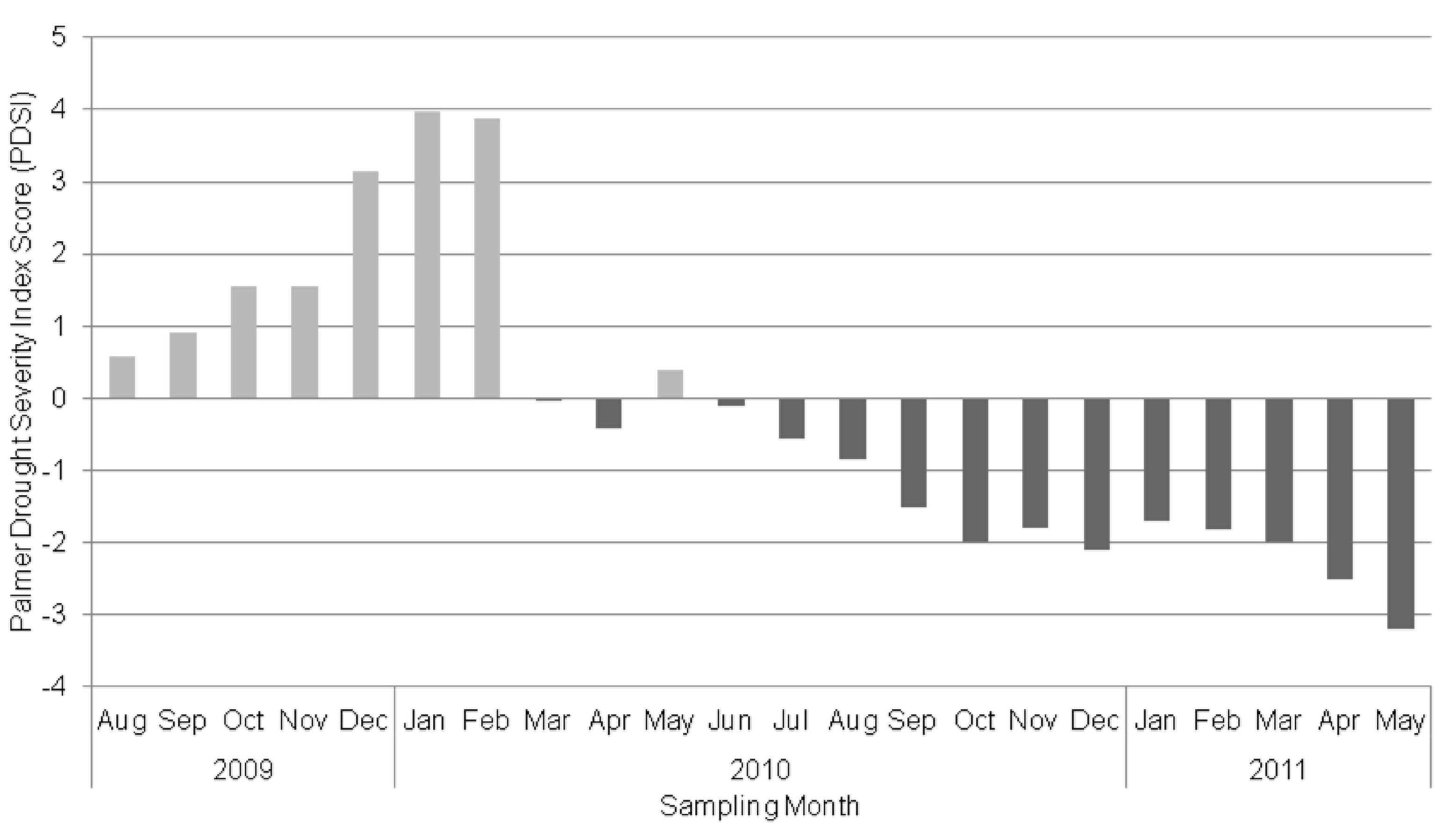


Figure 2-7. Monthly regional Palmer Drought Severity Index (PDSI) scores from the National Oceanic and Atmospheric Administration (NOAA) National Climatic Data Center (NCDC). All scores below zero represent drought conditions for the northwest Florida region.

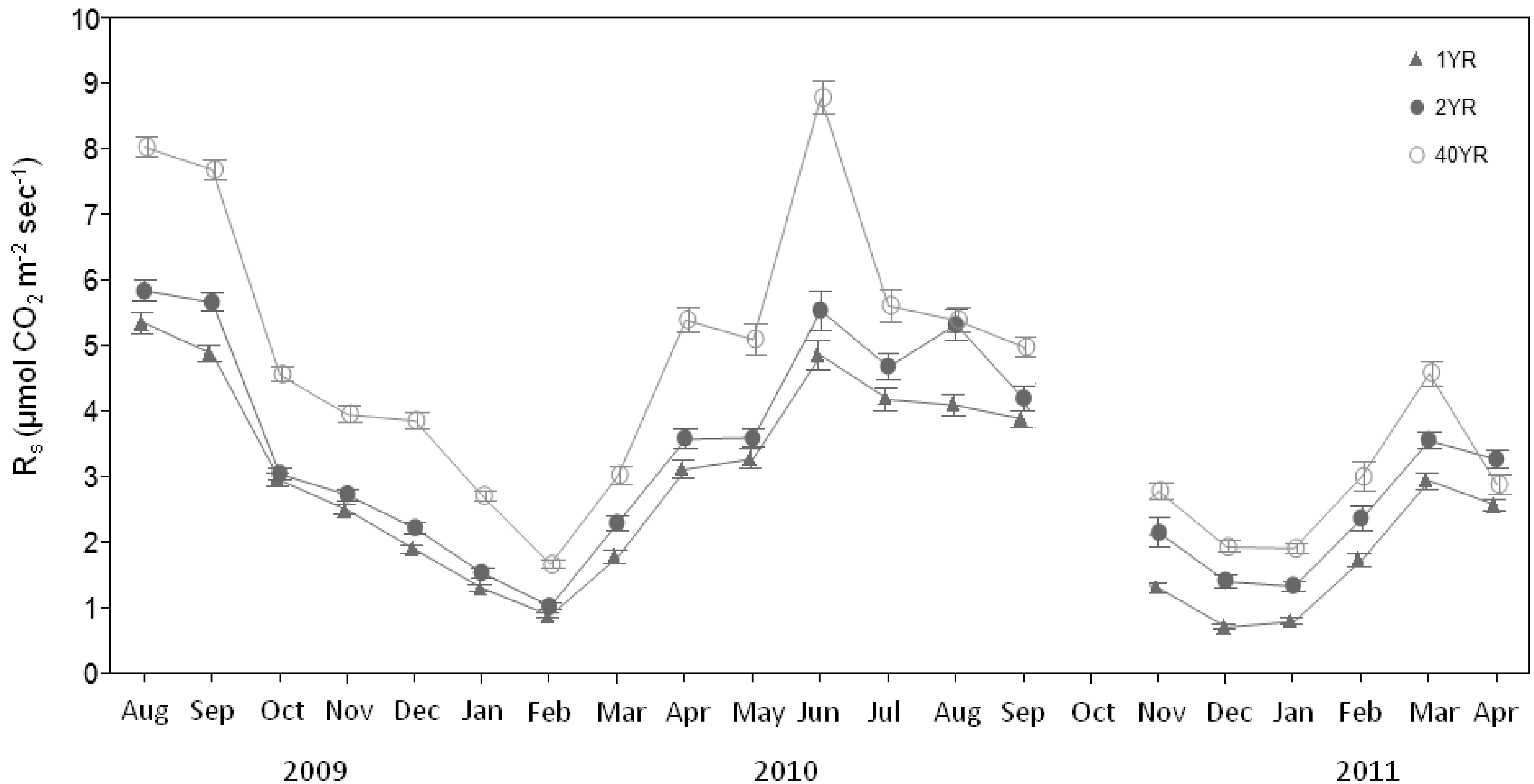


Figure 2-8. Monthly mean soil $CO_2$ efflux rates (µmol $CO_2$ $m^{-2}$ $sec^{-1}$) for three prescribed fire treatment types at the Tall Timbers Research Station near Tallahassee, Florida, USA. Data were from 27 sample points per treatment type, measured three-times daily once per month. Data were not recorded in the month of October 2010.

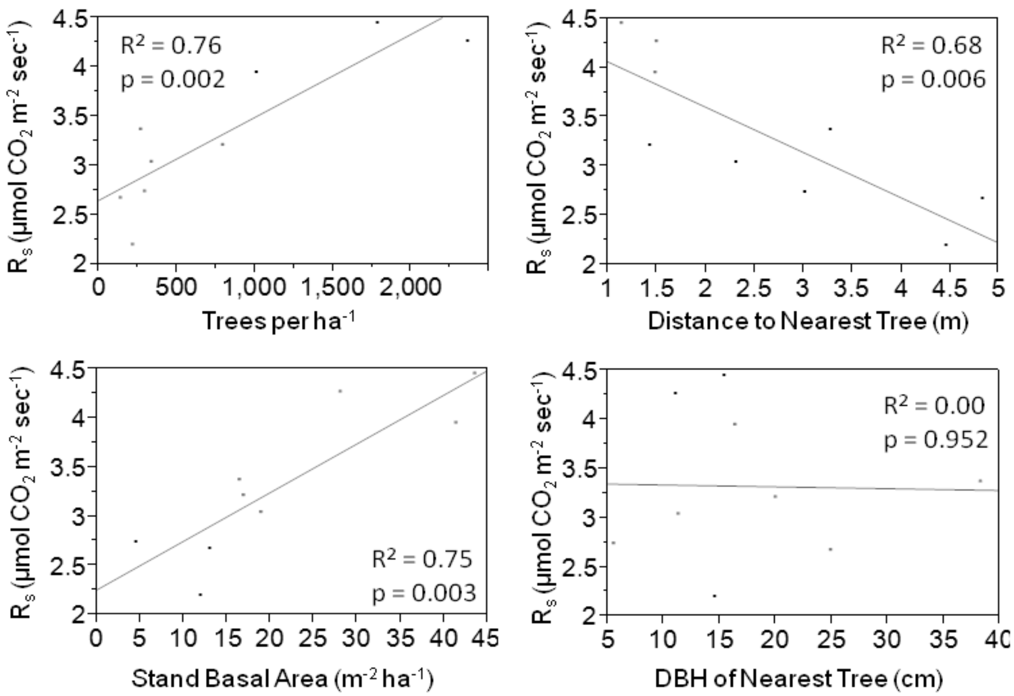


Figure 2-9. Linear regression of the relationships between mean soil $CO_2$ efflux rates ($R_s$) (µmol $CO_2$ $m^{-2}$ $sec^{-1}$) and mean: stand density (trees per $ha^{-1}$), distance to nearest tree (m), stand basal area ($m^{-2}$ $ha^{-1}$), and diameter at breast height of the nearest tree (cm). Each point represents entire study period means per sample plot with all treatments combined.

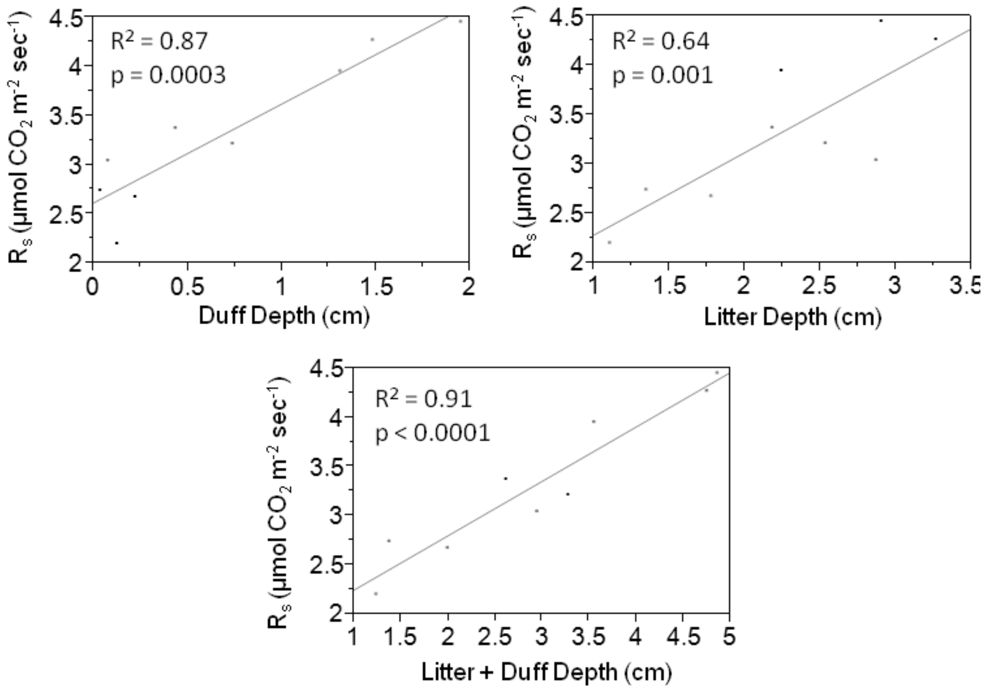


Figure 2-10. Linear regression of the relationships between mean soil $CO_2$ efflux rates ($R_s$) (µmol $CO_2$ $m^{-2}$ $sec^{-1}$) and mean: duff depth (cm), litter depth, and total litter+duff depth (cm). Each point represents entire study period means per sample plot with all treatments combined.

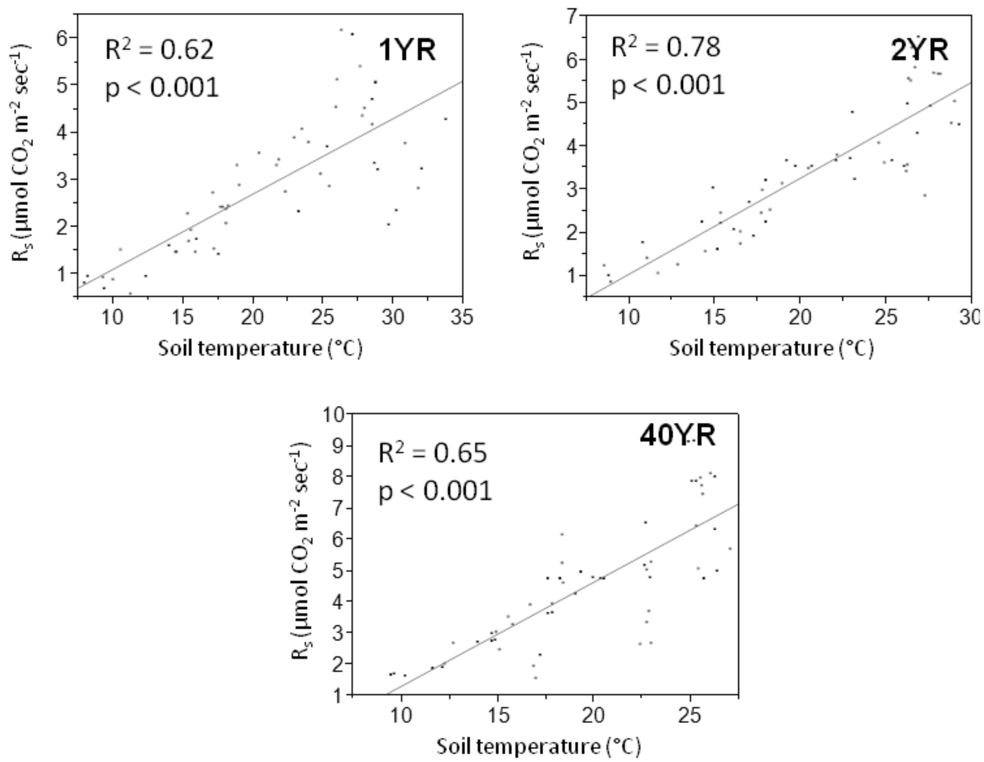


Figure 2-11. Linear regression of the relationships between monthly mean soil $CO_2$ efflux rates ($R_s$) (µmol $CO_2$ $m^{-2}$ $sec^{-1}$) and monthly mean soil temperature ($T_s$) (°C) for three prescribed fire intervals at the Tall Timbers Research Station near Tallahassee, Florida, USA. Each point represents monthly mean values per sample plot.

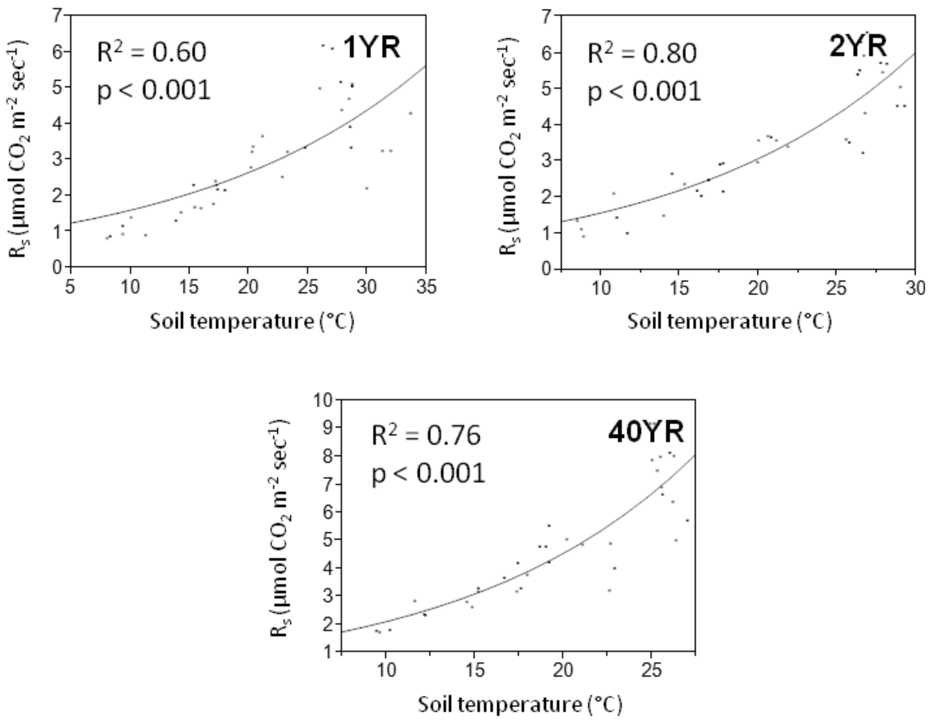


Figure 2-12. The relationship between monthly mean soil $CO_2$ efflux rates (µmol $CO_2$ $m^{-2}$ $sec^{-1}$) ($R_s$) and monthly mean soil temperature (°C) ($T_s$) as modeled using an exponential equation (Equation 2-2). Data presented are from sites at the Tall Timbers Research Station near Tallahassee, Florida, USA, representing three prescribed fire treatment intervals. Each point represents monthly mean values per sample plot.

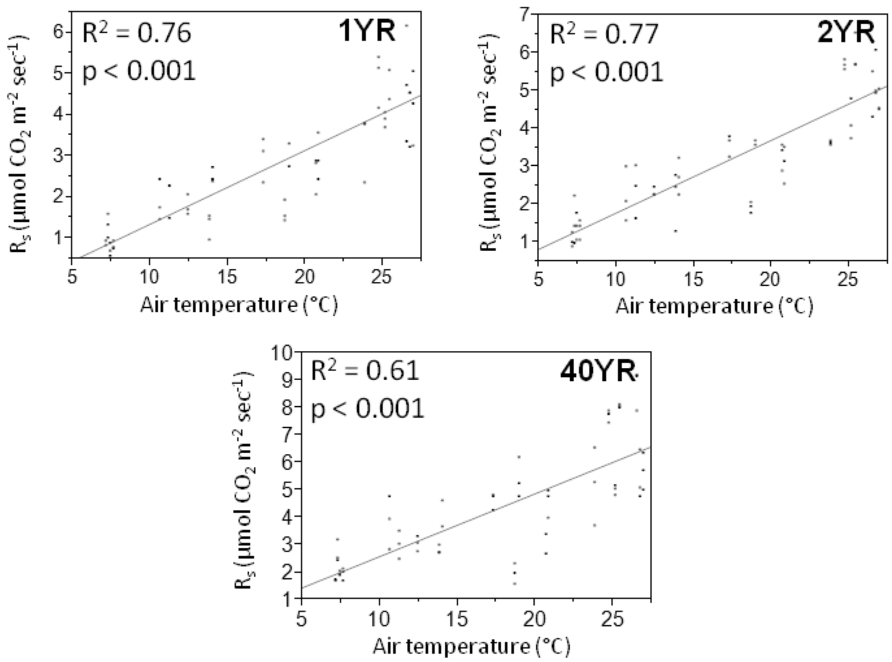


Figure 2-13. Linear regression of the relationships between monthly mean soil $CO_2$ efflux rates ($R_s$) (µmol $CO_2$ $m^{-2}$ $sec^{-1}$) and monthly mean air temperature (M Temp) (°C) for three prescribed fire intervals at the Tall Timbers Research Station near Tallahassee, Florida, USA. Monthly air temperature data were from the Florida Automated Weather Network Station (FAWNS) at Quincy, Florida, USA. Each point represents monthly mean values per sample plot.

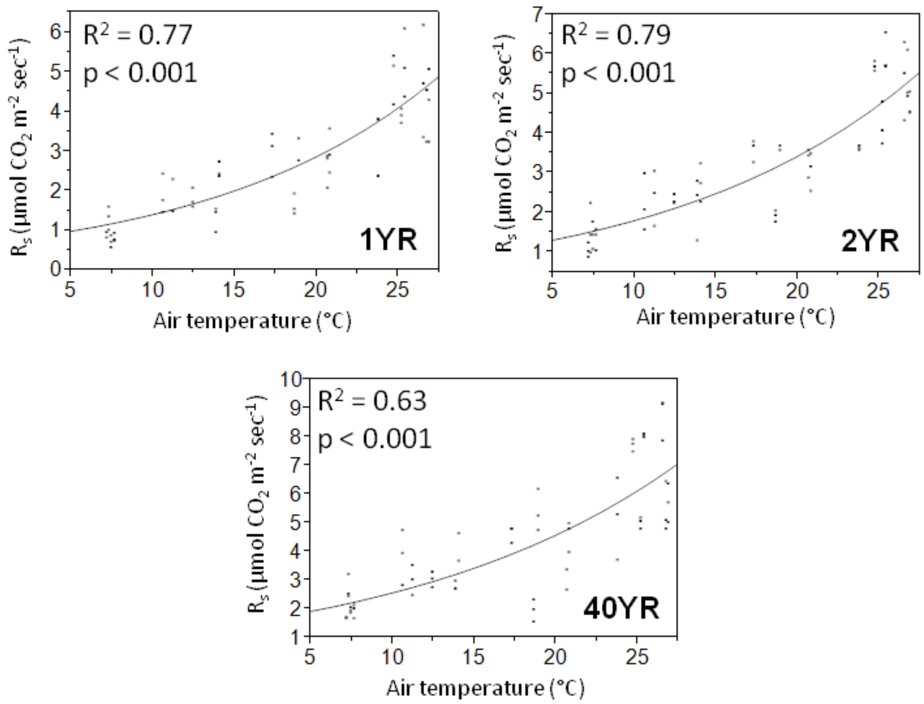


Figure 2-14. The relationship between monthly mean soil $CO_2$ efflux rates (μmol $CO_2$ $m^{-2}$ $sec^{-1}$) ($R_s$) and monthly mean air temperature (°C) (M Temp) as modeled using an exponential equation (Equation 2-2). Data presented are from sites at the Tall Timbers Research Station near Tallahassee, Florida, USA, representing three prescribed fire treatment intervals. Monthly air temperature data were from the Florida Automated Weather Network Station (FAWNS) at Quincy, Florida, USA. Each point represents monthly mean values per sample plot.

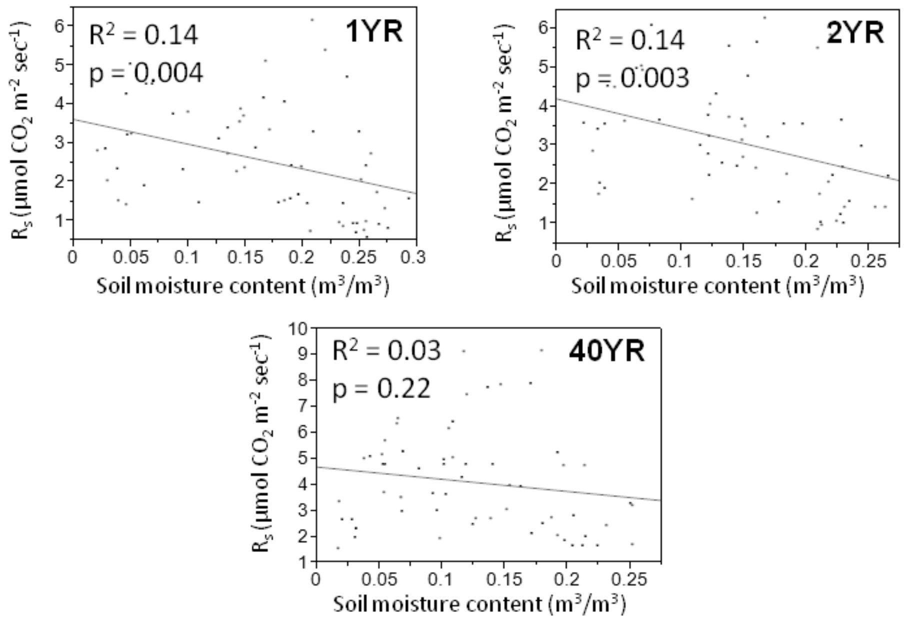


Figure 2-15. Linear regression of the relationships between monthly mean soil $CO_2$ efflux rates ($R_s$) (µmol $CO_2$ $m^{-2}$ $sec^{-1}$) and monthly mean soil moisture content ($M_s$) ($m^3/m^3$) for three prescribed fire intervals at the Tall Timbers Research Station near Tallahassee, Florida, USA. Each point represents monthly mean values per sample plot.

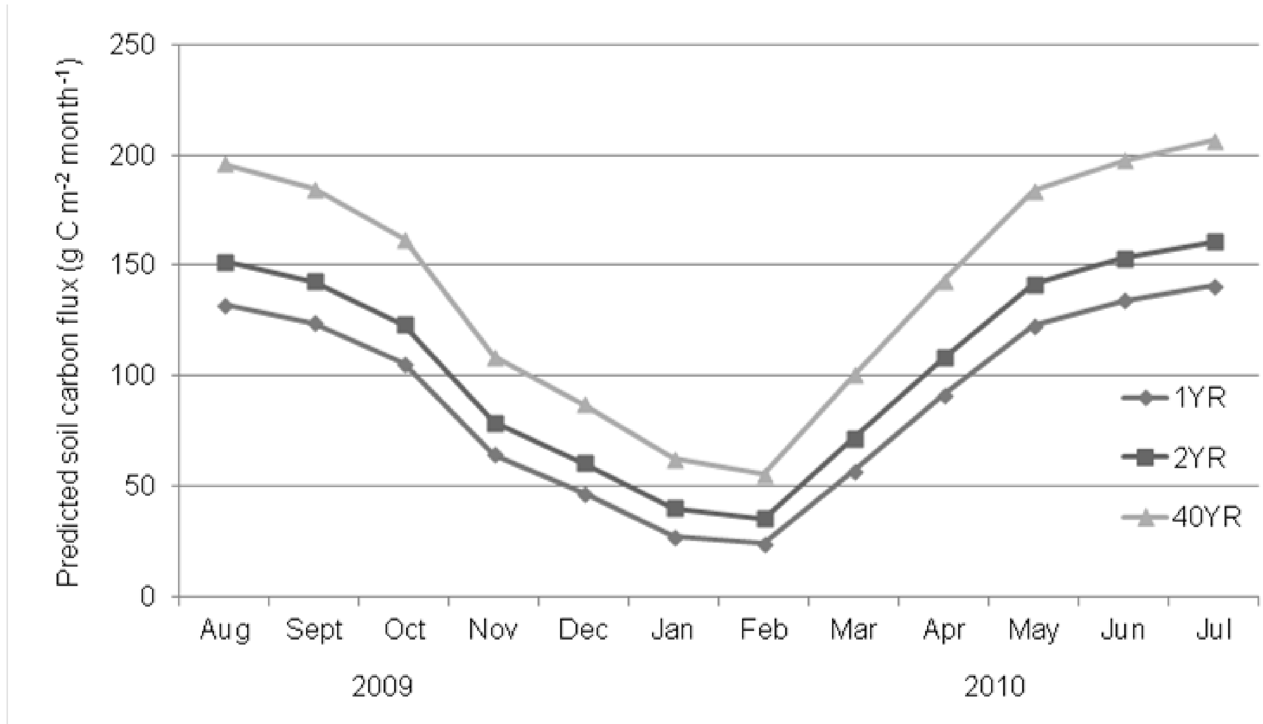


Figure 2-16. Predicted monthly total soil carbon flux from August 2009 to July 2010 by prescribed fire return interval (FRI). Flux values were predicted using FRI specific linear models of soil $CO_2$ efflux rate responses to 2 m ambient air temperature.

# CHAPTER 3
# THE EFFECTS OF LITTER INPUTS AND PRESCRIBED FIRE ON SOIL CO2 EFFLUX RATES IN NORTH FLORIDA OLD-FIELD FORESTS

## Background

Forests and forest soils are a significant repository of global carbon and represent 70% of the world's terrestrial carbon pool (Post et al., 1982; Luo and Zhou, 2006). In recent years forest management practices that reduce carbon emissions and increase carbon sequestration have been identified as a potential pathway towards reducing global atmospheric $CO_2$ concentrations (McKinley et al., 2011; Maier et al., 2012). One way that management practices have shown to influence forest carbon emissions is through their effect on soil $CO_2$ efflux rates (Luo and Zhou, 2006). Soil $CO_2$ efflux ($R_s$) represents one of the dominant fluxes of $CO_2$ from forested systems to the atmosphere, with the estimated global annual $R_s$ flux an order of magnitude greater than total anthropogenic emissions from fossil fuel combustion (Schlesinger and Andrews, 2000; Luo and Zhou, 2006). Given the magnitude of the $R_s$ flux and the significant role that forest soils play in global carbon dynamics it is important to understand the connections between forest management practices and the factors that drive soil $CO_2$ efflux rates.

Soil $CO_2$ efflux ($R_s$) is a combination of $CO_2$ respired by plant roots and associated rhizosphere fungi ($R_a$) and heterotrophic soil microorganisms ($R_h$). Methods of partitioning the relative contribution of $R_h$ and $R_a$ sources to $R_s$ have been discussed in detail recently by several authors (Hanson et al., 2000; Kuzyakov, 2006; Subke et al., 2006). It has been recognized that one of the greatest challenges to partitioning sources of $R_s$ is the delineation among sources in the field without disturbing the soil matrix and biota (Fenn et al., 2010). In place of invasive field methods of partitioning such as trenching and girdling, or *ex situ* methods such as laboratory incubation, some studies have investigated the specific response of $R_h$ relative to $R_s$ by manipulating labile carbon inputs (Cleveland et al., 2006; Salamanca et al., 2006; Zimmermann et al., 2009; Chemidlin Prévost-Bouré et al., 2010). While litter manipulation treatments are not substitutions for experimental partitioning methods, they can reveal information about the importance of aboveground inputs on soil $CO_2$ efflux without heavily impacting soil biotic and abiotic conditions.

It has been shown that litterfall and leaf litter can be a source of carbon for the heterotrophic soil microbes responsible for $R_h$ fluxes (Nahdelhoffer et al., 2004; Luo and Zhou, 2006; Sayer, 2006). Understanding the $R_s$ and $R_h$ response to variable vegetative aboveground inputs and management regimes is relevant for understanding and predicting soil carbon dynamics under changing climate and vegetation assemblages (Sayer, 2006). Improving the understanding of these mechanisms is particularly important as studies have suggested that increased atmospheric $CO_2$ and anthropogenic N deposition may lead to increased litterfall and altered soil carbon fluxes as heterotrophic soil microorganisms respond to changing carbon inputs (Zak et al., 2003; Quinn Thomas et al., 2009).

Many previous studies following direct leaf and needle litter additions have reported increased $R_s$ rates relative to controls, with the responses attributed to increased $R_h$ contributions to $R_s$ (Bowden et al., 1993; Jonasson et al., 2004; Salamanca et al., 2006; Sulzman et al., 2012). Aerobic soil microbial populations have also been shown to increase metabolic activity when presented with more targeted labile carbon additions such as: glucose, amino acids, root exudates, and dissolved organic matter (DOM) (Nobili et al., 2001; Cleveland et al., 2006). Temporal responses of soil microbial populations to carbon additions have proven to be relatively short, with elevated soil $CO_2$ efflux rates observed within ~12 hours of treatment with elevated rates lasting many days or months (Nobili et al., 2001; Cleveland et al., 2006; Chemidlin Prévost-Bouré et al., 2010). Seasonal variations in litter inputs to the soil have also been shown to influence $R_s$ rates, with increased rates observed in the autumn season - despite decreased aboveground photosynthetic activity and soil temperature (Kutsch et al., 2010). Such autumnal increases in $R_s$ have been attributed to the availability of labile carbon from deciduous leaf senescence during the autumn months (Kutsch et al., 2010).

Previous studies have found litter exclusion to reduce $R_s$ rates due to a reduction in available carbon for soil microbial metabolism. Li et al. (2004) reported that prolonged (7 years) litter exclusion in a natural *Pinus* stand in Puerto Rico reduced (54%) in-situ $R_s$ rates as well as soil microbial biomass (67%) relative to control. Similarly, in a hardwood forest in North Carolina, USA, Reynolds and Hunter (2001) found that litter exclusion during a six-month study significantly reduced $R_s$ rates relative to control. In a deciduous hardwood forest in Massachusetts, USA, Bowden et al. (1993) determined following a six-month litter exclusion experiment that the decomposition of recent leaf litter represented approximately 12% of total $R_s$ rates.

Our study sought to address the response of $R_s$ as a proxy for $R_h$ to changes in aboveground litterfall within forest stands representing three prescribed fire management regimes: annual prescribed fire (1YR), biennial prescribed fire (2YR) and fire exclusion (40YR). The intention of this study was to assess the relative influence of inputs of leaf litter as a labile carbon source for heterotrophic soil microorganism metabolism within each common fire management type. The manipulation of labile carbon inputs was intended to give insight into the magnitude, temporal, and seasonal response of the heterotrophic soil microorganisms to leaf litter carbon inputs. While not directly partitioning sources of $R_s$, this experiment specifically targeted the $R_h$ component of $R_s$ without invasive or destructive procedures. This study seeks to address the hypothesis that aboveground litter influences heterotrophic soil microbial decomposition and soil $CO_2$ efflux rates in both frequently burned and long-unburned old-field forests.

## Methods

### Study Site

The study sites were located within the Tall Timbers Fire Ecology Research Plots (Stoddard Fire Research Plots) at the Tall Timbers Research Station (TTRS) in Leon County, Florida, USA, approximately 30 km from the cities of Tallahassee, Florida (to the south) and Thomasville, Georgia (to the north) (30° 39'N, -084° 12'W) (Figure 3-1)( Clewell and Komarek, 1975; Glitzenstein et al., 2012). The Stoddard Fire Research Plots were established in the 1960s as a long-term study of the influence of prescribed fire frequency on old-field forest vegetation and soils (Clewell and Komarek, 1975; Glitzenstein et al., 2012). Prior to establishment of the plots most of the region was burned annually to improve hunting since the late 1800s and 1920s (K Robertson, 2012 pers. comm.). For this study, sampling took place within the annually burned (1YR), biennially burned (2YR) and fire excluded (40YR) Stoddard Fire Research Plots (Figure 3-2). The study site elevation was approximately 59 m a.s.l. Average annual precipitation was 137 cm with the majority falling during the summer months of June, July and August (National Climate Data Center 2009, Thomasville, Georgia). Mean maximum and minimum temperatures for January and July for the area from long-term records (1971-2000) were 16.8°C and 4.6°C for January and 33°C and 21.8°C for July (National Climate Data Center 2009, Thomasville, Georgia). Soils within the sites were heavily cultivated for corn and cotton from the 1820s-1920s and occasionally as recently as the 1950s, with subsequent soil and vegetation assemblages highly influenced by past agricultural practices (Clewell and Komarek, 1975). Soils were generally classified as fine-loamy, kaolinitic, thermic Typic Kandiudults of the Orangeburg and Faceville series (Natural Resource Conservation Service (NRC) Soil Survey Geographic Database (SSURGO)). Vegetation across the frequently burned sites consisted of an overstory mixture of naturally regenerated shortleaf pine (*Pinus echinata* P. Mill), and loblolly pine (*P. taeda* L.) and an understory composed of annual grasses and hardwood resprouts (Clewell and Komarek, 1975; Myers and Ewel, 1990; Engstrom and Palmer, 2005; Glitzenstein et al., 2012). Vegetation within the unburned sites consisted of a mixture of shortleaf pine, loblolly pine, sweetgum (*Liquidambar styraciflua* L.), mockernut hickory (*Carya alba* (L.) Nutt. ex Ell.), live oak (*Quercus virginiana* P. Mill.) and water oak (*Q. nigra* L.) (Clewell and Komarek, 1975; Myers and Ewel, 1990).

**Litter Manipulation and Sampling**

The seven-month litter manipulation and $R_s$ sampling experiment was established in May, 2011. From June, 2011 until December, 2011, soil $CO_2$ efflux rates ($R_s$) (μmol $CO_2$ $m^{-2}$ $sec^{-1}$), soil temperature ($T_s$) (°C), and soil volumetric moisture content ($M_s$) ($m^3/m^3$) were sampled three times a day once per month. Sampling took place within a total of nine plots established within three blocks, with each block consisting of a representative plot of three prescribed fire return interval (FRI) treatment types: annual burn (1YR), biennial burn (2YR) and long unburned (40YR) (Figure 3-2). To account for variability within the plot, each individual plot was comprised of nine 20 cm diameter PVC sample soil collars arranged in a 3 x 3 grid with 5 m separation following Kobziar and Stephens (2006). PVC sampling collars were constructed of Schedule 30 white 20 cm diameter pipe cut to 10 cm lengths and beveled along one edge. Collars were inserted beveled edge down into the soil or duff to a depth of approximately 8 cm using a rubber mallet. All collars were installed at least four weeks prior to the start of sampling to allow any soil disturbance from installation to normalize. During the course of study, any vegetative growth within the sample collars was clipped and removed prior to $R_s$ measurement.

Two experimental litter manipulations plus control were randomly assigned to collars within each plot: litter addition, (3 collars), litter exclusion (3 collars), and control (3 collars). Around each sampling collar a low rectangular frame measuring approximately 40 cm in length on each side and rising approximately 5 cm above the soil surface was installed (Figure 3-3). This “treatment box” was constructed of 2.54 cm x 5.08 cm pine lumber and was the unit of litter addition, exclusion, or control. The interior of each treatment box measured 0.16 $m^2$. The treatment box was designed to expand the area of litter manipulation beyond the confine of the PVC soil collar to include the area outside the collar where $T_s$ and $M_s$ measurements were taken. This was important as it was anticipated that the litter manipulations might influence microsite $T_s$ and $M_s$ conditions that would otherwise be unaccounted for if the unit of treatment were restricted to within the soil collar. The litter addition sample frames received a one-time addition of 140 g. of litter (the equivalent to 8750 kg $ha^{-1}$) during the spring season (May) (Figure 3-3). This litter addition represented a 47%, 38%, and 37% increase over the mean annual litterfall load at the 1YR, 2YR, and 40YR sites respectively (K. Robertson, unpublished data; Reid et al., 2012). To ensure that the litter addition composition was representative of natural inputs, fresh leaf litter material was gathered in each plot during the preceding autumn (2010). The gathered material represented a natural mixture of foliar material mostly from *Pinus*, *Carya*, and *Quercus* species. Leaf litter was bagged and oven dried at 50°C for one week to achieve uniform moisture content. It was then ground using a 5 mm sieve on a Wiley Mill (Thomas Scientific Inc., Swedesboro, NJ, USA) to improve microbial availability. The freshly ground litter was then applied one-time within three randomly selected sample frames per plot. Care was taken to evenly distribute the litter within the entire area of the sample frame - including within the PVC collar. Fresh litter input was excluded from three randomly selected treatment boxes per plot via the construction of an enclosure of flexible plastic mesh stapled to wooden survey stakes (Figure 3-3). This design facilitated the exclusion of vertical and horizontal litterfall, while still allowing for the free flow of air, precipitation, and sunlight; as well as access for the $R_s$, $T_s$, and $M_s$ measurements taken with the sampling instrument and sensor probes. Litterfall material collected on top of the exclusions was removed and discarded monthly to prevent shading of the treatment box. Three randomly selected treatment boxes per plot did not receive any manipulation and remained throughout the study as the experimental control.

Sampling of $R_s$ for all plots was conducted using a LI-COR Biosciences LI-8100 automated soil $CO_2$ sampling instrument with a 20 cm survey chamber (LI-COR

Biosciences Inc., Lincoln, NE, USA) (Figure 3-4). Concurrently with $R_s$ measurements, soil temperature ($T_s$) and moisture content ($M_s$) at 10 cm and 5 cm depths, respectively, were recorded onboard the LI-8100 using an Omega 8831 type E T-Handle temperature probe and a Decagon Systems EC-5 soil moisture probe (Omega Inc., Stamford, CT; Decagon Systems Inc., Pullman, WA). On the monthly sampling day, each treatment box was sampled three times: once in the morning, once at mid-day, and once again in the evening hours. A total of 243 measurements were taken per month (nine collars x three daily measurements x three fire treatment types x three replicates). The resulting dataset for the entire seven-month study totaled 1655 $R_s$ measurements after exclusions due to hazardous weather and equipment malfunctions. Problems with sampling equipment resulted in erroneous soil moisture content measurements during the month of June and erroneous soil temperature measurements during the month of August. Recorded soil moisture content values less than 0.00, and soil temperature measurements greater than 40 °C were ignored in analyses.

Plot level forest vegetative and forest floor characteristics were assessed in the winter and spring of 2011. Vegetation was sampled using a 15 m radius circular plot (0.07 ha) centered on the middle $R_s$ sample collar. The following field parameters with abbreviation and unit were recorded one-time per plot: basal area (BA) ($m^2$ $ha^{-1}$), hardwood basal area (HW BA) ($m^2$ $ha^{-1}$), pine basal area (P BA) ($m^2$ $ha^{-1}$), and stand density (TPH) (trees $ha^{-1}$). Plot level mean litter depth (Litter) (cm) and mean duff depth (Duff) (cm) came from the averages of measurements taken as part of a previous study in the Stoddard Fire Plots reported in Chapter 2 (this document).

Due to the technical difficulties that led to gaps in measurements taken by the on-site weather station, monthly mean ambient temperature (M Temp) measurements and precipitation totals were recorded by the Florida Automated Weather Network (FAWN) site at Quincy, Florida, approximately 30 km from Tall Timbers Research Station. During the period of study from June through December 2011, mean monthly ambient temperatures (M Temp), ranged from 13.67 - 27.82 °C (Figure 3-5) and total monthly precipitation ranged from 4.50 - 20.55 cm. In plot measured soil temperature ranged from 8.91 - 34.75 °C, while in plot measured soil moisture content ranged from 0.00 - 0.32 $m^3/m^3$. Regional precipitation totals during and prior to the start of the study were low enough to classify the region in a "severe" to "extreme" drought following the Palmer Drought Severity Index (PDSI)(Figure 3-6)(National Oceanic and Atmospheric Administration, National Climatic Data Center).

**Analysis**

To determine the overall effect of treatments, a repeated measures analysis of variance (ANOVA) was used to examine the effects of prescribed fire interval (FRI), litter treatment type, time (sample month), and interaction effects on plot-level monthly mean soil $CO_2$ efflux rates, soil temperature, and soil moisture content. Significant treatment effects were identified at p-value < 0.05. Where significant effects were identified, differences among treatment levels were analyzed using Tukey's HSD tests. To determine the effects of litter treatments on $R_s$, $T_s$, and $M_s$ within specific FRIs, additional repeated measures analysis of variance (ANOVA) tests were performed for each FRI, with significant differences among litter treatment types analyzed using Tukey's HSD tests. To assess for differences between plot level forest and stand characteristics by FRI, one-way ANOVA tests were used. Where significant differences were identified, differences among treatments were analyzed using Tukey's HSD test.

To examine the relationships between $R_s$ rates and $T_s$, $M_s$, and monthly mean air temperature (M Temp) and precipitation, linear (Equation 3-1) regression models were developed using monthly plot means per FRI and litter treatment. In addition, non-linear models of the relationships between monthly mean $R_s$ rates and $T_s$ and M Temp were explored using an exponential equation (Equation 3-2) frequently used to describe the response of $R_s$ rates to soil temperature (Lundegardh, 1927; Samuelson et al., 2004; Concilio et al., 2005; Kobziar and Stephens, 2006).

$$R_s = \beta_0 + \beta_1(parameter) \qquad (3\text{-}1)$$

$$R_s = \beta_0 e^{\beta_1(Ts)} \quad \text{or} \quad R_s = \beta_0 e^{\beta_1(M\,Temp)} \qquad (3\text{-}2)$$

$$Q_{10} = e^{10\beta_1} \qquad (3\text{-}3)$$

Where $\beta_0$, and $\beta_1$ were coefficients estimated through regression analysis. Residuals of regressions were checked for normality and heteroscedasticity. In addition to those mentioned previously, an exponential equation (Equation 3-3) describing the response of soil $CO_2$ efflux to a 10 °C change in soil temperature was developed per FRI and litter treatment type (Lundegardh, 1927; Samuelson et al., 2004; Concilio et al., 2005; Kobziar and Stephens, 2006). All statistical analyses were performed using JMP 9.0 (SAS Institute, Cary, NC, USA).

## Results

Plot level forest conditions and composition varied significantly between prescribed fire treatment types (FRI). Stand density (1716.41 trees $ha^{-1}$), basal area (37.72 $m^2$ $ha^{-1}$), duff (1.58 cm) and litter depth (2.81 cm) were all greatest in the 40YR

FRI and lowest in the 1YR FRI (282.93 trees $ha^{-1}$, 11.79 $m^2$ $ha^{-1}$, 0.08 cm, 1.77 cm, respectively) (Table 3-2). Both the pine and hardwood species components of total basal area increased from the 1YR to the 40YR FRI, with the most hardwood (15.73 $m^2$ $ha^{-1}$) and pine (21.99 $m^2$ $ha^{-1}$) basal area in the 40YR FRI and the least hardwood and pine basal area in the 1YR FRI (3.87 $m^2$ $ha^{-1}$ and 7.92 $m^2$ $ha^{-1}$, respectively) (Table 3-2). During the seven-month study period monthly mean $R_s$ rates varied considerably: 1YR: control (0.95 - 6.15 µmol $CO_2$ $m^{-2}$ $sec^{-1}$), litter addition (1.24 - 8.15 µmol $CO_2$ $m^{-2}$ $sec^{-1}$), and litter exclusion (0.92 - 6.44 µmol $CO_2$ $m^{-2}$ $sec^{-1}$); 2YR: control (0.88 - 7.36 µmol $CO_2$ $m^{-2}$ $sec^{-1}$), litter addition (1.45 - 10.42 µmol $CO_2$ $m^{-2}$ $sec^{-1}$), and litter exclusion (1.17 - 7.15 µmol $CO_2$ $m^{-2}$ $sec^{-1}$); 40YR: control (1.85 - 11.30 µmol $CO_2$ $m^{-2}$ $sec^{-1}$), litter addition (2.17 - 12.63 µmol $CO_2$ $m^{-2}$ $sec^{-1}$), and litter exclusion (1.60 - 10.53 µmol $CO_2$ $m^{-2}$ $sec^{-1}$).

In general, in all FRIs and litter treatments, soil moisture content ($M_s$) ($m^3/m^3$), soil temperature ($T_s$) (°C) and $R_s$ rates varied by sample month, with the highest $T_s$ and $R_s$ observed in the summer months and the lowest in the fall and winter months (Table 3-3) (Figures 3-7 and 3-8). $R_s$ and $T_s$ closely followed seasonal trends in ambient air temperature (Figure 3-5), with monthly mean $T_s$ in each litter treatment and FRI highly positively linearly correlated with monthly mean ambient air temperature ($R_2$ = 0.92 - 0.95) (Table 3-10). Soil moisture content did not follow the same seasonal trends as $R_s$ and $T_s$, with the highest $M_s$ observed in all FRIs and litter treatments in the summer and winter months and the lowest $M_s$ observed during the months of September and October (Figures 3-7 and 3-8). Soil moisture content throughout the study period was not significantly correlated with monthly precipitation (Figure 3-5) (Table 3-13) and was likely influenced by the effects of an on-going regional drought that started prior to and continued throughout the entire study period (Figure 3-6).

**Analysis of Treatment Effects**

Repeated measures ANOVA was used to identify significant overall treatment effects ($p < 0.05$) due to FRI, litter treatment type, sample month (time), and the interaction of FRI x month, litter x month, and FRI x litter (Table 3-3). When litter treatments were ignored and the data pooled, significant differences in monthly mean $R_s$ rates ($F = 24.20$ $p < 0.0001$), soil temperature ($T_s$) ($F = 6.80$ $p = 0.0016$), and soil moisture content ($M_s$) ($F = 43.06$ $p < 0.0001$) were found between the prescribed fire treatments (FRI). Similar to the results of Chapter 2 (this document) Tukey's HSD tests ($p < 0.05$) found that monthly mean $R_s$ rates were significantly higher in the 40YR FRI than in the 2YR and 1YR FRI (Tables 3-3 and 3-4). Similar tests found that monthly mean $M_s$ was significantly lower in the 40YR FRI, while monthly mean $T_s$ was significantly higher in the 1YR than the 40YR FRI (Table 3-4). The treatment effect of FRI on $R_s$ ($F = 3.92$ $p < 0.001$), $T_s$ ($F = 14.73$ $p < 0.001$), and $M_s$ ($F = 2.18$ $p = 0.0245$) varied significantly over time (Table 3-3) (Figure 3-8), with similar monthly and seasonal variations in $R_s$, $T_s$, and $M_s$ observed and discussed in Chapter 2 (this document).

When FRI was ignored and the effect of litter treatment type assessed exclusively, significant treatment effects on monthly mean $R_s$ ($F = 11.29$ $p < 0.0001$) and $M_s$ ($F = 7.00$ $p = 0.0014$) were identified (Table 3-3). Tukey's HSD tests found that overall, litter addition treatments resulted in significantly higher monthly mean $R_s$ rates than the exclusion and control treatments, while the litter exclusion treatments resulted in significantly lower overall monthly mean $M_s$ relative to the litter addition and control treatments (Table 3-5). Monthly mean soil temperature was not significantly influenced by litter manipulation treatments when FRI was ignored. The treatment effect of litter manipulation only varied significantly with time ($F = 1.51$ $p = 0.0402$) for $M_s$, (Table 3-5) (Figure 3-7).

While the overall trends in FRI and litter manipulation described previously (Table 3-3) provide insight into the broader effects of such treatments, the primary interest of this study was to identify the effects of litter manipulation treatments (litter addition, litter exclusion, and control) on $R_s$, $T_s$, and $M_s$ within each FRI (1YR, 2YR, and 40YR) (Tables 3-6 and 3-7). To accomplish this, separate repeated measures ANOVA and Tukey's HSD tests were run for each FRI and variable of interest ($R_s$, $T_s$, and $M_s$) (Table 3-6). Within the 1YR FRI, the control (3.05 μmol $CO_2$ $m^{-2}$ $sec^{-1}$) and litter exclusion treatment (3.06 μmol $CO_2$ $m^{-2}$ $sec^{-1}$) mean $R_s$ rates were significantly lower (28%) than the litter addition treatment (4.21 μmol $CO_2$ $m^{-2}$ $sec^{-1}$). Within the 2YR FRI, the control (3.68 μmol $CO_2$ $m^{-2}$ $sec^{-1}$) treatment mean $R_s$ rates were significantly lower (32%) than the litter addition treatment (5.45 μmol $CO_2$ $m^{-2}$ $sec^{-1}$) (Table 3-6) (Figures 3-9 and 3-10). Litter manipulation had no significant effect on $R_s$ rates in the 40YR FRI. Soil moisture content ($M_s$) varied by litter treatment only within the 1YR prescribed fire treatment (Tables 3-6 and 3-7) (Figures 3-11 and 3-12). In the 1YR FRI, litter exclusion (0.12 $m^3/m^3$) reduced soil moisture content relative to the control (0.16 $m^3/m^3$) but not the litter addition (0.14 $m^3/m^3$) (Table 3-6). No significant differences in soil temperature ($T_s$) were found among litter treatment types within the FRI sites (Tables 3-6 and 3-7) (Figures 3-13 and 3-14).

**Effects of Treatments on the Response of $R_s$ to Abiotic Factors**

Simple linear regression models (Equation 3-1) and non-linear (Equation 3-2) exponential models were developed by litter treatment type and fire return interval to assess the influence of litter treatments on the relationships between $R_s$ rates and soil temperature (Tables 3-8 and 3-9). The linear regression models indicated that positive relationships between monthly mean $R_s$ rates and $T_s$ existed for all fire return intervals and litter treatment types ($R^2$ = 0.38 - 0.61) (Table 3-8) (Figures 3-15, 3-16, and 3-17). Litter manipulation appeared to slightly weaken the relationships between $R_s$ and $T_s$ in all FRIs. In general, the regression coefficients of all $R_s$ and $T_s$ models were slightly lower than those developed in Chapter 2 of this document. The non-linear exponential models also indicated that positive relationships between monthly mean $R_s$ rates and $T_s$ existed for all fire return intervals and litter treatment types ($R^2$ = 0.36 - 0.58) (Table 3-9) (Figure 3-18, Figure 3-19, and Figure 3-20). Like the linear regression models, litter manipulation generally appeared to slightly weaken the relationships between $R_s$ rates and $T_s$ with the highest regression coefficients in the control litter treatments in the 1YR and 2YR FRIs and the litter exclusion treatment in the 40YR FRI (Table 3-9). Using the β1 estimate from Equation 3-2 in the $Q_{10}$ model (Equation 3-3), the response of $R_s$ rates to 10 °C changes in $T_s$ ($Q_{10}$ value) were calculated for each litter treatment type and FRI ($Q_{10}$ = 1.57 - 3.40) (Table 3-9). In the 2YR and 40YR FRIs, $Q_{10}$ values were highest in the litter addition treatments ($Q_{10}$ = 2.10 and $Q_{10}$ = 3.40, respectively) while in the 1YR FRI, $Q_{10}$ values were highest in the control treatment (Table 3-9).

Additional simple linear regression models using Equation 3-1 were developed per litter treatment type and FRI to assess the relationships between monthly mean soil moisture content ($M_s$), monthly total precipitation (Precip), and monthly mean $R_s$ rates. In all litter treatment and FRI models, no significant relationships were found between $R_s$ rates and $M_s$ ($R^2$ = 0.00 - 0.18 $p > 0.05$) (Table 3-11). These results are similar to those of Chapter 2 (this document) wherein $M_s$ explained little of the temporal variation in monthly mean $R_s$ rates ($R^2$ = 0.03 - 0.14). In contrast, simple linear regression models (Equation 3-1) by litter treatment type and FRI of the relationships between monthly mean $R_s$ rates and monthly total precipitation (Precip) identified strong linear relationships in all models ($R_2$ = 0.46 - 0.75) (Table 3-12). Further analysis found that the monthly pattern of precipitation during the study period followed similar seasonal variations in soil and ambient air temperature (Figure 3-5) that resulted in $T_s$ and Precip being strongly correlated ($R^2$ = 0.58 - 0.64) (Table 3-14). This multicollinearity between $T_s$ and Precip limited further interpretation of the effects of monthly precipitation patterns on the temporal variations in monthly mean $R_s$ rates.

## Discussion

Many of the studies of soil $CO_2$ efflux rates available for comparison in the southeastern US took place in industrial plantation forests and as such some differences in results were not surprising (Ewel et al., 1987a; Ewel et al., 1987b; Fang et al., 1998; Gough and Seiler, 2004; Samuelson et al., 2004; Gough et al., 2005). The range of monthly mean $R_s$ rates observed in the litter control units in this study were similar but generally higher than those reported elsewhere in several other studies of southeastern US soil $CO_2$ efflux rates (Maier and Kress, 2000; Gough and Seiler, 2004; Maier et al., 2004; Gough et al., 2005; Samuelson et al., 2004; Samuelson and Whitaker, 2012). For example, in a study of a Georgia, USA, loblolly pine plantation Samuelson et al. (2004) reported $R_s$ rates ranging from 1 - 6 μmol $CO_2$ $m^{-2}$ $sec^{-1}$ while Butnor et al. (2003) reported $R_s$ rates ranging from 2.23 - 6.63 μmol $CO_2$ $m^{-2}$ $sec^{-1}$ in a loblolly pine plantation in North Carolina, USA. In another example, monthly mean $R_s$ rates from a yearlong study in a similarly structured frequently burned, natural longleaf pine forest in Coastal Alabama, USA ranged from 1.6 - 6.4 μmol $CO_2$ $m^{-2}$ $sec^{-1}$ (Samuelson and Whitaker, 2012). Not surprisingly the range of $R_s$ rates in the litter control treatments in this study were similar to those reported in Chapter 2 of this document following a nearly two-year survey of monthly and seasonal variability of $R_s$ rates in the Stoddard Fire Plots. It is possible that the higher $R_s$ rates observed in this study in comparison to those cited previously may have been due to differences in the soil $CO_2$ efflux measurement systems. While research by Madsen et al. (2008) has shown that there are no significant differences in estimated $R_s$ flux rates between the commonly used LI-6400 and LI-8100 instruments, previous research by Heinemeyer and McNamara (2011) has shown that soil $CO_2$ efflux measurement chamber type can significantly influence measured flux rates, with closed static chambers consistently underestimating $R_s$ fluxes (21-39%) compared to closed dynamic chambers like the LI-8100 instrument used in this study (LI-COR Biosciences, Inc. Lincoln, NE, USA).

**Effect of Prescribed Fire Management**

Our results found that the three prescribed fire management methods assessed in this study (1YR, 2YR, and 40YR) significantly altered $R_s$ rates regardless of litter manipulation type, with the highest mean $R_s$ rates in the long unburned (40YR) sites and the lowest in the 1YR sites. While temporal variations in $R_s$ rates across all treatments were generally well explained by positive correlations with soil temperature ($T_s$), neither $T_s$ nor $M_s$ explained the differences in $R_s$ rates between FRIs. These results were consistent with those reported in Chapter 2 (this document). The observed differences in monthly mean $R_s$ rates between FRI sites were likely due to variations in stand level biomass and productivity (Raich and Tufekciogul, 2000), vegetative composition (Wang et al., 2006), and disturbance history (Hanula et al., 2012) that facilitated higher $R_a$ and $R_h$ contributions to total $R_s$ in the 40YR sites than the 1YR and 2YR sites. See Chapter 2 of this document for further discussion of the variations in mean monthly $R_s$ rates between the 1YR, 2YR, and 40YR Stoddard Fire Plots.

**Effect of Litter Addition**

The results of our litter manipulation found that $R_s$ rates in the frequently burned sites responded positively to the litter supplements as litter additions led to significant increases (28% and 32%) in $R_s$ rates in the 1YR (4.21 µmol $CO_2$ $m^{-2}$ $sec^{-1}$) and 2YR (5.45 µmol $CO_2$ $m^{-2}$ $sec^{-1}$) prescribed fire treatments relative to controls (3.05 µmol $CO_2$ $m^{-2}$ $sec^{-1}$ and 3.68 µmol $CO_2$ $m^{-2}$ $sec^{-1}$, respectively). Other studies of litter manipulation have reported results similar to those described here. For example, in a litter addition experiment in the Cascade Mountains of Oregon, USA, Sulzman et al. (2012) reported a 34% increase in $R_s$ rates relative to control following conifer needle litter additions. In another study, Chemidlin Prévost-Bouré et al. (2010) reported mean $R_s$ rates increased 60-120% relative to controls following litter additions in a field study in France.

It is important to consider that the elevated $R_s$ rates observed following litter additions in the 1YR and 2YR treatments in our study may have been artificially influenced by the experimental methods used. For example, grinding the litter applied to the litter addition treatments may have facilitated a more rapid microbial decomposition and subsequent $R_h$ response than would have otherwise occurred had whole litter been applied to the treatment sites. Due to the decreased surface to volume ratio and increased particle size, it is possible that litterfall under natural field conditions may elicit less of an immediate microbial response. Additional study of $R_s$ rates within the Stoddard Fire Plots using natural litter additions may provide insight into this potential bias.

It has been shown elsewhere that increases in labile soil carbon inputs can induce subsequent rapid and prolonged increases in soil microbial metabolic activity, such that microbial populations mineralize not only the recently added carbon but also older and more recalcitrant soil carbon sources in a process known as *priming* (Chemidlin Prévost-Bouré et al., 2010; Kuzyakov, 2010; Blagodatskaya et al., 2011). In a study of $R_h$ rates in France, Chemidlin Prévost-Bouré et al. (2010) reported evidence of a microbial priming effect within two-months of litter additions that persisted for well over a year and resulted in a 32% increase in $R_s$ rates. It has been suggested that microbial priming may cause significant changes in soil carbon pools as some global climate change and atmospheric nitrogen deposition models forecast increased litterfall in some regions (Hoosbeek, 2004; Kuzyakov, 2010; Sulzman et al., 2012). Given the seven-month study period reported here, it is difficult to say whether or not evidence of a real or prolonged microbial priming effect was observed in the litter additions (Chemidlin Prévost-Bouré et al., 2010; Sulzman et al., 2012).

In the 40YR prescribed fire treatments, litter additions recorded a non-significant increase (7%) in $R_s$ rates (5.49 μmol $CO_2$ $m^{-2}$ $sec^{-1}$) relative to the control (5.09 μmol $CO_2$ $m^{-2}$ $sec^{-1}$). Given that litter additions in the 40YR sites did not increase $R_s$ rates significantly, heterotrophic sources of $R_s$ in the 40YR sites may not have been carbon limited. The significantly higher basal area, litter depth, and duff depth in the 40YR sites may have provided ample aboveground carbon inputs and belowground root exudates (and turnover) to support heterotrophic microbial activity. One possible response to these results would be to suggest a trenching or exclusion study to remove the inputs of recent photosynthate from roots and then reapply fresh litter (Hanson et al., 2000;

Sapronov and Kuzyakov, 2007). Trenching and exclusion studies however invariably disturb the soil microenvironment often through alterations of soil moisture content due to limitations in lateral diffusion of soil water, increases in dead roots due to severing, and limitations in the lateral diffusion of soil $CO_2$ (Kutsch et al., 2010; G. Lokuta, 2012 pers. comm).

Given the monthly interval for sampling $R_s$ rates in this study, additional short-term pulses in soil $CO_2$ efflux following litter treatments may have gone undetected. Recent research has demonstrated that soil $CO_2$ efflux rates are tightly temporally coupled with above and belowground carbon inputs (Stoy et al., 2007). For example, recent research using canopy level $^{13}C$ isotope sampling in a loblolly pine forest in North Carolina, USA, detected increases in soil $CO_2$ efflux $^{13}C$ fractioning within 3-6 days of the initial canopy exposure (Warren et al., 2012). In another recent example from the Everglades region of Florida, USA, Medvedeff (2012) found that increases in $R_h$ in response to experimental ash additions were detectable within two-days of treatment. Importantly, Medvedeff (2012) also noted that the treatment effects of ash additions were no longer detectable thirty-days post treatment. We suggest that future studies investigating the influence of forest management methods on soil carbon dynamics utilize carbon isotope pulses and repeated short and long-term sampling. Though costly, these methods may allow for the differentiation of $R_a$ and $R_h$ while capturing the highly variable temporal responses of heterotrophic soil microbes following carbon inputs. In addition, such techniques may also provide evidence for microbial priming through the potential identification of the source of soil $CO_2$ efflux carbon ("old carbon" vs. "new carbon") (Epron et al., 2012).

### Effect of Litter Exclusion

In our study litter exclusion did not reduce $R_s$ rates within any prescribed fire interval. The lack of a significant treatment effect may have been the result of the study duration or season. Litter exclusion tents were installed in May 2011 after the majority of the deciduous tree and annual grass litter from the previous growing season were shed. Previous research from a similar old-field loblolly-shortleaf pine successional study site in Mississippi, USA, reported that 90% of the annual deciduous leaf litter load fell between the months of October and December (Hinesley and Nelson, 1991). Given the results of Hinesley and Nelson (1991), it is possible that had the exclusion treatments in our study been installed in September or October of 2010, the exclusion of the litter inputs from the peak 2010-year litterfall period might have influenced $R_s$ rates during the sample period. This is supported by the results of Kutsch et al. (2010) who found that models of monthly $R_h$ rates for an old-growth deciduous forest in Germany were strongly correlated with the litter production from the previous year. Our results are similar to those of Garten (2009) who reported that $R_s$ rates within litter exclusion treatments in a temperate forest in Tennessee, USA, were not significantly different ($p > 0.05$) from control, while litter additions in the same study resulted in a significant increase (62%) in mean $R_s$ rates. In contrast, other studies have found longer-term litter exclusion treatments to significantly reduce total $R_s$ rates (Bowden et al., 1993; McCarthy and Brown, 2006; Chemidlin Prévost-Bouré et al., 2010). In an experimental burning and litter manipulation study in Ohio, USA, McCarthy and Brown (2006) found that litter exclusion and the removal of existing forest floor litter significantly reduced $R_s$ rates relative to control. In a field study near Paris, France, Chemidlin Prévost-Bouré et al. (2010) reported a significant decrease (25-45%) in $R_s$ rates relative to control due to litter exclusion. Similarly, Bowden et al. (1993) reported a persistent reduction (non-significant) in $R_s$ rates during a June - July study following litter exclusion during the previous September-October in a mixed hardwood forest in Massachusetts, USA.

The duration of our study and litter exclusion treatments may have also contributed to the lack of a significant treatment effect from litter exclusion. Preliminary research on carbon turnover using $^{14}C$ isotopic sampling in the 40YR and 3YR Stoddard Research Plots has indicated that the residence time of soil carbon ranges from 11 years in the 3YR Stoddard plots to 5.5 years in the 40YR plots (P. Hsieh and K. Robertson, unpublished data). These results and those of others discussed by Sayer (2006), suggest that a 7-month litter exclusion period may not have been long enough to elicit a change in microbial decomposition and subsequent $R_s$ rates. During our sampling period, existing organic matter in and above the soils in the litter exclusion treatments may have been sufficient to sustain heterotrophic microbial metabolism and subsequent $R_h$ rates (Sayer, 2006).

A lack of a litter exclusion treatment effect could also indicate that in these systems, aboveground inputs such as litterfall may not be as important in driving $R_s$ rates as recently fixed photosynthate. Recent research has shown that both recent photosynthate and fine root turnover can be important sources of carbon for forest soil $CO_2$ efflux in the short-term (Epron et al., 2012; Warren et al., 2012). The importance of aboveground litter as a source for soil heterotrophic microbial decomposition may also vary seasonally. For example, Warren et al. (2012) found evidence suggesting that the role of recent photosynthate in soil $CO_2$ efflux in a loblolly pine forest in North Carolina, USA declined in importance during the autumn months as other sources of labile carbon become more important for heterotrophic decomposition during that period. Future studies that include prolonged litter exclusion treatments and periodic litter additions that vary seasonally may provide insight into these relationships between aboveground inputs and soil $CO_2$ efflux rates.

**Importance of Soil Temperature**

In our study, soil and ambient temperature explained much of the temporal variation in $R_s$ rates, regardless of prescribed fire interval or litter treatment type. Temperature regulates $R_s$ rates through the metabolic influence on microbial enzyme activity and is correlated with the seasonal photosynthetic activity of plants (Luo and Zhou, 2006). Our results were consistent with the results of many other studies of upland ecosystems of the southeastern US. For example, Reinke et al. (1981) found that ambient air temperature was highly ($R^2$ = 0.73) correlated with $R_s$ rates in a South Carolina, USA, longleaf pine forest, while Fang et al. (1998) found that soil temperature explained > 90% of the observed variability of $R_s$ rates in a Florida, USA, slash pine plantation.

The positive correlations observed in many ecosystems between soil $CO_2$ efflux rates and soil temperature has led some to raise concerns regarding the future of landscape level and global soil $CO_2$ efflux rates under warmer climate conditions (Bond-Lamberty and Thomson, 2010). Others have further suggested that as $R_s$ rates increase in response to global climate change, the elevated atmospheric $CO_2$ and global temperature may drive a positive feed-back mechanism resulting in increased $R_s$ rates and loss of soil carbon stocks (Rustad et al., 2000). However it is important to consider in these discussions the intricate relationships that exist between aboveground vegetation and belowground soil microbial assemblages, as experimental manipulations have found that increases in atmospheric $CO_2$ concentrations and temperature can result in positive, negative, and or neutral $R_s$ responses from belowground soil microbial populations (Wardle et al., 2004; Garten, 2009; Lau and Lennon, 2012).

The estimated $Q_{10}$ values that describe the response of $R_s$ to changes in soil temperature ranged from $Q_{10}$ = 1.57 - 3.40 in our study. These values were similar to those reported in Chapter 2 (this document) following a previous multi-year study in the Stoddard Fire Plots. In addition, Wang et al. (2006) reported similar $Q_{10}$ values for a range of forest types in China ($Q_{10}$ = 2.61 - 3.75), while Samuelson and Whitaker (2012) reported similar $Q_{10}$ values ($Q_{10}$ = 2.81) following a year-long study in a natural longleaf pine forest in Alabama, USA. In our study, the highest $Q_{10}$ values were observed in the 40YR FRI and the lowest in the 1YR FRI, with litter addition treatments resulting in slightly higher $Q_{10}$ values in the 2YR and 40YR FRIs. The results of Bhupinderpal-Singh et al. (2003) and Zhou and Zhou (2012) suggest that variability in $Q_{10}$ values among treatments and study sites may indicate differences in the relative contributions of $R_h$ and $R_a$ sources to $R_s$. In a few studies (Bhupinderpal-Singh et al., 2003; Luan et al., 2011; Zhou and Zhou, 2012) it has been shown through experimental manipulation that heterotrophic sources of $R_s$ have higher $Q_{10}$ values than autotrophic sources of $R_s$. If that is the case, then our results indicate that litter additions may have increased the importance of heterotrophic microbial contributions to total $R_s$ in the 2YR and 40YR sites. Given that we observed increases in $R_s$ rates in all FRIs following litter additions, it makes sense that labile carbon supplements would increase heterotrophic microbial activity similar to the results of Medvedeff (2012). It is not clear however, why litter additions in the 1YR treatment, which did increase $R_s$ rates, did not result in increased estimated $Q_{10}$ values. In addition, the results of Bhupinderpal-Singh et al. (2003), Luan et al (2011), and Zhou and Zhou (2012) suggest that heterotrophic sources of $R_s$ were more significant in the 40YR FRI (litter control $Q_{10}$ = 3.16) than in the 1YR (litter control $Q_{10}$ = 1.74) and 2YR (litter control $Q_{10}$ = 1.92) FRIs. Previous research using $^{14}C$ isotope analysis has shown that soil carbon turnover time in the 40YR treatments is much faster (5.5 years) than in the 3YR Stoddard Fire Plots (11 years) (P. Hsieh, unpublished data). While the 3YR Stoddard Fire Plots were not assessed in this study, they are similar in structure and composition to the 2YR sites. The results of P. Hsieh along with those of Hanula et al. (2012) from a study in the Osceola National Forest, suggest that frequent prescribed fire may either directly or indirectly reduce microbial decomposition rates.

It must be considered that the use of $Q_{10}$ values for partitioning sources of $R_s$ is not a practice well established in the literature. Many previous partitioning studies (Boone et al., 1998; Saiz et al., 2006; Sulzman et al., 2012) have found $Q_{10}$ values that contrast with those of Bhupinderpal-Singh et al. (2003), Luan et al. (2011), and Zhou and Zhou (2012). For example, following a physical $R_s$ partitioning study of a mixed hardwood deciduous forest in Massachusetts, USA, Boone et al., (1998) reported $Q_{10}$ values of $Q_{10}$ = 4.6 for autotrophic $CO_2$ efflux, $Q_{10}$ = 2.5 for heterotrophic sources of $CO_2$ efflux, and $Q_{10}$ = 3.5 for bulk soil (control). We are hopeful that future studies using isotopic sampling or other methods may provide guidance on the disagreement between the results of $Q_{10}$ studies as the methods and results of Bhupinderpal-Singh et al. (2003), Luan et al (2011), and Zhou and Zhou (2012) could provide a low-cost method of identifying the relative contributions of the sources of soil $CO_2$ efflux without disturbing integrated soil biogeochemical processes.

**Importance of Soil Moisture**

In our study, regardless of prescribed fire treatment or litter manipulation method, soil moisture content did not explain a significant amount of the temporal variation in $R_s$ rates. These results are consistent with those of other studies in southeastern US upland ecosystems that found little to no correlation between soil moisture content and $R_s$ rates (Fang et al., 1998; Gough and Seiler, 2004; Samuelson et al., 2004; Whitaker, 2010). Given that the observed soil moisture content values were not significantly related to the monthly precipitation values, as was expected, we propose three possible situations that may have occurred that explain the lack of agreement. First, soil moisture measurements represented a once per month sample of soil moisture conditions within the plot, while total monthly precipitation represented a cumulative monthly figure. The lack of correlation may have been due to temporal gaps between the two measurements types. Second, due to large data gaps caused by technical difficulties with the onsite weather station, the monthly precipitation data were recorded at an automated weather station located 30 km from the sample plots. Given the highly heterogeneous nature of precipitation events (Bellon and Austin, 1986), it is possible that the monthly precipitation values for the off-site weather station were not representative of the precipitation amounts received at the plots. Finally, we suggest similar to Kutsch et al. (2010), that it is also possible that soil moisture content measurements were biased due to the measurement instrument, as the 5 cm EC-5 probe (Decagon Systems, Pullman, Washington, USA) used to sample soil moisture content during $R_s$ measurements may not have been long enough to measure mineral soil moisture content given the depth of the duff and litter layers in the 40YR plots (4.39 cm) as compared to the 1YR (1.85 cm) and 2YR treatments (2.63 cm). Recent research from the southeastern US suggests that soil moisture and prolonged drought events can reduce total ecosystem respiration (Bracho et al., 2012) and soil $CO_2$ efflux (Noormets et al., 2010) in upland forested ecosystems. Given that our study took place during a prolonged regional drought, the results of Bracho et al. (2012) and Noormets et al. (2010) should be taken into consideration when making comparisons with studies conducted during periods with more or less precipitation.

## Conclusions

Our results have shown that prolonged prescribed fire management practices can significantly influence forest soil $CO_2$ efflux rates in the loblolly pine - shortleaf pine old-field forests of North Florida, USA. Frequent burning reduces soil $CO_2$ efflux rates in the study area relative to fire exclusion, with annual burning resulting in lower monthly mean soil $CO_2$ efflux rates than biennial burning. Our results also found that soil $CO_2$ efflux rates can increase for a period of several months following one-time litter additions, with the greatest increases in the annually and biennially burned sites. At the same time, soil $CO_2$ efflux rates in both frequently burned and long fire-excluded sites do not appear sensitive to short-term reductions in leaf litter inputs. Even though a positive soil $CO_2$ efflux response was detected following experimental litter additions, it remains to be seen whether litter represents a significant, dominant, or seasonal source of labile carbon for soil heterotrophic microbial respiration, as previous studies in other systems have reported the importance of fine-root turnover and root exudates in supplying heterotrophic microbial respiration. Our results provided some evidence to suggest that the role of leaf litter in soil $CO_2$ efflux differs between sites managed with various prescribed fire management regimes.  Future research from a soil microbial ecology perspective may allow for a better understanding of how prolonged prescribed fire management regimes, and vegetative above and belowground inputs shape soil bacterial and fungal populations responsible for heterotrophic soil $CO_2$ efflux.

Table 3-1. Plot level variables investigated for their influence on soil $CO_2$ efflux rates at the Tall Timbers Research Station, FL

| Parameter category | Plot variable | Abbreviation | Measured | Measurement location |
|---|---|---|---|---|
| Microclimate | Soil temperature | $T_s$ (°C) | 3x daily | 5 - 15 cm of collar |
| | Soil moisture content | $M_s$ ($m^3/m^3$) | 3x daily | 5 - 15 cm of collar |
| Vegetation | Basal area | BA ($m^2$ $ha^{-1}$) | Winter 2011 | 15 m radius circular plot from center collar |
| | Pine basal area | PBA ($m^2$ $ha^{-1}$) | Winter 2011 | 15 m radius circular plot from center collar |
| | Hardwood basal area | HWBA ($m^2$ $ha^{-1}$) | Winter 2011 | 15 m radius circular plot from center collar |
| | Stand density | TPH (trees $ha^{-1}$) | Winter 2011 | 15 m radius circular plot from center collar |
| Forest floor | Duff depth | Duff (cm) | Spring 2011 | Avg. of three measurements within 30 cm of collar |
| | Litter depth | Litter (cm) | Spring 2011 | Avg. of three measurements within 30 cm of collar |
| | Total duff and litter depth | DL (cm) | Spring 2011 | Avg. of three measurements within 30 cm of collar |
| Weather | Total precipitation | Precip (cm) | Monthly | Quincy, FL FAWNS station |
| | Mean air temperature (2 m) | Temp (°C) | Monthly | Quincy, FL FAWNS station |
| | Palmer drought severity index | PDSI | Monthly | Northwest Florida regional estimate from NOAA-NCDC |

Table 3-2. Mean forest characteristics per prescribed fire treatment type at the Tall Timbers Research Station, FL

| FRI | Year | Trees (ha) | Hardwood basal area ($m^2$ $ha^{-1}$) | Pine basal area ($m^2$ $ha^{-1}$) | Total basal area ($m^2$ $ha^{-1}$) | Duff depth (cm) | Litter depth (cm) | Annual litterfall (t $ha^{-1}yr^{-1}$) |
|---|---|---|---|---|---|---|---|---|
| 1YR | 2011 | 282.93 (64.83) b | 3.87 (6.28) b | 7.92 (3.68) a | 11.79 (7.22) b | 0.08 (0.06) c | 1.77 (0.91) c | 4.63 (1.53) a |
| 2YR | 2011 | 400.81 (344.87) b | 6.30 (4.28) ab | 9.16 (6.14) a | 15.45 (2.15) b | 0.46 (0.41) b | 2.17 (0.79) b | 5.42 (0.69) a |
| 40YR | 2011 | 1716.41 (681.42) a | 15.73 (3.59) a | 21.99 (11.22) a | 37.72 (8.36) a | 1.58 (0.55) a | 2.81 (0.58) a | 5.47 (1.37) a |

FRI is fire return interval. Letters per column show significant differences between fire return intervals (Tukey's HSD test; Tukey 1953). Litterfall rates provided by K. Robertson (unpublished data).

Table 3-3. Results of the repeated measures ANOVA for soil $CO_2$ efflux ($R_s$), soil temperature ($T_s$), and soil moisture content ($M_s$) means at the Tall Timbers Research Station, FL

| | $R_s$ | | | $T_s$ | | | $M_s$ | | |
|---|---|---|---|---|---|---|---|---|---|
| Term | df | F | p | df | F | p | df | F | p |
| FRI | 2 | 24.20 | < 0.0001 | 2 | 6.80 | 0.0016 | 2 | 43.06 | < 0.0001 |
| Litter | 2 | 11.29 | < 0.0001 | 2 | 0.03 | 0.9677 | 2 | 7.00 | 0.0014 |
| Time | 6 | 69.89 | < 0.0001 | 5 | 918.45 | < 0.0001 | 5 | 59.86 | < 0.0001 |
| FRI*Time | 12 | 3.92 | < 0.0001 | 10 | 14.73 | < 0.0001 | 10 | 2.18 | 0.0245 |
| Litter*Time | 12 | 0.49 | 0.9150 | 10 | 0.08 | 1.0000 | 10 | 1.20 | 0.0402 |
| FRI*Litter | 4 | 1.36 | 0.2514 | 4 | 0.01 | 1.0000 | 4 | 1.51 | 0.2039 |

For each month, daily measurements per soil collar were averaged and the three soil collar means per litter treatment type were then averaged to produce a plot-level mean value for each month.

Table 3-4. Mean soil $CO_2$ efflux rate, soil temperature, and soil moisture content for the entire study period by prescribed fire treatment at the Tall Timbers Research Station, FL

| Fire return interval (FRI) | Mean $R_s$ (µmol $CO_2$ $m^{-2}$ $sec^{-1}$) | Mean $T_s$ (°C) | Mean $M_s$ ($m^3/m^3$) |
|---|---|---|---|
| 1YR | 3.44 (2.57) c | 21.21 (7.33) a | 0.40 (0.08) a |
| 2YR | 4.50 (3.45) b | 20.88 (6.35) ab | 0.13 (0.07) a |
| 40YR | 5.15 (3.92) a | 20.46 (4.64) b | 0.08 (0.06) b |

Values are means with standard deviation in parentheses. Means are for fire return intervals with litter treatments grouped. Letters indicate significant differences among FRI means using Tukey's HSD Test. Data were recorded three times daily once per month from June - December 2011.

Table 3-5. Mean soil $CO_2$ efflux rate, soil temperature, and soil moisture content for the entire study period by litter treatment type at the Tall Timbers Research Station, FL

| Litter treatment type | Mean $R_s$ (µmol $CO_2$ $m^{-2}$ $sec^{-1}$) | Mean $T_s$ (°C) | Mean $M_s$ ($m^3/m^3$) |
|---|---|---|---|
| Addition | 5.05 (3.93) a | 20.83 (6.24) a | 0.12 (0.08) a |
| Exclusion | 4.10 (3.18) b | 20.83 (6.20) a | 0.10 (0.07) b |
| Control | 3.94 (3.01) b | 20.89 (6.22) a | 0.13 (0.08) a |

Values are means with standard deviation in parentheses. Means are for litter treatment types with prescribed fire return interval (FRI) grouped. Letters indicate significant differences among FRI means using Tukey's HSD Test. Data were recorded three times daily once per month from June - December 2011.

Table 3-6. Results of the repeated measures ANOVA for soil $CO_2$ efflux ($R_s$), soil temperature ($T_s$), and soil moisture content ($M_s$) means within prescribed fire treatments at the Tall Timbers Research Station, FL

| | | $R_s$ | | | $T_s$ | | | $M_s$ | | |
|---|---|---|---|---|---|---|---|---|---|---|
| FRI | Term | df | F | p | df | F | p | df | F | p |
| 1YR | Litter | 2 | 6.65 | 0.0031 | 2 | 0.01 | 0.9885 | 2 | 6.39 | 0.0042 |
| | Time | 6 | 17.28 | < 0.0001 | 5 | 212.54 | < 0.0001 | 5 | 24.94 | < 0.0001 |
| | Litter*Time | 12 | 0.34 | 0.9770 | 10 | 0.03 | 1.0000 | 10 | 1.52 | 0.1738 |
| 2YR | Litter | 2 | 7.42 | 0.0017 | 2 | 0.02 | 0.9846 | 2 | 0.49 | 0.6153 |
| | Time | 6 | 20.28 | < 0.0001 | 5 | 459.17 | < 0.0001 | 5 | 22.66 | < 0.0001 |
| | Litter*Time | 12 | 0.54 | 0.8740 | 10 | 0.10 | 0.9997 | 10 | 0.36 | 0.9544 |
| 40YR | Litter | 2 | 0.94 | 0.3974 | 2 | 0.03 | 0.9961 | 2 | 2.69 | 0.0814 |
| | Time | 6 | 36.31 | < 0.0001 | 5 | 777.91 | < 0.0001 | 5 | 14.07 | < 0.0001 |
| | Litter*Time | 12 | 0.18 | 0.9988 | 10 | 0.10 | 0.9997 | 10 | 1.30 | 0.2681 |

For each month, daily measurements per soil collar were averaged and the three soil collar means per litter treatment type were then averaged to produce a plot-level mean value for each month.

Table 3-7. Soil $CO_2$ efflux, soil temperature, and soil moisture content means by litter treatment type and fire return interval for the Tall Timbers Research Station, FL

| Fire return interval (FRI) | Litter treatment | Mean $R_s$ (μmol $CO_2$ $m^{-2}$ $sec^{-1}$) | Mean $T_s$ (°C) | Mean $M_s$ ($m^3/m^3$) |
|---|---|---|---|---|
| 1YR | Litter | 4.21 (3.05) a | 21.12 (7.38) a | 0.14 (0.08) ab |
| 1YR | Exclusion | 3.06 (2.07) b | 21.22 (7.34) a | 0.12 (0.08) b |
| 1YR | Control | 3.05 (2.34) b | 21.28 (7.34) a | 0.16 (0.08) a |
| 2YR | Litter | 5.45 (4.55) a | 20.89 (6.41) a | 0.13 (0.07) a |
| 2YR | Exclusion | 4.38 (2.72) ab | 20.84 (6.26) a | 0.12 (0.07) a |
| 2YR | Control | 3.68 (2.47) b | 20.92 (6.44) a | 0.13 (0.07) a |
| 40YR | Litter | 5.49 (3.93) a | 20.48 (4.64) a | 0.09 (0.06) a |
| 40YR | Exclusion | 4.86 (4.12) a | 20.42 (4.74) a | 0.06 (0.04) a |
| 40YR | Control | 5.09 (3.68) a | 20.47 (4.56) a | 0.07 (0.06) a |

Values are means with standard deviation in parentheses. Means are for litter treatment type by fire return interval. Letters indicate significant differences among litter treatment type means per fire return interval using Tukey's HSD Test. Data were recorded three times daily once per month from June-December 2011 for three prescribed fire treatment intervals.

Table 3-8. Linear regression models of the relationships between soil $CO_2$ efflux rates and soil temperature by fire return interval and litter treatment type

| FRI | Litter treatment | Model and estimates | F | $R^2$ | p |
|---|---|---|---|---|---|
| 1YR | Litter | $R_s = 0.1074 + 0.1768*T_s$ | 9.77 | 0.38 | 0.0065 |
| 1YR | Exclusion | $R_s = -0.1272 + 0.1320*T_s$ | 14.03 | 0.47 | 0.0018 |
| 1YR | Control | $R_s = -0.5696 + 0.1547*T_s$ | 17.41 | 0.52 | 0.0007 |
| 2YR | Litter | $R_s = -2.4001 + 0.3508*T_s$ | 18.80 | 0.54 | 0.0005 |
| 2YR | Exclusion | $R_s = -1.1155 + 0.2418*T_s$ | 22.60 | 0.59 | 0.0002 |
| 2YR | Control | $R_s = -1.1360 + 0.2089*T_s$ | 24.47 | 0.61 | 0.0001 |
| 40YR | Litter | $R_s = -4.2070 + 0.4523*T_s$ | 9.78 | 0.38 | 0.0065 |
| 40YR | Exclusion | $R_s = -3.7433 + 0.3982*T_s$ | 11.23 | 0.41 | 0.0041 |
| 40YR | Control | $R_s = -3.8450 + 0.4130*T_s$ | 10.94 | 0.41 | 0.0044 |

Model data are mean monthly measurements from June-December 2011 taken at the Tall Timbers Research Station near Tallahassee, Florida, USA. $R_s$ is soil $CO_2$ efflux rate (μmol $CO_2$ $m^{-2}$ $sec^{-1}$), $T_s$ is soil temperature (°C).

Table 3-9. Non-linear exponential models of the relationships between soil $CO_2$ efflux rates ($R_s$) and soil temperature by fire return interval and litter treatment type r

| Fire return interval (FRI) | Treatment | Coefficient β0 | Coefficient β1 | $Q_{10}$ | $R^2$ | p |
|---|---|---|---|---|---|---|
| 1YR | Litter | 1.4158 | 0.0450 | 1.57 | 0.36 | 0.0086 |
| 1YR | Exclusion | 0.9192 | 0.0476 | 1.61 | 0.43 | 0.0030 |
| 1YR | Control | 0.7791 | 0.0556 | 1.74 | 0.49 | 0.0013 |
| 2YR | Litter | 0.9544 | 0.0741 | 2.10 | 0.52 | 0.0007 |
| 2YR | Exclusion | 1.0081 | 0.0621 | 1.86 | 0.55 | 0.0004 |
| 2YR | Control | 0.7652 | 0.0653 | 1.92 | 0.58 | 0.0003 |
| 40YR | Litter | 0.3507 | 0.1224 | 3.40 | 0.44 | 0.0028 |
| 40YR | Exclusion | 0.3257 | 0.1197 | 3.31 | 0.46 | 0.0020 |
| 40YR | Control | 0.3819 | 0.1150 | 3.16 | 0.45 | 0.0023 |

Data are results of non-linear exponential models ($R_s = \beta 0 \, e^{\beta 1 T s}$) of soil $CO_2$ efflux rate ($R_s$) (μmol $CO_2$ $m^{-2}$ $sec^{-1}$) responses to soil temperature ($T_s$). Data are presented by prescribed fire return interval (FRI) and litter manipulation treatment type. Coefficients were estimated using statistical software SAS JMP 9.0. $Q_{10}$ was calculated using the exponential equation $Q_{10} = e^{10\beta 1}$ (Lundegardh, 1927) where β1 was the coefficient estimated in the initial non-linear model.

Table 3-10. Linear regression of soil temperature and monthly mean ambient air temperature by litter treatment type and fire return interval

| Fire return interval (FRI) | Litter treatment | Relationship | $R^2$ | F | p |
|---|---|---|---|---|---|
| 1YR | Addition | Pos | 0.92 | 188.12 | < 0.0001 |
| 1YR | Exclusion | Pos | 0.92 | 180.88 | < 0.0001 |
| 1YR | Control | Pos | 0.93 | 197.22 | < 0.0001 |
| 2YR | Addition | Pos | 0.94 | 257.95 | < 0.0001 |
| 2YR | Exclusion | Pos | 0.95 | 298.56 | < 0.0001 |
| 2YR | Control | Pos | 0.94 | 251.76 | < 0.0001 |
| 40YR | Addition | Pos | 0.95 | 292.70 | < 0.0001 |
| 40YR | Exclusion | Pos | 0.94 | 252.98 | < 0.0001 |
| 40YR | Control | Pos | 0.95 | 280.16 | < 0.0001 |

Soil temperature data ($T_s$) (°C) were recorded in sample plots at Tall Timbers Research Station, Florida, USA. Monthly mean ambient air temperature (M Temp) (°C) data were means from hourly 2 m measurements recorded at the Florida Automated Weather Network Station (FAWNS) in nearby Quincy, FL.

Table 3-11. Linear regression of the relationships between soil $CO_2$ efflux rates and soil moisture content by litter treatment type and fire return interval

| FRI | Litter treatment | Model and estimates | F | $R^2$ | p |
|---|---|---|---|---|---|
| 1YR | Litter | $R_s$ = 2.6386 + 10.1666*$M_s$ | 2.38 | 0.13 | 0.1422 |
| 1YR | Exclusion | $R_s$ = 3.7252 – 6.4439*$M_s$ | 1.13 | 0.07 | 0.3039 |
| 1YR | Control | $R_s$ = 2.6459 + 2.0158*$M_s$ | 0.13 | 0.01 | 0.7357 |
| 2YR | Litter | $R_s$ = 3.9793 + 8.7733*$M_s$ | 0.72 | 0.04 | 0.7154 |
| 2YR | Exclusion | $R_s$ = 4.7924 – 4.6506*$M_s$ | 0.23 | 0.01 | 0.6381 |
| 2YR | Control | $R_s$ = 3.5785 – 0.2566*$M_s$ | 0.00 | 0.00 | 0.9732 |
| 40YR | Litter | $R_s$ = 3.6307 + 21.6083*$M_s$ | 1.63 | 0.09 | 0.2200 |
| 40YR | Exclusion | $R_s$ = 4.4822 + 3.2570*$M_s$ | 0.02 | 0.00 | 0.8887 |
| 40YR | Control | $R_s$ = 3.1391 + 23.5037*$M_s$ | 3.59 | 0.18 | 0.0765 |

Model data are mean monthly measurements from June-December 2011 taken at the Tall Timbers Research Station near Tallahassee, Florida, USA. $R_s$ is soil $CO_2$ efflux rate (μmol $CO_2$ $m^{-2}$ $sec^{-1}$), $M_s$ is soil moisture content ($m^3/m^3$).

Table 3-12. Linear regression of the relationships between soil $CO_2$ efflux rates and monthly precipitation by litter treatment type and fire return interval

| FRI | Litter treatment | Model and estimates | F | $R^2$ | p |
|---|---|---|---|---|---|
| 1YR | Litter | $R_s$ = 1.0919 + 0.2961*Precip | 19.94 | 0.51 | 0.0003 |
| 1YR | Exclusion | $R_s$ = 0.6766 + 0.2268*Precip | 16.34 | 0.46 | 0.0007 |
| 1YR | Control | $R_s$ = 0.4195 + 0.2507*Precip | 25.98 | 0.58 | < 0.0001 |
| 2YR | Litter | $R_s$ = 0.6896 + 0.4484*Precip | 24.61 | 0.56 | < 0.0001 |
| 2YR | Exclusion | $R_s$ = 1.2985 + 0.2936*Precip | 19.41 | 0.51 | 0.0003 |
| 2YR | Control | $R_s$ = 0.8007 + 0.2743*Precip | 20.29 | 0.52 | 0.0002 |
| 40YR | Litter | $R_s$ = -0.4857 + 0.5698*Precip | 52.57 | 0.73 | < 0.0001 |
| 40YR | Exclusion | $R_s$ = -0.4015 + 0.5011*Precip | 53.82 | 0.74 | < 0.0001 |
| 40YR | Control | $R_s$ = -0.2653 + 0.5111*Precip | 57.08 | 0.75 | < 0.0001 |

Model data are mean monthly measurements from June-December 2011 taken at the Tall Timbers Research Station near Tallahassee, Florida, USA. $R_s$ is soil $CO_2$ efflux rate (µmol $CO_2$ $m^{-2}$ $sec^{-1}$), Precip is monthly total precipitation for the region from measurements recorded at the Florida Automated Weather Network Station (FAWNS) in nearby Quincy, FL.

Table 3-13. Linear regression of soil moisture content and monthly precipitation by litter treatment type and fire return interval

| Fire return interval (FRI) | Litter treatment | Relationship | $R^2$ | F | p |
|---|---|---|---|---|---|
| 1YR | Addition | Pos | 0.14 | 2.62 | 0.1250 |
| 1YR | Exclusion | Neg | 0.07 | 1.20 | 0.2892 |
| 1YR | Control | Pos | 0.08 | 1.47 | 0.2428 |
| 2YR | Addition | Pos | 0.15 | 2.92 | 0.1070 |
| 2YR | Exclusion | Pos | 0.02 | 0.41 | 0.5324 |
| 2YR | Control | Pos | 0.03 | 0.43 | 0.5232 |
| 40YR | Addition | Pos | 0.10 | 1.83 | 0.1946 |
| 40YR | Exclusion | Neg | 0.02 | 0.27 | 0.6092 |
| 40YR | Control | Pos | 0.23 | 4.89 | 0.0420 |

Model soil moisture content ($M_s$) ($m^3/m^3$) data are mean monthly measurements from June-December 2011 taken at the Tall Timbers Research Station near Tallahassee, Florida, USA. $R_s$ is soil $CO_2$ efflux rate (μmol $CO_2$ $m^{-2}$ $sec^{-1}$), Precip is monthly total precipitation for the region from measurements recorded at the Florida Automated Weather Network Station (FAWNS) in nearby Quincy, FL.

Table 3-14. Linear regression of soil temperature and monthly precipitation by litter treatment type and fire return interval

| Fire return interval (FRI) | Litter treatment | Relationship | $R^2$ | F | p |
|---|---|---|---|---|---|
| 1YR | Addition | Pos | 0.60 | 24.00 | 0.0002 |
| 1YR | Exclusion | Pos | 0.58 | 21.92 | 0.0003 |
| 1YR | Control | Pos | 0.58 | 22.46 | 0.0002 |
| 2YR | Addition | Pos | 0.63 | 27.13 | < 0.0001 |
| 2YR | Exclusion | Pos | 0.62 | 25.88 | 0.0001 |
| 2YR | Control | Pos | 0.61 | 24.80 | 0.0001 |
| 40YR | Addition | Pos | 0.63 | 27.70 | < 0.0001 |
| 40YR | Exclusion | Pos | 0.62 | 25.91 | 0.0001 |
| 40YR | Control | Pos | 0.63 | 27.29 | < 0.0001 |

Soil temperature data ($T_s$) (°C) data are mean monthly measurements from June-December 2011 taken at the Tall Timbers Research Station near Tallahassee, Florida, USA. Precipitation is monthly total precipitation for the region from measurements recorded at the Florida Automated Weather Network Station (FAWNS) in nearby Quincy, FL.

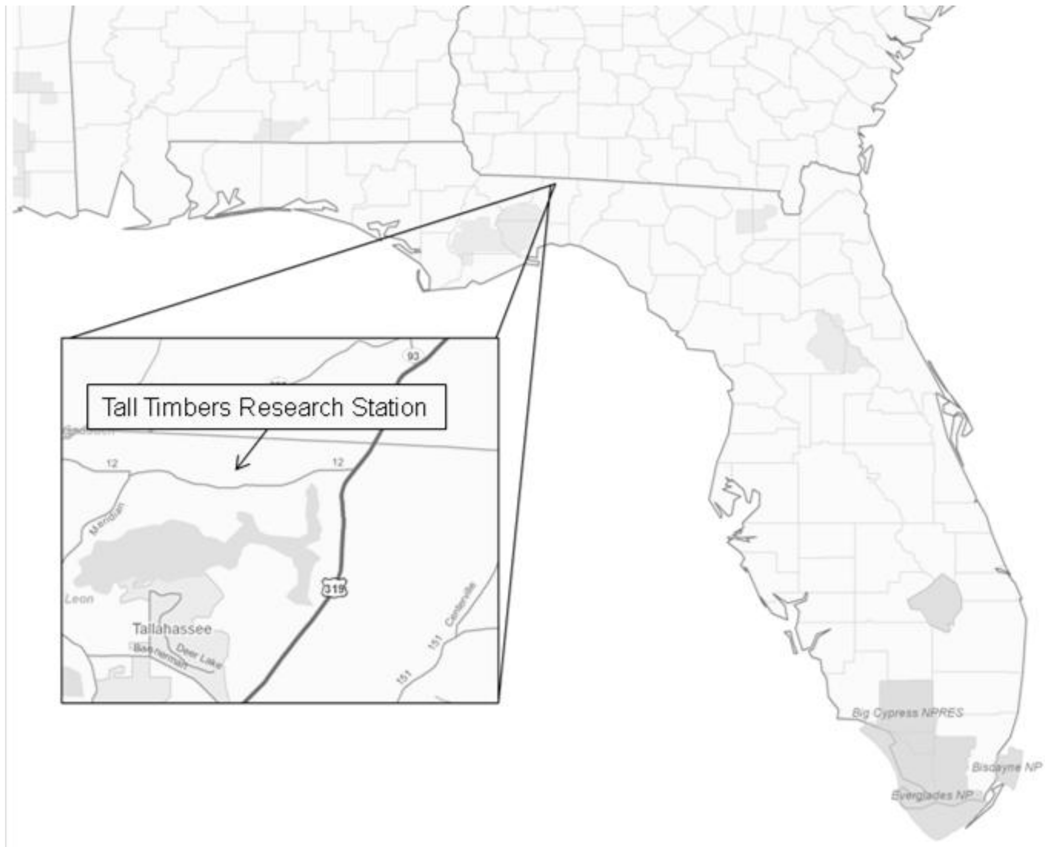


Figure 3-1. Map of the study area at the Tall Timbers Research Station in Leon County, Florida, USA. Map produced by David Godwin.

Figure 3-2. Ground (left) and aerial (right) images of three of the soil $CO_2$ efflux sampling plots located within the Tall Timbers Research Station in Leon County, Florida, USA. The top images show an annual burn frequency site (1YR), the middle images a two-year burn frequency site (2YR), and the bottom image a site unburned since 1966. Ground images original to the author. Ground photographs courtesy of David Godwin. Aerial images courtesy of Microsoft Bing Maps.

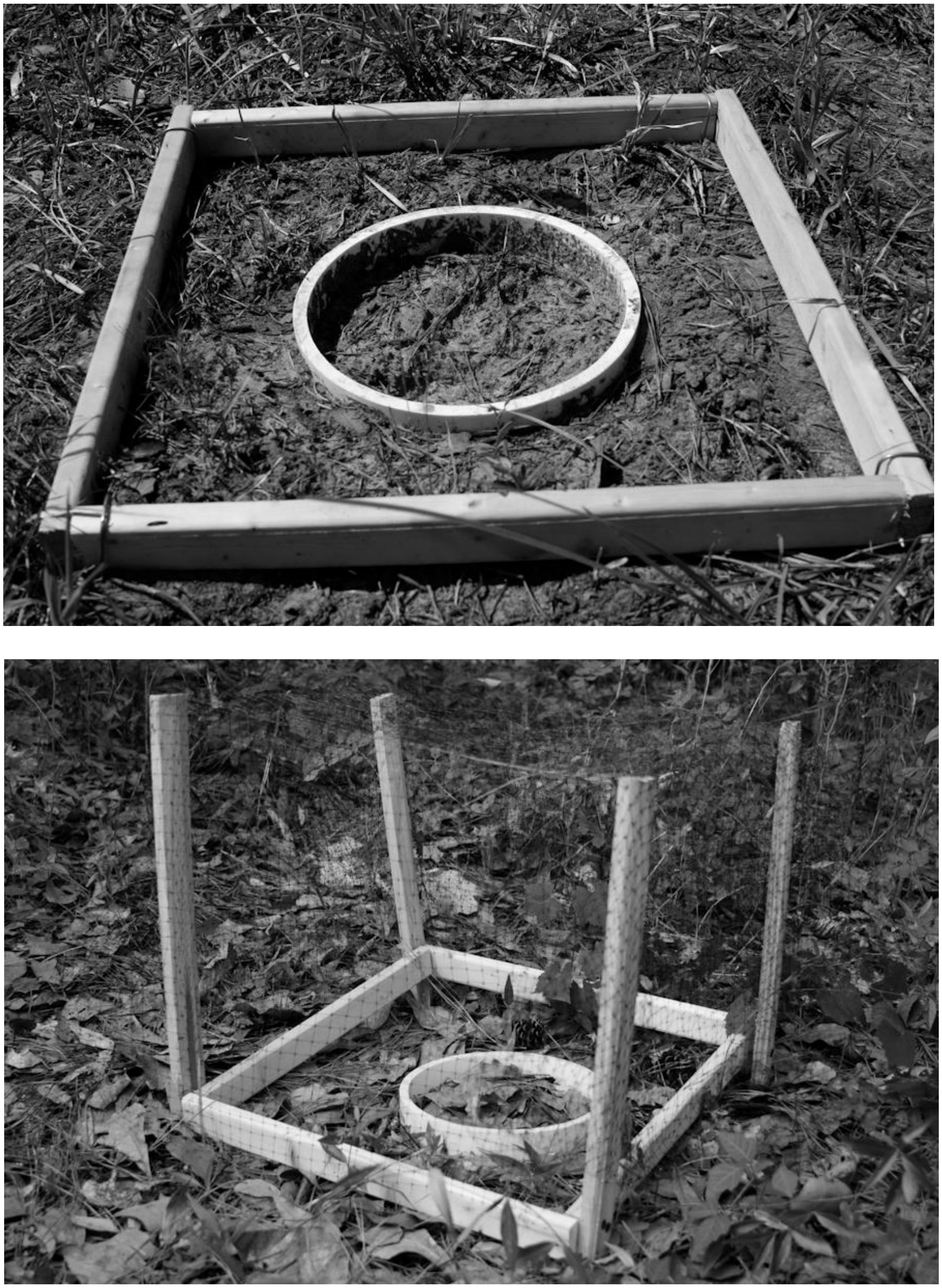

Figure 3-3. Photograph of a 20 cm soil $CO_2$ efflux sample collar and 0.16 $m^2$ wood treatment box (top) and litter exclusion enclosure (bottom) at the Tall Timbers Research Station, Florida, USA. Photographs courtesy of David Godwin.


Figure 3-4. Photograph of the LICOR Biosciences LI-8100 soil $CO_2$ efflux sampling instrument with 20 cm survey chamber and soil moisture and temperature probes. Photograph courtesy of David Godwin.

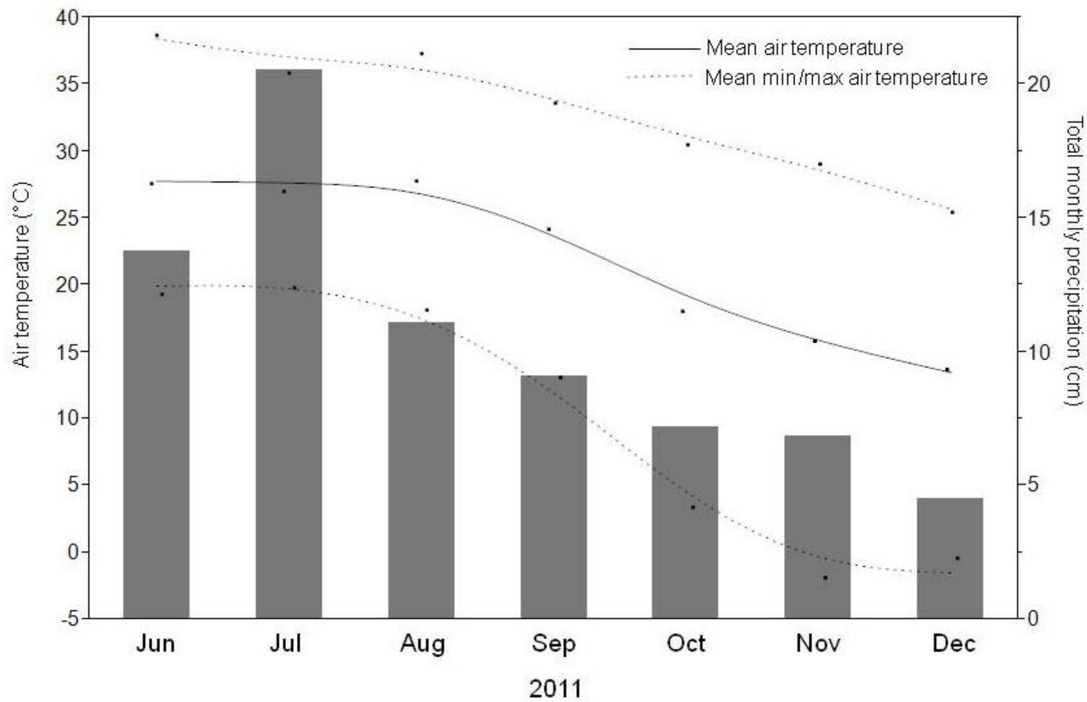


Figure 3-5. Plot of seven months of 2 m air temperature records and precipitation for the year 2011 from the Florida Automated Weather Network (FAWN) site at Quincy, Florida, approximately 30 km from Tall Timbers Research Station, Florida, USA.

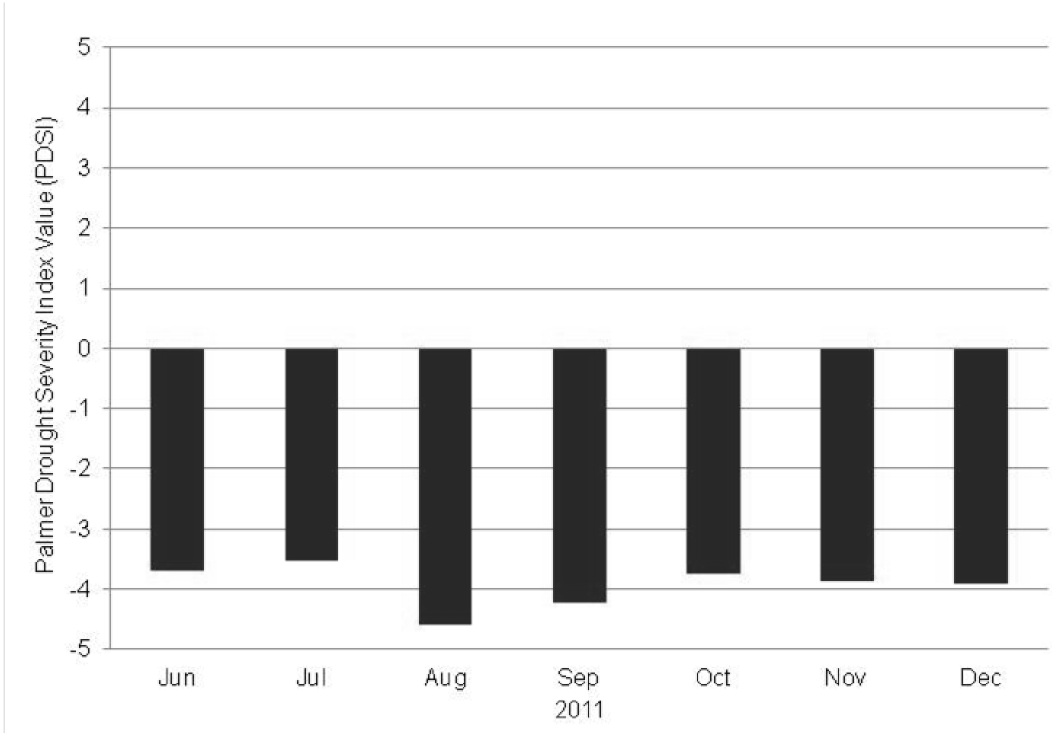


Figure 3-6. Plot of seven months of monthly Palmer Drought Severity Index (PDSI) values for the year 2011 from the National Oceanic and Atmospheric Administration (NOAA) National Climatic Data Center (NCDC). All scores below zero represent drought conditions for the region.

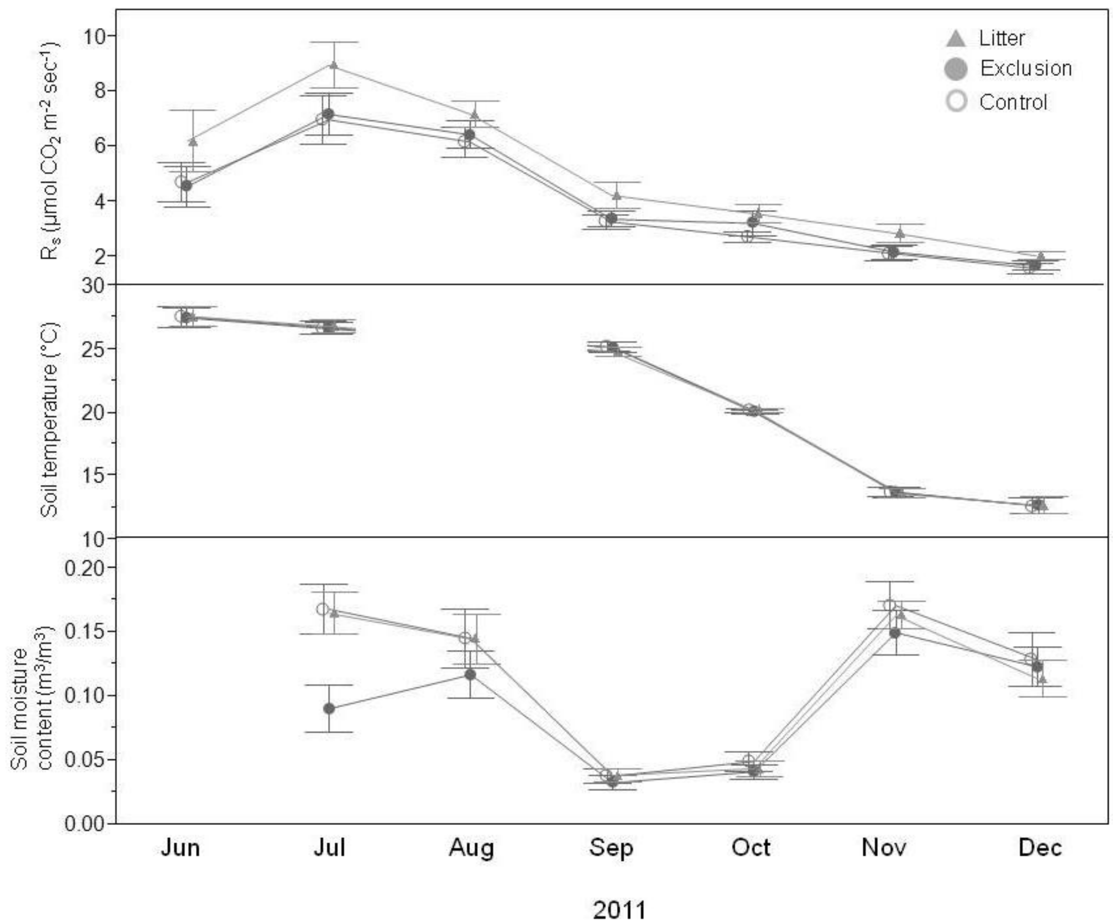


Figure 3-7. Monthly mean soil $CO_2$ efflux rates ($R_s$) (μmol $CO_2$ $m^{-2}$ $sec^{-1}$), soil temperature ($T_s$) (°C), and soil moisture content ($M_s$) ($m^3/m^3$) by litter treatment type (litter addition, litter exclusion, and control). Points indicate monthly means of all study data with FRI treatment type ignored. Equipment problems resulted in no $M_s$ data collected during the month of June and no $T_s$ data collected during the month of August.

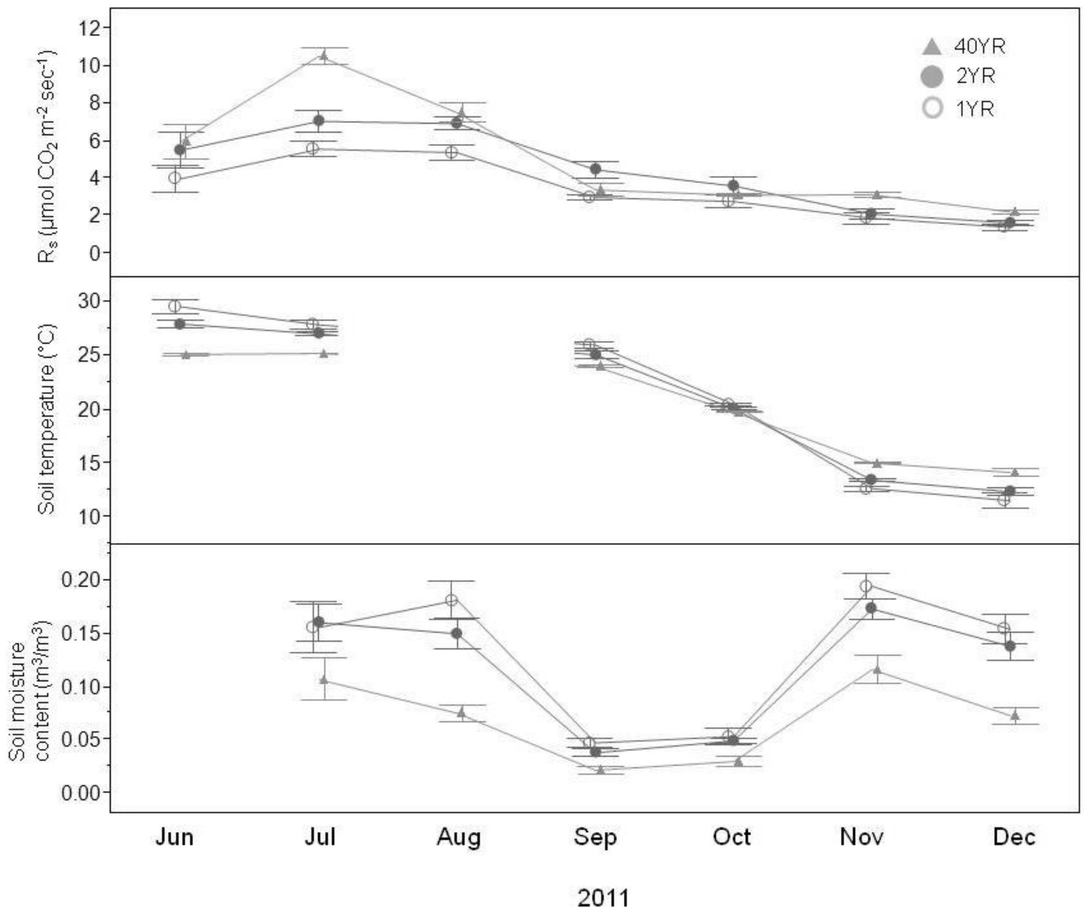


Figure 3-8. Monthly mean soil $CO_2$ efflux rates ($R_s$) (µmol $CO_2$ m$^{-2}$ sec$^{-1}$), soil temperature ($T_s$) (°C), and soil moisture content ($M_s$) (m$^3$/m$^3$) prescribed fire management type (1YR, 2YR, and 40YR). Points indicate monthly means of all study data with litter treatment type ignored. Equipment problems resulted in no $M_s$ data collected during the month of June and no $T_s$ data collected during the month of August.

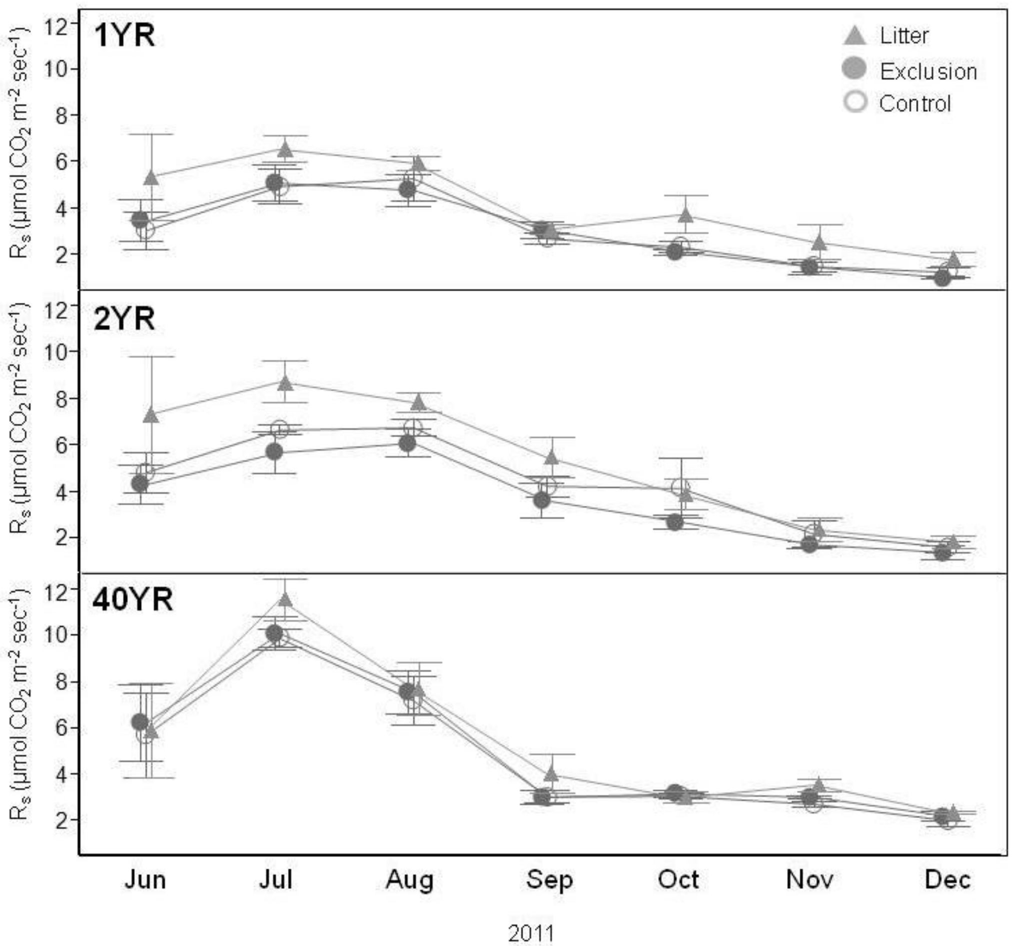


Figure 3-9. Monthly mean soil $CO_2$ efflux rates ($R_s$) (µmol $CO_2$ $m^{-2}$ $sec^{-1}$) by litter (litter addition, litter exclusion, and control) and fire (1YR, 2YR, and 40YR) treatment type. Points indicate soil respiration rate monthly averages for the study period June – December 2011.

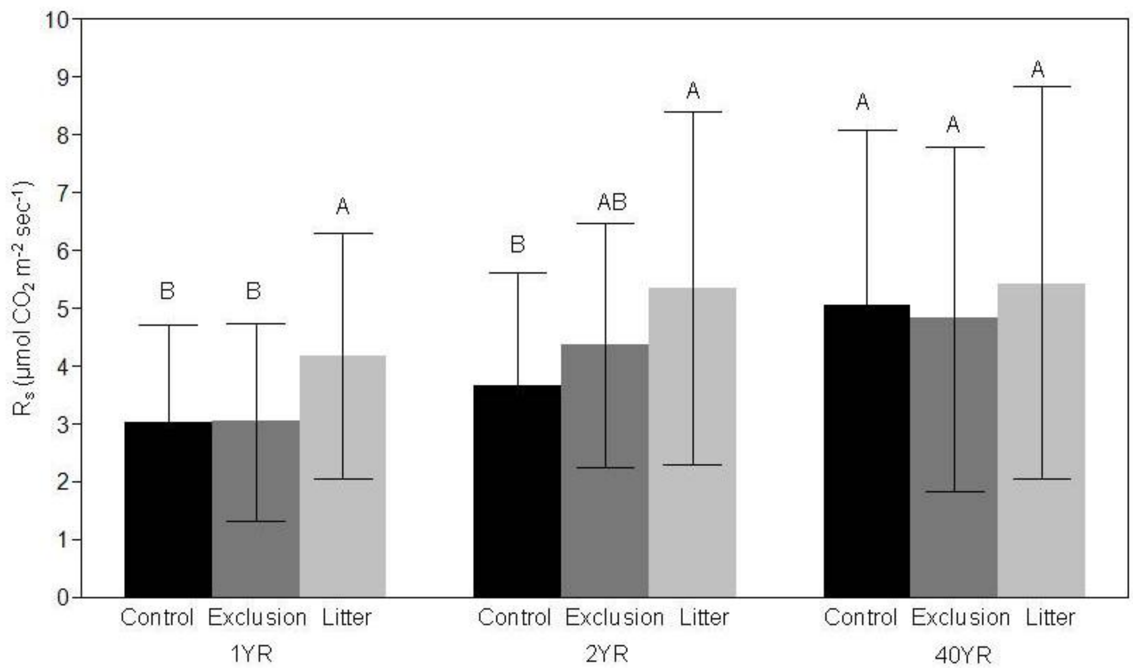


Figure 3-10. Overall mean soil $CO_2$ efflux rates ($R_s$) (µmol $CO_2$ $m^{-2}$ $sec^{-1}$) by litter manipulation treatment (litter addition, exclusion, and control) within fire return interval treatment (1YR, 2YR, and 40YR). Letters indicate significant differences among litter treatments within each fire treatment (Tukey's HSD test α = 0.05). Data are means for the study period June – December 2011.

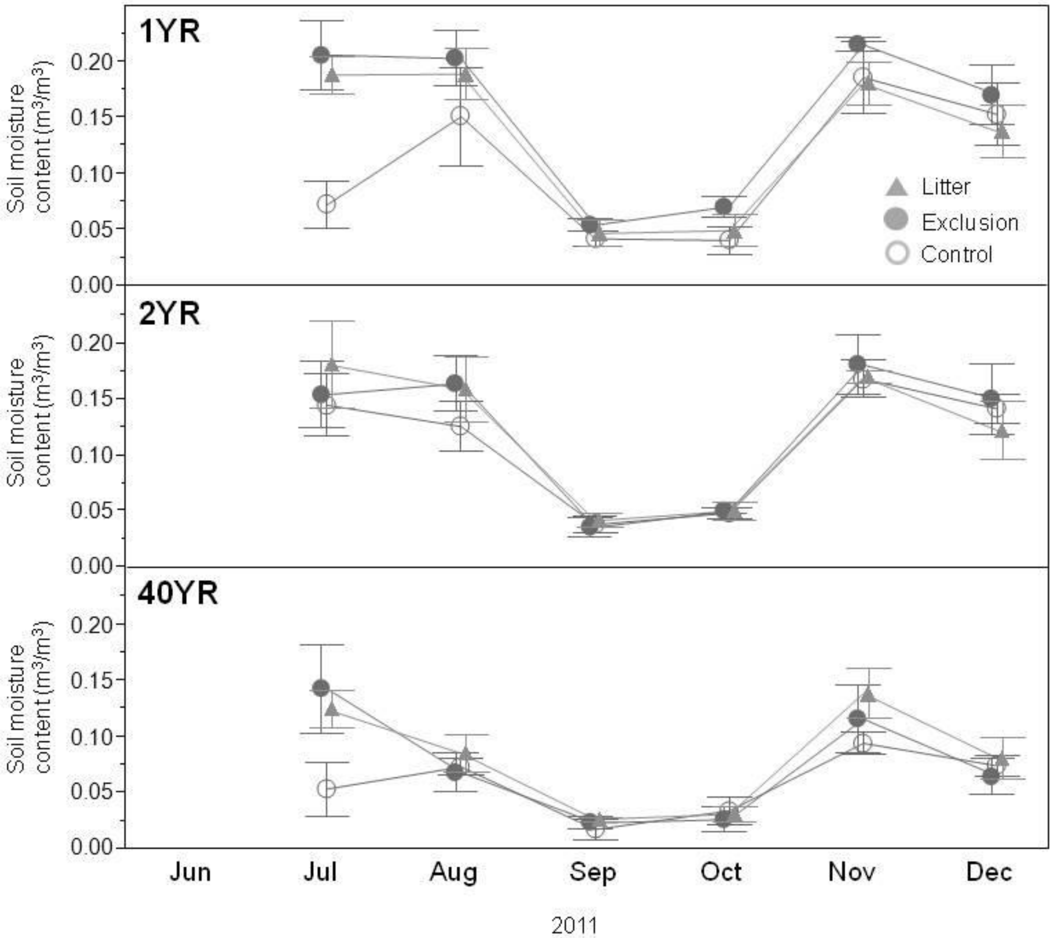


Figure 3-11. Monthly mean soil moisture content ($M_s$) ($m^3/m^3$) by litter (litter addition, litter exclusion, and control) and fire (1YR, 2YR, and 40YR) treatment type. Points indicate soil moisture content monthly means for the study period June – December 2011. Equipment problems resulted in no data collected during the month of June.

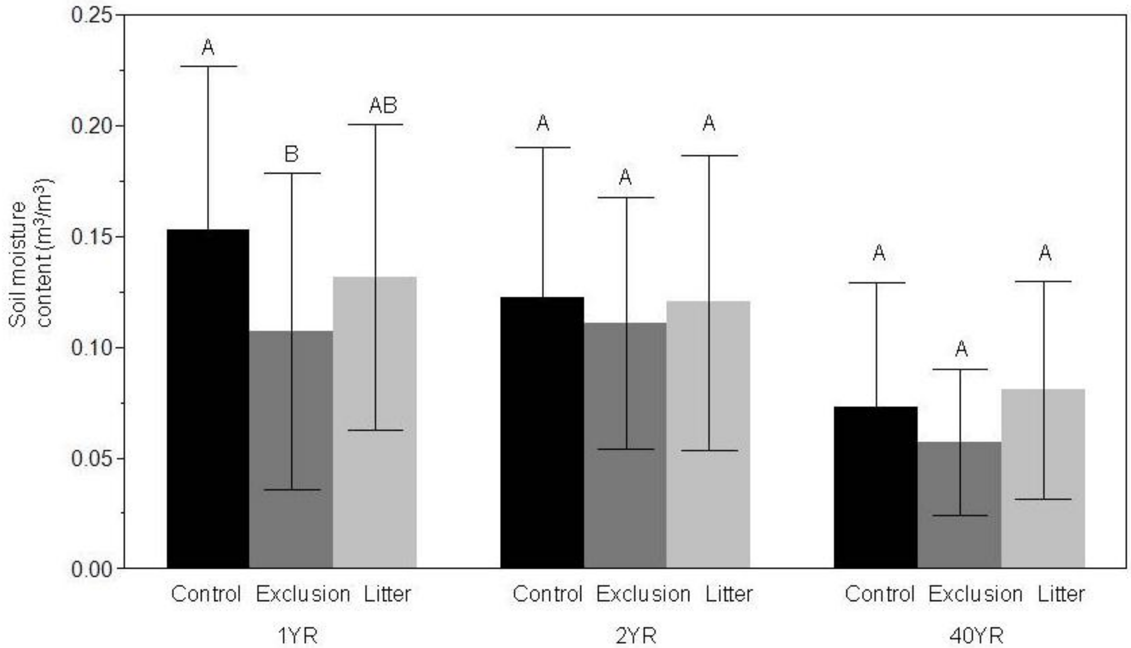


Figure 3-12. Overall mean soil moisture content ($M_s$) ($m^3/m^3$) by litter manipulation treatment (litter addition, exclusion, and control) within fire return interval treatment (1YR, 2YR, and 40YR). Letters indicate significant differences among litter treatments within each fire treatment (Tukey's HSD test α = 0.05). Data are means for the study period June – December 2011.

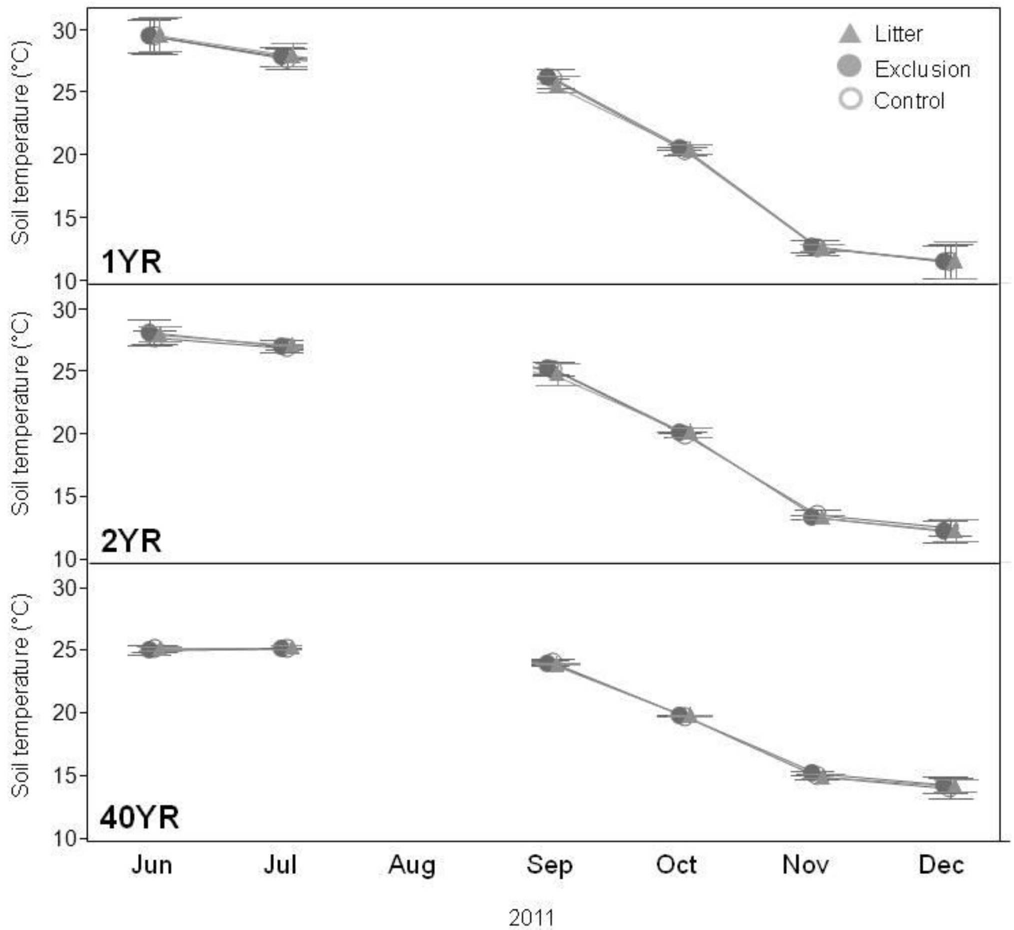


Figure 3-13. Monthly mean soil temperature ($T_s$) (°C) by litter (litter addition, litter exclusion, and control) and fire (1YR, 2YR, and 40YR) treatment type. Points indicate soil temperature monthly averages for the study period June – December 2011. Equipment problems resulted in no data collected during the month of August.

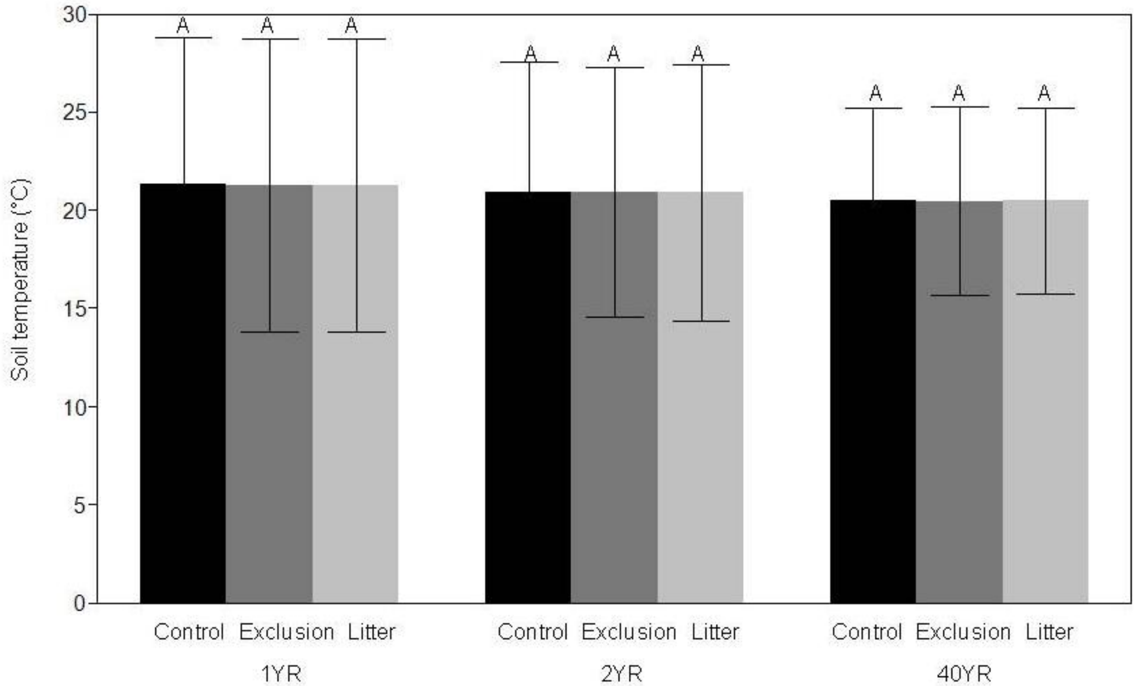


Figure 3-14. Overall mean soil temperature ($T_s$) (°C) by litter manipulation treatment (litter addition, exclusion, and control) within fire return interval treatment (1YR, 2YR, and 40YR). Letters indicate significant differences among litter treatments within each fire treatment (Tukey's HSD test α = 0.05). Data are means for the study period June – December 2011.

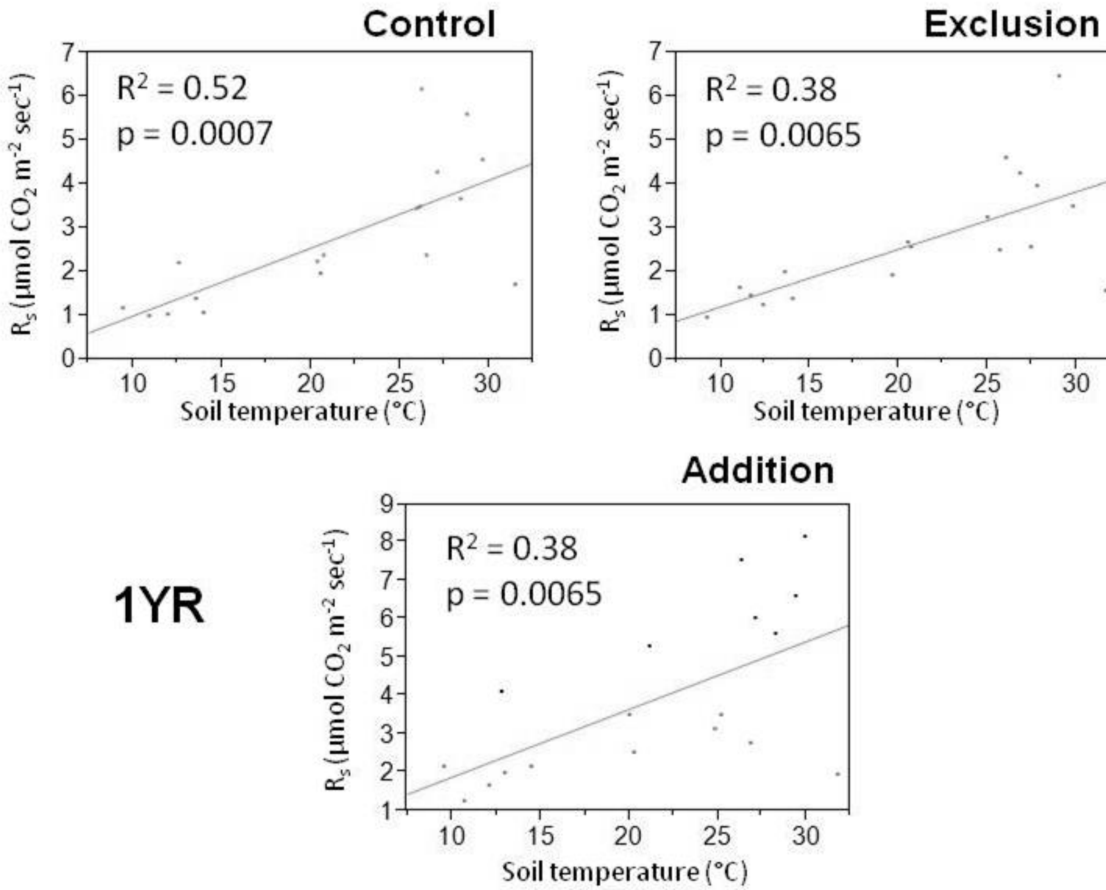


Figure 3-15. Linear regression of the relationships between monthly mean soil $CO_2$ efflux rates ($R_s$) (µmol $CO_2$ $m^{-2}$ $sec^{-1}$) and soil temperature ($T_s$) (°C) for three litter treatment types within the 1YR prescribed fire interval at the Tall Timbers Research Station near Tallahassee, Florida, USA. Each point represents monthly mean values per sample plot.

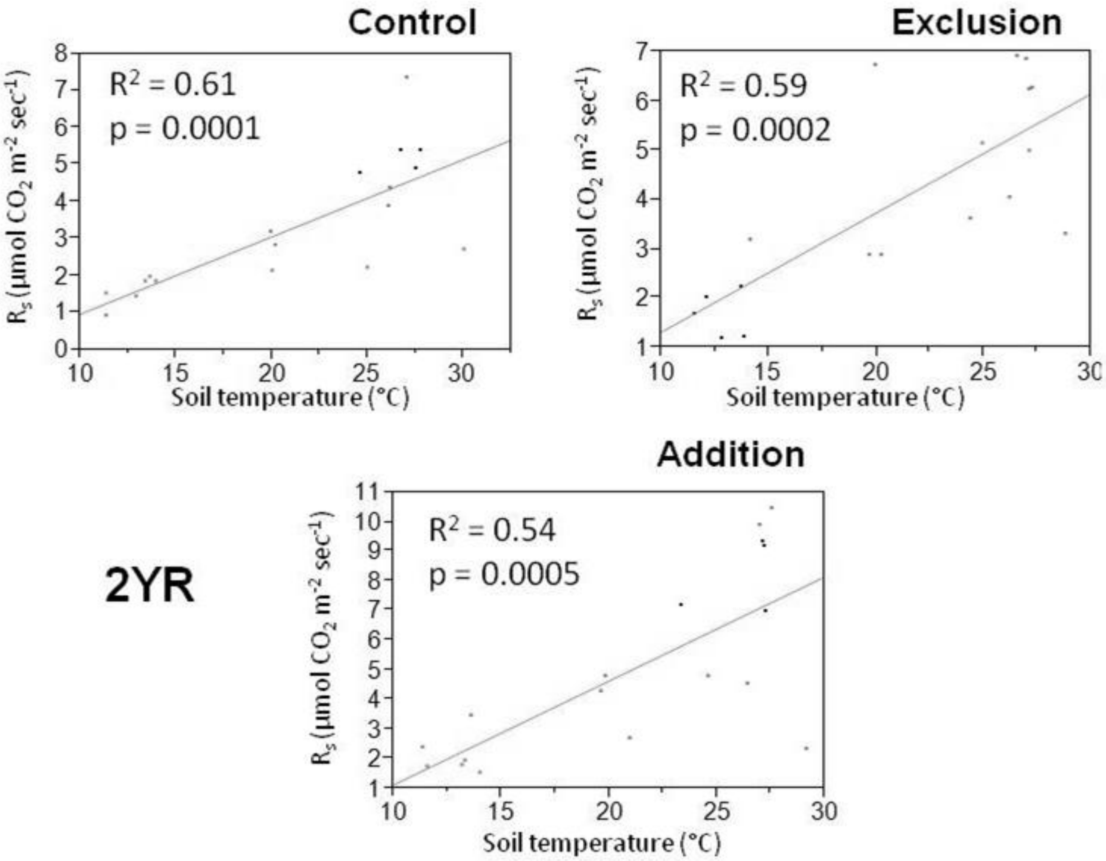


Figure 3-16. Linear regression of the relationships between monthly mean soil $CO_2$ efflux rates ($R_s$) (µmol $CO_2$ $m^{-2}$ $sec^{-1}$) and soil temperature ($T_s$) (°C) for three litter treatment types within the 2YR prescribed fire interval at the Tall Timbers Research Station near Tallahassee, Florida, USA. Each point represents monthly mean values per sample plot.

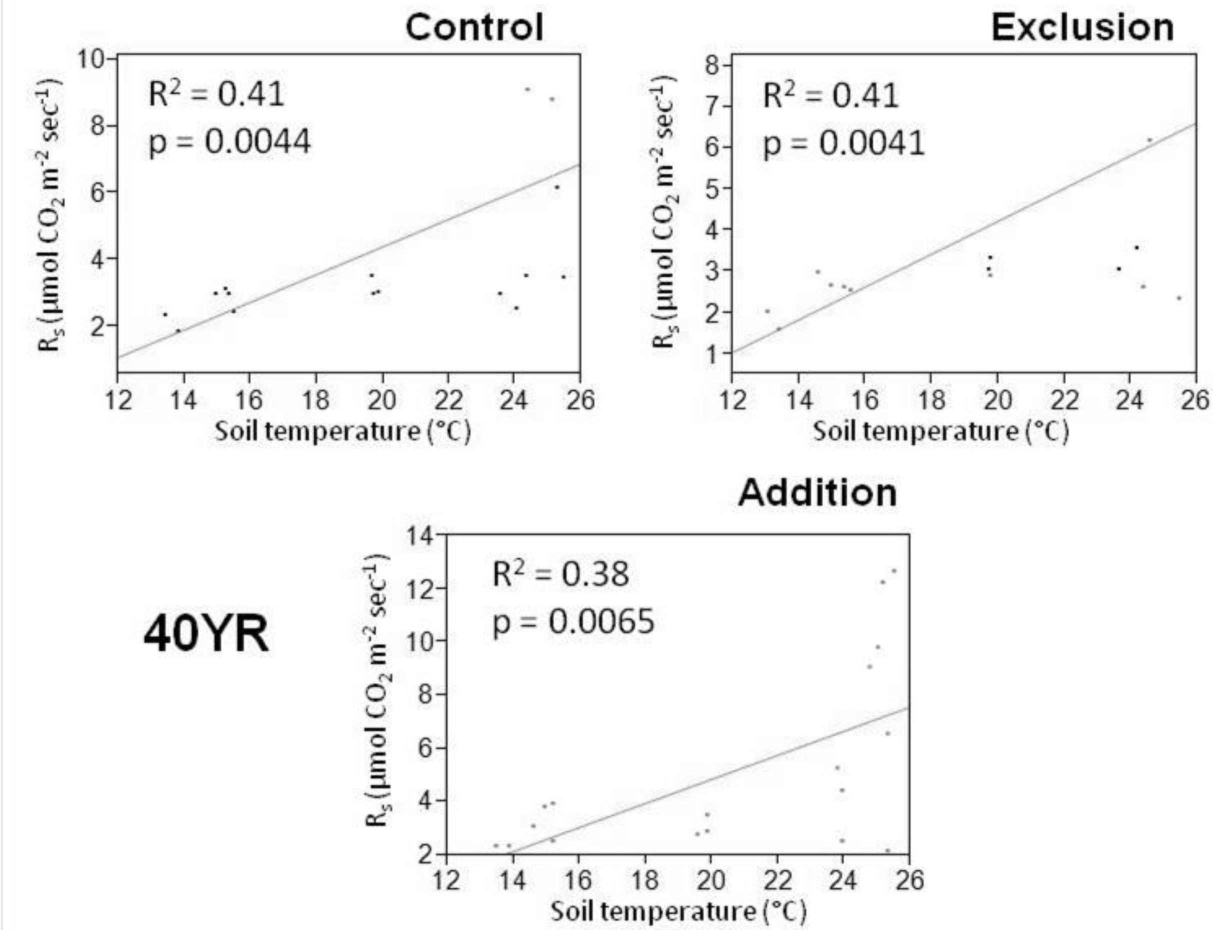


Figure 3-17. Linear regression of the relationships between monthly mean soil $CO_2$ efflux rates ($R_s$) (µmol $CO_2$ $m^{-2}$ $sec^{-1}$) and soil temperature ($T_s$) (°C) for three litter treatment types within the 40YR prescribed fire interval at the Tall Timbers Research Station near Tallahassee, Florida, USA. Each point represents monthly mean values per sample plot.

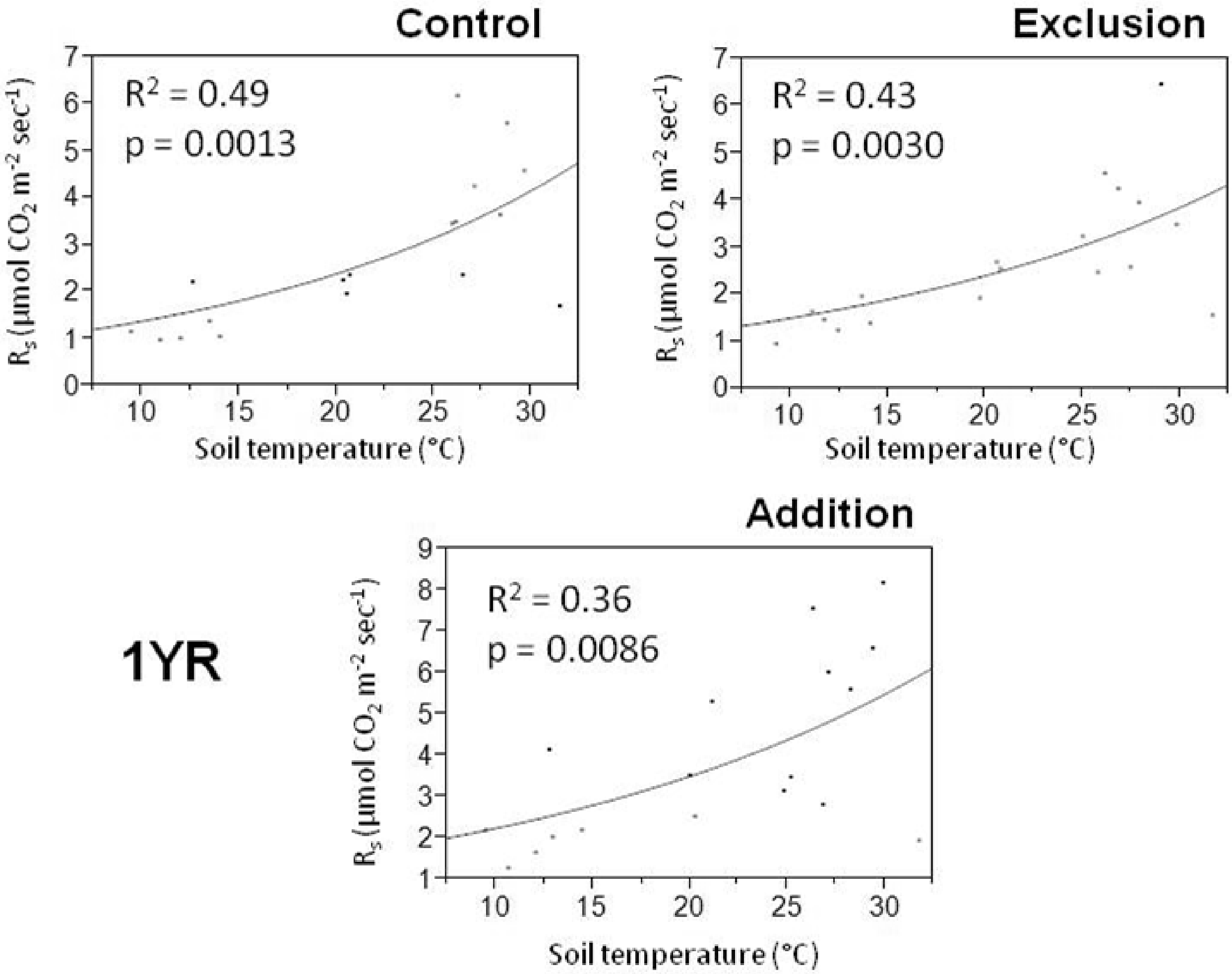


Figure 3-18. The relationship between monthly mean soil $CO_2$ efflux rates (µmol $CO_2$ $m^{-2}$ $sec^{-1}$) ($R_s$) and monthly mean soil temperature (°C) ($T_s$) as modeled using an exponential equation (Equation 3-2). Data presented are from the 1YR prescribed fire treatment interval litter treatment types. Each point represents monthly mean values per sample plot.

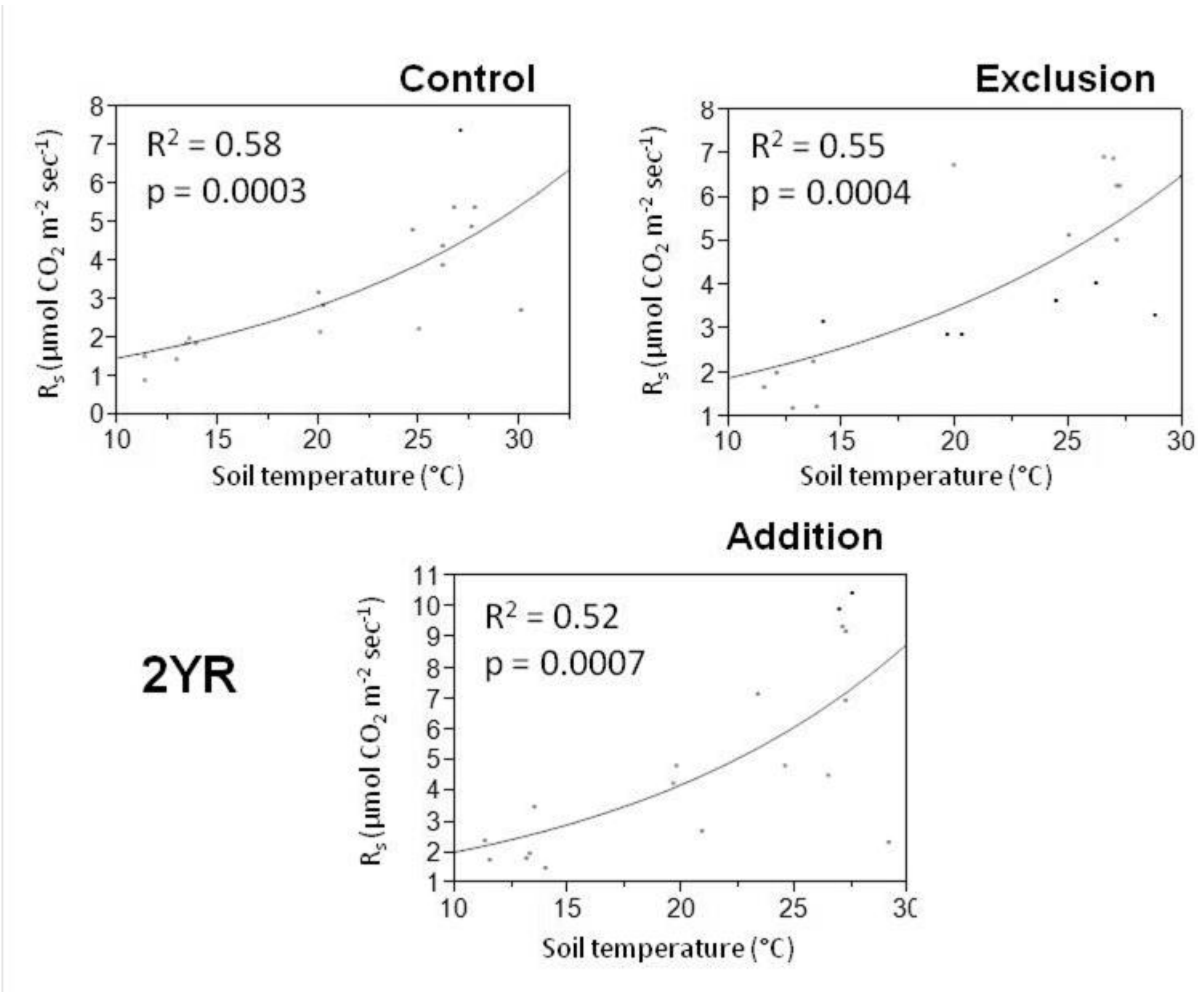


Figure 3-19. The relationship between monthly mean soil $CO_2$ efflux rates (μmol $CO_2$ $m^{-2}$ $sec^{-1}$) ($R_s$) and monthly mean soil temperature (°C) ($T_s$) as modeled using an exponential equation (Equation 3-2). Data presented are from the 2YR prescribed fire treatment interval litter treatment types. Each point represents monthly mean values per sample plot.

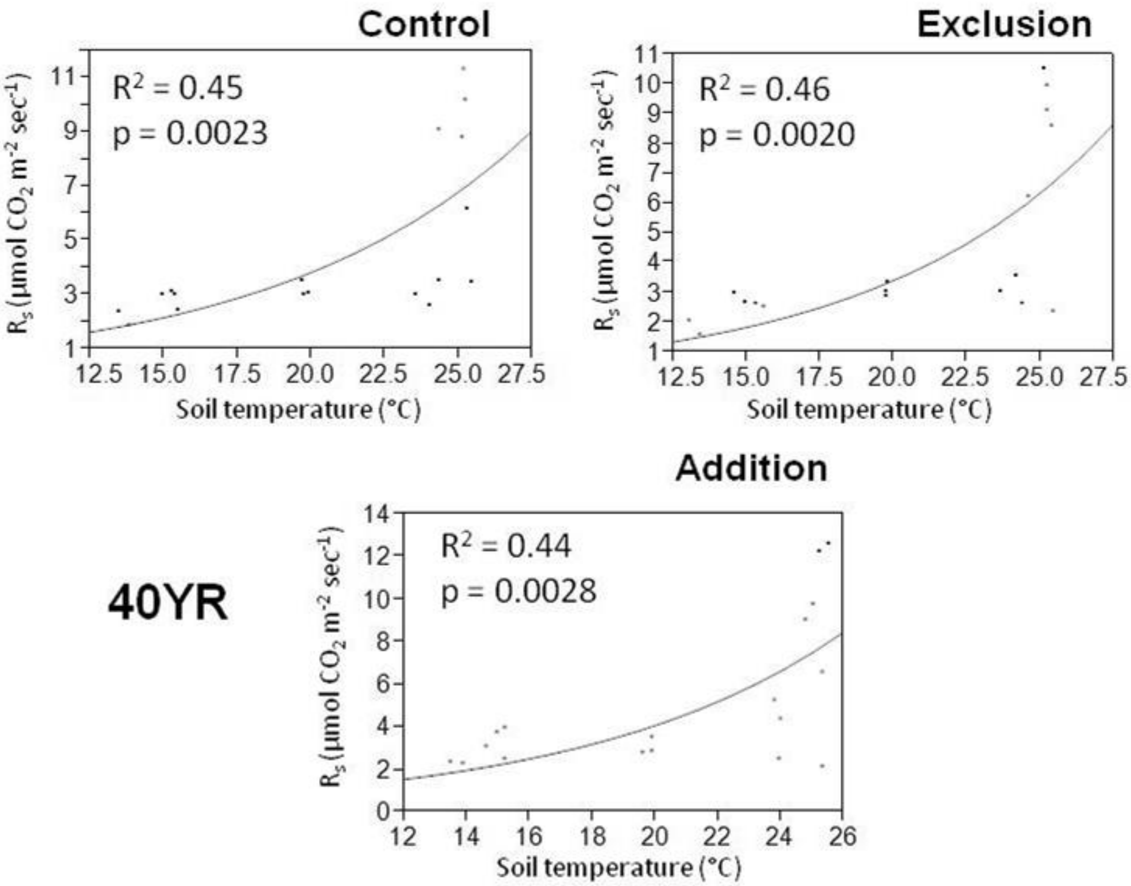


Figure 3-20. The relationship between monthly mean soil $CO_2$ efflux rates (µmol $CO_2$ $m^{-2}$ $sec^{-1}$) ($R_s$) and monthly mean soil temperature (°C) ($T_s$) as modeled using an exponential equation (Equation 3-2). Data presented are from the 40YR prescribed fire treatment interval litter treatment types. Each point represents monthly mean values per sample plot.

# CHAPTER 4
# THE INFLUENCE OF PRESCRIBED FIRE AND UNDERSTORY FUELS MASTICATION ON SOIL CO2 EFFLUX RATES IN TWO NORTH FLORIDA FLATWOODS FORESTS

## Background

It is important to understand the implications of forest management practices on soil carbon dynamics as forests and forest soils play significant roles in global carbon cycles. In temperate forest ecosystems, approximately 50-60% of ecosystem carbon is found within the soils, with soil $CO_2$ efflux ($R_s$) comprising 50-60% of total ecosystem carbon budgets (Raich and Schlesinger, 1992; Lal, 2005; Noormets et al. 2010). One method for assessing how management affects forest carbon dynamics is the measurement of soil $CO_2$ efflux rates. A variety of forest management activities, including prescribed fire and mechanical fuels mastication, have been shown to significantly influence soil $CO_2$ efflux rates in the western United States (US), yet these relationships are not well known in southeastern US forests (Concilio et al., 2005; Kobziar, 2007; Ryu et al., 2009). Prescribed fire is one of the most prevalent forest management tools employed in the southeastern US with over 2.4 million ha burned in 2011 and mechanical fuels mastication treatments are becoming more common in the region as concerns over wildfire in the wildland urban interface grow (Agee and Skinner, 2005; Waldrop and Goodrick, 2012). This study seeks to understand the influence of prescribed fire management regimes and mechanical fuels mastication treatments on soil $CO_2$ efflux rates in mature pine flatwoods forests of north central Florida, USA.

Flatwoods are the most common forested ecosystem in Florida totaling over 5.2 million ha (Myers and Ewel, 1990). Given the prevalence of this forest type, public and private interest in the effect of forest management activities on forest carbon dynamics are expected to be significant (Law and Harmon, 2011). With the possibility of future federal land management goals including carbon sequestration, understanding the effect of management regimes on carbon dynamics is critical (Exec. Order No. 13,513, 2009). In flatwoods managed for conservation, prescribed fire is one of the most frequently utilized management tools for maintaining ecosystem composition and structure and reducing wildfire risk (Outcalt and Wade, 1999). For wildfire risk reduction in flatwoods forests, prescribed fire is typically applied on a 3-5 year interval to remove the accumulation of saw palmetto (*Serenoa repens* (Bartr.) Small) and other understory vegetative fuels that tend to drive fire behavior in these systems (Brose and Wade, 2002). Given the importance of prescribed fire in these forests and the potential ecological and economic benefits of carbon credits for carbon sequestration, it is important to understand the influence of these management fires on soil $CO_2$ efflux rates.

As the extent of the wildland urban interface (WUI) has expanded in the later part of the 20$^{th}$ and early 21$^{st}$ century, so has the social and political pressure to reduce the risk of property damage in the interface from wildfires (Vince et al., 2005). There are three primary methods which have been employed to alter forest structure in efforts to reduce such risk: prescribed fire, mechanical mastication and a combination of mechanical mastication followed by prescribed fire (Agee and Skinner, 2005; Kobziar and Stephens, 2006; Hurteau and North, 2009). Mechanical fuels mastication is used to reduce understory fuel heights, thereby increasing the height to live crowns, which has been shown to reduce fire behavior in both western and eastern US forests (Agee and Skinner, 2005; Glitzenstein et al., 2006; Kobziar et al., 2009). In many WUI areas in the southeastern US, prescribed fire has become difficult for land managers to implement due to concerns from adjacent and nearby landowners over smoke and wildfire risk or because of prolonged fire suppression and subsequent hazardous fuel load accumulations (Miller and Wade, 2003; Long et al., 2004). The use of mechanical fuels treatments with or without prescribed fire has increased in recent years in Florida, USA, as land managers seek to maintain and restore forest structure in areas where the implementation of prescribed fire has proven difficult. Pre-burning mechanical techniques are also applied to alter the arrangement of vegetative fuels to decrease fire intensity and severity upon the subsequent reintroduction of prescribed fire (Menges and Gordon, 2010). As the implementation of these mechanical treatments becomes more widespread, it will become even more important to understand their influence on forest carbon. Previous studies of mechanical fuels mastication have shown that treatments can significantly alter soil $CO_2$ efflux rates (Kobziar and Stephens, 2006) as well as influence soil environmental factors such as soil temperature and soil moisture content; factors that are known to drive soil $CO_2$ efflux rates in some ecosystems (Concilio et al., 2005; Kobziar and Stephens, 2006; Xu et al., 2011).

Mechanical fuels mastication treatments and prescribed fire can influence soil $CO_2$ efflux rates by altering soil and environmental physical, chemical, and abiotic factors that affect the sources of heterotrophic and autotrophic $R_s$. For example, fire has been shown to alter forest floor litter and duff loads, carbon and nitrogen pools, soil temperature, pH, and microbial activity in multiple ecosystems (Neary, 1999; Debano, 2000). In addition, mechanical fuels mastication treatments have been shown to influence forest floor litter and duff loads and average soil temperature and moisture content which can also influence heterotrophic and autotrophic sources of $R_s$ (Luo and Zhou, 2006; Kobziar, 2007). Finally, both treatments have clear impacts on understory forest vegetation through physical mastication or damage, combustion, injury, or competitive release that can alter vegetative activity and belowground carbon allocation.

Numerous studies have investigated carbon dynamics in flatwoods and similar commercial slash pine forests of the southeastern US, however none known have specifically addressed the effects of mechanical fuels mastication treatments and prescribed fire management regimes on soil $CO_2$ efflux rates (Ewel et al., 1987a; Ewel et al.,1987b; Fang et al., 1998; Clark et al., 2004; Powell et al., 2008; Meigs et al., 2009; Lavoie et al., 2010; Bracho et al., 2012). By investigating prescribed fire, mechanical fuels mastication, and mechanical fuels mastication followed by prescribed fire in the context of two flatwoods ecosystems managed for conservation and multiple-use purposes, this study sought to address the following research questions: (1) How do prescribed fire and understory fuels mastication treatments influence monthly, seasonal, and annual soil $CO_2$ efflux rates, and, (2) How do prescribed fire and mastication treatments affect forest conditions that will likely influence long-term site level soil $CO_2$ efflux rates and soil carbon dynamics? For managers and researchers alike, this study provides insight into linkages between forest management, soil carbon storage and flux, and the physical and biotic variables influencing those fluxes that are likely to be influenced by global climate change.

## Methods

### Study Areas

The first study sites were located within the 80,000 ha United States Forest Service (USFS) Osceola National Forest (Osceola) in Columbia County, FL, USA approximately 20 km from the town of Lake City (30° 14'N, -082° 31'W) (Figure 4-1). The area is within the Gulf Coastal Plain region and is generally flat with little to no perceptible slope. The study sites are located approximately 44 m above sea level. Average annual precipitation was 132 cm with the majority falling during the summer months of June, July and August (National Climate Data Center 2009). Mean maximum and minimum temperatures for January and July for the study area from long-term records were 18.9 °C and 6.1 °C for January and 32.7 °C and 21.7 °C for July (National Climate Data Center 2009). Soils within the site are generally poorly drained sandy, siliceous, hyperthermic Ultic Alaquods of the Mascotte and Olustee series (Natural Resource Conservation Service (NRCS) Soil Survey Geographic Database (SSURGO)). Vegetation across all sites consisted of an overstory mixture of naturally regenerated slash pine (*Pinus elliottii* Engelm) and longleaf pine (*P. palustris* P. Mill) and an understory composed of saw palmetto (*Serenoa repens* (W. Bartram) Small), gallberry (*Ilex glabra*), and deerberry (*Vaccinium stamineum*) shrubs (Myers and Ewel 1990). Across the study area stand age averaged 80 years (Osceola National Forest staff pers. comm.). Prior to the start of the study, all plots had been unburned for at least 11 years (Jesse Kreye, pers. comm.).

The second study site was located within the 840 ha University of Florida Austin Cary Memorial Forest (ACMF) in Alachua County, Florida, USA approximately 14 km from the city of Gainesville (29° 44' N, -082° 14' W) (Figure 4-1). The site is approximately 44 m a.s.l. and generally flat with no perceptible slope. Average annual precipitation is 123 cm with the majority falling during the summer months National Climate Data Center 2009). Mean maximum and minimum temperatures for January and July for the study area from long-term records are 19 °C and 6.1°C for January and 36.6 °C and 22.9 °C for July (National Climate Data Center 2004). Soils within the site are generally poorly drained sandy, siliceous, hyperthermic Ultic Alaquods of the Pomona series (NRCS SSURGO). Vegetation across all sites consists of an overstory mixture of naturally regenerated slash pine and longleaf pine and an understory composed of saw palmetto, gallberry, and deerberry shrubs (Myers and Ewel 1990). Across the study area stand age averaged 80 years with an average height of 24 m (Daniel Schultz pers. comm.).

**Sampling**

The Osceola National Forest study consisted of twelve sample plots representing four treatment types: prescribed fire (burn), mechanical fuel mastication (mow), mechanical mastication + prescribed fire (mow+burn), and unburned control (control) (Figure 4-2). Plots were established in three 2 ha experimental treatment blocks, with each block containing a representative plot of each treatment. Three sampling plots were randomly located within each treatment type in each block. Mechanical fuel mastication in the mow and mow+burn plots took place during the summer of 2010. Prescribed burning in the mow and mow+burn plots took place in February, 2011, with two blocks burned on one day and one block burned the next day. Blocks were burned by hand using low intensity strip-head fires. Air temperature on the days of burning ranged from 17-24°C and relative humidity (RH) ranged from 47-62%. Regional Keetch-Byram Drought Index at the time of burning was 107.

The ACMF study consisted of six sample plots representing two treatment types: three-year prescribed fire interval (3YR), and fire exclusion (40YR) (Figure 4-3). The study was arranged in a pseudo-replicate sampling design due to the limited availability of treatments, with three sample plots randomly established within each 20 ha treatment type. Fire had been excluded from the 40YR treatment for at least forty years while the nearby 3YR treatment area had been maintained in a three-year dormant season prescribed fire interval for at least twelve years prior to the study and had been frequently burned prior to that (Daniel Schultz pers. comm.). Plots in the 3YR treatment were last prescribed burned in February of 2009 using strip-head fires. Further descriptions of the conditions and fire behavior during the day of prescribed burning in 2009 were not available.

**Field Measurements**

Soil $CO_2$ efflux sample plots were established in the early winter of 2009 at the ACMF and in the early winter of 2010 at the Osceola study sites. Each sample plot consisted of nine permanently installed 20 cm diameter independent PVC collars arranged in a 3 x 3 grid with 5 m separation following Kobziar and Stephens (2006). PVC sampling collars were constructed of Schedule 30 white 20 cm diameter pipe cut to 10 cm lengths and beveled along one edge. Collars were inserted beveled edge down into the soil or duff to a depth of approximately 8 cm using a rubber mallet. All collars were installed at least four weeks prior to the start of sampling to allow any soil disturbance from installation to normalize. During the course of study, any vegetative growth within the sample collars was clipped and removed prior to $R_s$ measurement. A LI-COR Biosciences LI-8100 Automated Soil $CO_2$ Flux System attached to a 20 cm survey chamber was used to measure soil $CO_2$ efflux rates ($R_s$) (µmol $CO_2$ $m^{-2}$ $sec^{-1}$) at each collar (LI-COR Biosciences, Inc., Lincoln, NE). Concurrently with soil $CO_2$ efflux measurements, soil temperature at 10 cm depth (°C) ($T_s$) and soil volumetric moisture content ($m^3$ x $m^3$) ($M_s$) at 5 cm depth were recorded onboard the LI-8100. Soil temperature ($T_s$) was measured using an Omega 8831 type E T-Handle temperature probe, while soil moisture content ($M_s$) was measured using a Decagon Systems EC-5 soil moisture probe (Omega Inc., Stamford, CT; Decagon Systems Inc., Pullman, WA). Both probes were inserted into the soil at random azimuths approximately 5 - 15 cm from the collar and remained undisturbed in the soil during the 120-second $R_s$ measurement period. To assess temporal and seasonal variations in $R_s$ rates, $T_s$, and $M_s$, collars were sampled monthly over the course of one (ACMF) or two days (Osceola) on an approximately four-week rotation. To account for diurnal variations measurements at the ACMF plots were taken three times per day between 0800 and 1900 local time and measurements at the Osceola plots were taken twice per day between 0800 and 1700 local time.

Monthly mean 2 m ambient air temperature (°C) records (M Temp) from hourly meteorological observations at the Olustee, Florida remote automated weather station (RAWS) (approximately 7 km from the Osceola sites) and the Austin Cary Memorial Forest AmeriFlux tower (located within the ACMF 3YR treatment stand) were recorded throughout the study periods. Soil temperature (°C) at 10 cm soil depth measured hourly at the nearby Florida Automated Weather Network (FAWN) stations in Macclenny, Florida (approximately 30 km from the Osceola study sites) and Putnam Hall, Florida (approximately 21 km from the ACMF study sites) were recorded throughout the study periods. The FAWN station hourly 10 cm soil temperature measurements were used as input for the total monthly and annual carbon flux models per site. Monthly total precipitation (cm) measurements from the Olustee RAWS station and Austin Cary Forest staff meteorological records were also recorded and assessed for their influence on $R_s$ rate variability. Monthly sampling of $R_s$, $T_s$, and $M_s$ at the ACMF study site began in March 2010 and concluded in June 2011, while monthly sampling at the Osceola study site began in March 2011 and concluded in March 2012. At the ACMF study site, monthly $R_s$ measurements were not collected during the months of August and December of 2010 due to hazardous weather conditions while measurements collected during September 2010 were discarded due to sampling equipment error. At the Osceola study site, monthly measurements were not collected during the month of September 2011 due to hazardous weather conditions. Errors encountered with the soil temperature probe resulted in $T_s$ measurement gaps during the months of July 2010 and January 2011 at the ACMF study site and July and August of 2011 at the Osceola study site. Errors encountered with the soil moisture probe resulted in $M_s$ measurement gaps during the month of June 2010 at the ACMF study site. Recorded soil moisture content values less than 0.00, and soil temperature measurements greater than 40°C were excluded from the analyses, as they resulted from equipment malfunction.

Plot characteristics and vegetative sampling were conducted in the winter of 2011 at both the ACMF and Osceola study sites (Table 4-1). Overstory vegetation was sampled using a 15 m radius circular plot (0.07 ha) centered on the middle $R_s$ sample collar. The following field parameters with abbreviation and unit were recorded for each $R_s$ sample collar per plot: linear distance (m) from the sample collar to the nearest tree with a diameter at 1.3 m height (DBH) > 10 cm (Dnearest), diameter (cm) at breast height of the nearest tree to the sample collar (DBH), linear distance (m) from the sample collar to the nearest palmetto, mean litter or masticated vegetative depth (cm) from three measurements within 30 cm of the sample collar (Litter), mean duff depth (cm) from three measurements taken within 30 cm of the sample collar (Duff), and total mean duff and litter depth (cm) from three measurements taken within 30 cm of the sample collar (DL). The following stand condition parameters with abbreviation and units were recorded one time per sample plot: total basal area ($m^2$ $ha^{-1}$) (BA) and stand density (trees $ha^{-1}$) (TPH).

The following soil characteristics were measured one time in all plots: soil organic matter (SOM) (%) and total soil carbon (TC) (%). Three soil sub-samples per plot at two soil depths from the mineral layer (0 - 5 cm and 5 -10 cm) were collected for analysis. Soil samples were collected using a 2.22 cm AMS soil sampler after removing litter and duff layers (AMS, Inc., American Falls, Idaho, USA). To account for the spatial variability of soils within the plot the three sub-samples per plot were bagged per depth class and homogenized. Soil samples for the Osceola and ACMF study areas were collected in the winter of 2011 approximately ten months following the burn treatment in the Osceola and approximately seventeen months following mastication in the Osceola. Samples were bagged and shipped to Waters Agricultural Laboratories, Inc. (Camilla, Georgia, USA) for analysis.

**Analysis**

The data collected from each study site were analyzed separately. At the ACMF study site, prescribed fire treatments were analyzed as random samples representing two treatment sites. At the Osceola study site, treatments were analyzed as a randomized complete block design with understory vegetative fuel treatment type (Osceola) as the main treatments. For each month, daily measurements of $R_s$, $T_s$, and $M_s$ per soil collar were averaged, and the nine soil collar means were then averaged to produce a plot-level mean for each treatment and month. This resulted in a sample size of three for each treatment (Osceola total n = 12 and ACMF total n = 6) per month. One-way (ACMF) and two-way (Osceola) repeated measures analysis of variance (ANOVA) was used to test for differences in monthly means of $R_s$, $T_s$, and $M_s$ among treatments at each study site. Significant treatment effects were identified at p-value $<$ 0.05. To assess differences between field parameters by treatment at each study site, one-way ANOVA (Osceola) and student's t-tests (ACMF) were used. Where significant differences were identified in the ANOVA, differences among treatments were analyzed using Tukey's HSD test. With treatments ignored and all monthly means pooled, Pearson's correlation coefficients and linear regression were used to assess for relationships between overall study period mean plot $R_s$ rates and $T_s$, $M_s$, and field parameters following Gough et al. (2004). Additional linear (Equation 4-1) and nonlinear (Equation 4-2) regression models were developed per treatment and measurement season (growing vs. dormant) to assess the influence of treatments on the relationships between monthly per plot mean $R_s$ rates and $T_s$, $M_s$, and the field parameters listed in Table 4-1. At both study sites the growing season was defined as the months of March - September while the dormant season was defined as October - February (Gholz and Clark 2002). Non-linear models of the relationships between $R_s$ rates and $T_s$ and M Temp per entire study period and season were explored using an exponential equation (Equation 4-2) frequently used to describe the response of $R_s$ rates to soil temperature (Lundegardh, 1927; Samuelson et al., 2004; Concilio et al., 2005; Kobziar and Stephens, 2006). Following Samuelson et al. (2004) and Ryu et al. (2009) multiple regression using a forward step-wise procedure was used to develop models per study site and treatment of monthly mean $R_s$ rates using Equation 4-3, utilizing measured parameters that best explained the observed variability in $R_s$ rates (using $R^2$ and p-value), while minimizing multicollinearity and BIC scores.

$$R_s = \beta_0 + \beta_1(parameter) \tag{4-1}$$

$$R_s = \beta_0 e^{\beta_1(Ts)} \quad \text{or} \quad R_s = \beta_0 e^{\beta_1(M\,Temp)} \tag{4-2}$$

$$R_s = \beta_0 + \beta_1(parameter_1) + \beta_2(parameter_2) + \beta_i(parameter_i) \tag{4-3}$$

Coefficients $\beta_0$, $\beta_1$, $\beta_2$, and $\beta_i$ were estimated through regression analysis. Residuals of regressions were checked for normality and heteroscedasticity, and where necessary model terms were transformed to meet assumptions. The $\beta_1$ estimates developed using Equation 4-2 were used to estimate the $Q_{10}$ value per treatment, season, and study site using Equation 4-4 following Kobziar and Stephens (2006) (Lundegardh, 1927). The $Q_{10}$ value is often reported in studies of $R_s$ to describe the response of $R_s$ to a 10 °C change in soil temperature (Luo and Zhou, 2006).

$$Q_{10} = e^{10\beta_1} \tag{4-4}$$

The linear models developed per study site and treatment (using Equation 4-1) of the relationships between soil temperature ($T_s$) and $R_s$ rates were used to estimate hourly, monthly, and total annual soil carbon fluxes following Samuelson et al. (2004). The hourly 10 cm depth soil temperature (°C) measurements from the Macclenny, Florida and Putnam Hall, Florida FAWN stations were used as model input.

All statistical analyses were performed using JMP 9.0 (SAS Institute, Cary, NC, USA).

## Results

### Treatment Effects

Vegetative conditions varied significantly ($p < 0.05$) by treatment within the study areas (Table 4-2). At the ACMF site, significantly higher basal area (27.03 $m^{-2}$ $ha^{-1}$), stand density (773.33 tree $ha^{-1}$), duff (2.87 cm), and litter depth (4.11 cm) were observed in the long unburned treatment (40YR) than in the more frequently burned treatment (3YR). Analysis of soil samples at the ACMF at either the 0 - 5 cm depth or 5 - 10 cm depth found no significant differences between treatments in SOM (%) or TC (%). At the Osceola site, there were no significant ($p < 0.05$) differences between treatments in stand basal area, stand density, or duff depths. Prescribed burning was shown to significantly reduce litter depth in the burn (1.57 cm) and mow+burn (1.18 cm) treatments relative to the mow (3.50 cm) and control (4.50 cm) treatments (Table 4-2). At the Osceola site like the ACMF site, no significant treatment effects were observed for SOM or TC, for either sample depth.

At both study sites soil $CO_2$ efflux rates ($R_s$) (μmol $CO_2$ $m^{-2}$ $sec^{-1}$) and soil temperature ($T_s$) (°C) for all treatments tended to be highest during the late spring, summer, and early autumn months and lowest during the winter months (Figure 4-4 and Figure 4-5). Soil moisture content across all treatments and study sites was highly variable over time, with $M_s$ content generally highest during the winter and fall months and lowest during the summer months at the Osceola study site, while $M_s$ content for both treatments at the ACMF study site appeared to be strongly influenced by regional drought conditions as indicated by the Palmer Drought Severity Index (Figure 4-6).

At the Osceola site over 2,800 soil $CO_2$ efflux rate measurements were taken during the twelve-month sampling period, with plot level monthly mean $R_s$ rates ranging from 1.16 – 8.73 μmol $CO_2$ $m^{-2}$ $sec^{-1}$. Repeated measures ANOVA found monthly mean soil $CO_2$ efflux rates were not significantly different between Osceola treatments ($F = 0.86$ $p = 0.4985$) (Tables 4-3 and 4-4) (Figure 4-7). Soil $CO_2$ efflux rates did vary significantly by month ($F = 35.69$ $p < 0.0001$) but did not show an interaction between treatment effect and time (treatment x month) ($F = 0.66$ $p = 0.9123$). While not significantly different, the lowest mean $R_s$ rates were generally in the burn treatment (3.44 μmol $CO_2$ $m^{-2}$ $sec^{-1}$) with some monthly variation in the order of treatments observed (Table 4-4) (Figure 4-4). When treatment effects on $R_s$ rates were assessed separately by season (growing vs. dormant), there were no significant differences observed, and only the effect of time (month) was significant for either season (Tables 4-3 and 4-5).

At the Osceola study site, soil temperature ($T_s$) (°C) ranged from 13.71 – 25.76 °C during the entire study period and varied significantly by sample month ($F = 321.78$ $p < 0.0001$) and treatment ($F = 11.42$ $p = 0.0029$) (Table 4-3). Mean overall soil temperature was significantly higher in all treatments relative to the control, with no other significant differences between treatments observed (Tables 4-3 and 4-4) (Figure 4-7). The effect of treatment did not vary significantly with time (treatment x month) ($F = 1.30$ $p = 1932$). In the growing season, all treatments had significantly higher mean $T_s$ ($F = 31.86$ $p < 0.0001$) relative to the control, while the mow+burn treatment recorded significantly warmer soil temperatures than the mow only treatment (Table 4-3 and Table 4-5). In contrast, during the cooler dormant season, treatment did not have a significant effect on soil temperature (Tables 4-3 and 4-5).

Soil moisture content at the Osceola study sites ranged from 0.04 – 0.27 $m^3/m^3$ during the study period and varied significantly by sample month ($F = 22.57$ $p < 0.0001$) and treatment x time ($F = 1.88$ $p = 0.0106$), but not treatment ($F = 2.33$ $p = 0.1503$) (Tables 4-3 and 4-4) (Figure 4-7). During the seasonal assessment, no significant differences in $M_s$ were found between the treatments during either the growing season ($F = 2.68$ $p = 0.12$) or the dormant season ($F = 1.24$ $p = 0.36$) (Table 4-5). Soil moisture content over all study and monthly means showed a consistent non-significant trend among treatments as mow+burn generally had the highest mean $M_s$ while the control generally had the lowest mean $M_s$, with variation observed between the burn and mow treatments. (Tables 4-3 and 4-5) (Figure 4-4).

At the ACMF study site over 1860 individual soil $CO_2$ efflux rate measurements were taken during the 14-month sampling period with plot level monthly mean $R_s$ rates ranging from 1.30 – 6.34 μmol $CO_2$ $m^{-2}$ $sec^{-1}$ (Figure 4-5). Repeated measures ANOVA of monthly mean $R_s$ rates analyzed for the entire study period found no significant differences between treatments ($F = 0.35$ $p= 0.5888$) with the overall mean $R_s$ rate in the 3YR treatment (4.12 μmol $CO_2$ $m^{-2}$ $sec^{-1}$) slightly lower than the mean $R_s$ rate in the 40YR treatment (4.25 μmol $CO_2$ $m^{-2}$ $sec^{-1}$) (Tables 4-3 and 4-4) (Figure 4-8). The effects of time (sample month) on $R_s$ rates at the ACMF study site was highly significant ($F = 63.08$ $p < 0.0001$) while the interaction of time and treatment (treatment x time) on overall mean $R_s$ rates was also significant ($F = 2.43$ $p = 0.0187$, respectively) (Table 4-3). The season specific assessments (growing vs. dormant) found that mean $R_s$ rates during the growing season were higher, though not significantly in the 3YR treatments (4.48 μmol $CO_2$ $m^{-2}$ $sec^{-1}$) than the 40YR treatments (4.37 μmol $CO_2$ $m^{-2}$ $sec^{-1}$) (Table 4-

3 and Table 4-5). In contrast, during the dormant season $R_s$ rates were significantly lower in the 3YR treatments (3.42 μmol $CO_2$ $m^{-2}$ $sec^{-1}$) than the 40YR treatments (4.00 μmol $CO_2$ $m^{-2}$ $sec^{-1}$) ($F = 11.15$ $p = 0.0288$) (Tables 4-3 and 4-5).

Plot level monthly mean soil temperatures at the ACMF ranged from 12.49 – 26.59 °C during the study period. Repeated measures ANOVA found that $T_s$ differed significantly by sample month ($F = 900.65$ $p <0.0001$) and treatment x time interaction (month x treatment) ($F = 31.09$ $p < 0.0001$), but not by treatment type ($F = 5.74$ $p = 0.0746$) (Tables 4-3 and 4-4) (Figures 4-5 and 4-8). A similar analysis found that during the growing season mean soil temperature in the 3YR treatment (20.81 °C) was significantly ($F = 11.23$ $p = 0.0286$) warmer than in the 40YR treatment (19.76 °C) (Tables 4-3 and 4-5). There were no significant differences in $T_s$ due to treatment during the cooler dormant season ($F = 0.00$ $p = 0.9789$) (Table 4-3).

Overall plot level monthly mean soil moisture content at the ACMF ranged from 0.02 – 0.38 $m^3/m^3$ during the study period. A repeated measures ANOVA found that $M_s$ differed significantly by sample month ($F = 45.57$ $p < 0.0001$), treatment x time interaction ($F = 3.80$ $p = 0.0008$), and treatment ($F = 7.88$ $p = 0.0484$), with overall study period mean $M_s$ highest in the 3YR treatment (0.11 $m^3/m^3$) and lowest in the 40YR treatment (0.07 $m^3/m^3$) (Table 4-3 and Table 4-4) (Figures 4-5 and 4-8). When $M_s$ was assessed by season, significant differences ($F = 8.64$ $p = 0.0434$) between treatments were identified only in the growing season with the highest mean $M_s$ in the 3YR treatment (0.14 $m^3/m^3$) and the lowest in the 40YR treatment (0.08 $m^3/m^3$) (Tables 4-3 and 4-5). In general, the plot of the monthly means indicated that $M_s$ tended to be higher in the 3YR treatment than in the 40YR treatment, with the difference between treatments most pronounced during the first four months of sampling prior to the establishment of a prolonged regional drought (Figures 4-5 and 4-6).

**Overall Drivers of Soil $CO_2$ Efflux**

When treatments were ignored at each study site and all monthly mean plot values pooled, Pearson's Correlation coefficients and linear regressions were used to identify broad overall relationships between $R_s$, $T_s$, and $M_s$ and plot vegetative and meteorological conditions. At the Osceola study site, Pearson's Correlation coefficients indicated positive relationships between $R_s$ and $T_s$ (0.63) and $R_s$ and M Temp (0.52) (Table 4-6). Pearson's Correlation coefficients also indicated that $T_s$ and M Temp were not surprisingly strongly correlated (0.77) at the Osceola study site (Table 4-6). Also surprisingly, $R_s$ at the Osceola study site indicated a negative relationship with soil moisture content (-0.13) while also demonstrating a positive relationship with monthly precipitation patterns (0.35). Vegetative conditions were shown to have a small influence on overall $R_s$ rates as litter depth (0.06), duff depth (0.08), stand density (0.00), and basal area (0.11) were only weakly correlated with $R_s$ rates at the Osceola study site. Negative correlations observed between $R_s$ rates and distance to nearest tree (-0.06) and distance to nearest palmetto (-0.18) suggested that there was a small yet positive influence of the proximity of measurement points to trees and palmettos. In the Osceola study site, linear regressions of pooled monthly mean values, soil temperature ($R^2 = 0.40$ $p < 0.0001$) and M Temp ($R^2 = 0.27$ $p < 0.0001$) were also positively linearly correlated with overall mean $R_s$ rates, while plot level vegetative characteristics such as basal area ($R^2 = 0.01$ $p = 0.1772$), stand density ($R^2 = 0.00$ $p = 0.9991$), distance to nearest tree ($R^2 = 0.00$ $p = 0.4682$), and distance to nearest palmetto ($R^2 = 0.03$ $p = 0.0274$) were not correlated with $R_s$ rates (Figure 4-9). At the

ACMF study site, Pearson's Correlation coefficients indicated a strong positive relationship between $R_s$ and $T_s$ (0.89) and $R_s$ and M Temp (0.82). Similar to the Osceola study site, a negative relationship was identified between $R_s$ and $M_s$ (-0.25) while a contrasting positive relationship was identified between $R_s$ and monthly precipitation (0.24). The Pearson's Correlation coefficients indicated that overall mean $R_s$ rates were not correlated with vegetative characteristics including stand density (0.01), basal area (-0.03), distance to nearest palmetto (0.00), duff depth (0.02), and litter depth (0.05) (Table 4-7). Like $R_s$, $T_s$ means were weakly correlated with vegetative and characteristics, while $M_s$ means were negatively associated with $T_s$ (-0.50), stand density (-0.25), basal area (-0.23), duff depth (-0.28), and litter depth (-0.38) and showed a positive association with the distance to the nearest tree (0.27) and monthly total precipitation (0.40). In the ACMF study site linear regressions of pooled monthly mean values soil temperature ($R^2$ = 0.80 $p < 0.0001$) and monthly mean air temperature ($R^2$ = 0.68 $p < 0.0001$) were positively linearly correlated with $R_s$ rates while $M_s$ ($R^2$ = 0.06 $p = 0.0332$) and monthly precipitation ($R^2$ = 0.06 $p = 0.0414$) were significantly, but only weakly correlated with $R_s$ rates (Figure 4-11). Similar to the results of the Osceola study site simple linear regressions of the pooled ACMF study site data found no significant correlations between $R_s$ rates and basal area, stand density, distance to nearest tree, distance to nearest palmetto, or duff and litter depth (Figures 4-11 and 4-12).

**Treatment Specific Drivers of Soil $CO_2$ Efflux**

To assess the influence of $T_s$, $M_s$, and vegetative and meteorological conditions on monthly mean $R_s$ rates within treatments at each study site, simple linear regression models (Equation 4-1) were developed for each parameter and treatment (Table 4-8).

At the ACMF study site, simple linear regression models identified significant positive linear relationships between $R_s$ rates and soil temperature ($T_s$) in the 3YR ($R^2 = 0.83$ $p < 0.0001$) and 40YR treatments ($R^2 = 0.85$ $p < 0.0001$) (Table 4-8) (Figure 4-14). Similarly, the relationships between $R_s$ rates and monthly mean air temperature were also significantly linearly related for both the 3YR and 40YR treatments ($R^2 = 0.74$ $p < 0.0001$ and $R^2 = 0.62$ $p < 0.0001$, respectively) (Table 4-8) (Figure 4-14). Soil moisture content was significantly negatively linearly correlated with $R_s$ in the 40YR treatment ($R^2 = 0.12$ $p = 0.0380$) but not in the 3YR treatment ($R^2 = 0.04$ $p = 0.2565$). In the ACMF simple linear regression models no other plot level vegetative or meteorological characteristics were significantly linearly correlated ($p < 0.05$) with $R_s$ or had $R^2 > 0.10$.

At the Osceola study site similar to the results of the ACMF study site, the simple linear regression models by treatment identified significant positive relationships between soil $CO_2$ efflux rates ($R_s$) and soil temperature ($T_s$) ($R^2 = 0.33 - 0.58$) and monthly mean ambient air temperature (Temp) ($R^2 = 0.24 - 0.34$) (Table 4-8) (Figure 4-13). Only a weak linear relationship was identified between $R_s$ rates and soil moisture content ($M_s$) ($R^2 = 0.02 - 0.12$) at the Osceola treatments, with one treatment having a positive relationship with $M_s$ (Control) and the remainder having a negative relationship with $M_s$ (Burn, Mow, Mow+Burn) (Table 4-8). Some of the vegetative characteristics were significantly linearly correlated with monthly mean $R_s$ rates in the Burn treatment ($R^2 = 0.17 - 0.20$), while all other vegetative characteristics and treatments had non-significant ($p > 0.05$) or low correlation coefficient ($R^2 < 0.10$) relationships with $R_s$ or (Table 4-8).

In addition to the simple linear models, nonlinear exponential models (Equation 4-2) were used to further explore the relationships between monthly mean $R_s$ and $T_s$ by study site and treatment. At the ACMF study site, nonlinear regression indicated a strong positive relationship between $R_s$ and $T_s$ for both the 3YR ($R^2$ = 0.80) and 40YR treatment ($R^2$ = 0.82) (Table 4-9) (Figure 4-16). At the Osceola study site the fit of the $R_s$ and $T_s$ nonlinear regression models ($R^2$ = 0.32 - 0.56) were similar to that of the simple linear regression models ($R^2$ = 0.32 - 0.56) described previously (Table 4-9) (Figure 4-15). Nonlinear model coefficients $\beta_0$ and $\beta_1$ (Equation 4-2) were similar to estimates reported by Samuelson et al. (2004) and Kobziar and Stephens (2006) (Table 4-9).

**Seasonal Drivers of Soil $CO_2$ Efflux**

To assess seasonal variations in the relationships between $R_s$ and $T_s$, $M_s$, and plot vegetative and meteorological characteristics, additional simple linear (Equation 4-1) and nonlinear (Equation 4-2) regression models were developed per study site, treatment, and season (growing and dormant) (Tables 4-10 and 4-11) (Figures 4-17, 4-18, 4-19, and 4-20). At the ACMF study site, models for both treatments indicated that the relationships between $R_s$ and $T_s$ varied seasonally, with both linear (Table 4-10) (Figure 4-19) and non-linear models (Table 4-11) (Figure 4-20) showing that soil temperature explained much more of the variability in $R_s$ rates during the growing season ($R^2$ = 0.89 - 0.90) than during the dormant season ($R^2$ = 0.50 - 0.53). In contrast, linear models for both treatments identified negative relationships between $R_s$ rates and $M_s$, with $M_s$ explaining much more of the variability in $R_s$ rates during the dormant season ($R^2$ = 0.74 - 0.50) than during the growing season ($R^2$ = 0.29 - 0.19) (Table 4-10).

At the Osceola study site, linear and nonlinear models of all treatments found that the relationships between $R_s$ and $T_s$ and $R_s$ and $M_s$ varied seasonally (Table 4-10 and Table 4-11). At the Osceola study site, in contrast to the ACMF study site, positive linear models of $T_s$ explained much more of the variability in $R_s$ rates during the cooler dormant season ($R^2$ = 0.69 - 0.79) than during the warmer growing season ($R^2$ = 0.30 - 0.60) (Table 4-10) (Figure 4-17). Similarly, positive non-linear models of $T_s$ explained much more of the variability in $R_s$ rates during the dormant season ($R^2$ = 0.64 - 0.76) than during the growing season ($R^2$ = 0.30 - 0.58) (Table 4-11) (Figure 4-18). For either season or modeling type (linear or non-linear), the burn treatment recorded the weakest relationship between $R_s$ and $T_s$, while the mow treatment recorded the strongest relationship (Table 4-10 and Table 4-11). In the soil moisture content linear models, monthly mean $R_s$ was more closely correlated (negatively) with $M_s$ during the dormant season ($R^2$ = 0.24 - 0.67) than during the growing season ($R^2$ = 0.09 - 0.53) in all treatments except for the burn treatment (Table 4-10). In the burn treatment, $R_s$ was more closely correlated with $M_s$ during the growing season ($R^2$ = 0.44) than the dormant season ($R^2$ = 0.11) (Table 4-10).

**Multiple Regression Models**

Multiple linear regression models using Equation 4-3 were developed per study site, treatment, and season to identify the influence of treatment (Table 4-12) and season (Table 4-13) on the drivers (Table 4-1) of soil $CO_2$ efflux rates. Models were developed using a forward step-wise approach (minimum parameter input and retention $p < 0.05$) using the stand and plot characteristics described in Table 4-1 as potential parameters. Models were developed to minimize BIC score and parameter multicollinearity while maximizing model coefficient of variation ($R^2$). The ACMF study site all-season multiple linear regression models explained a significant amount of the observed variation in $R_s$ rates for both the 3YR ($R^2$ = 0.90 $p < 0.0001$) and 40YR treatments ($R^2$ = 0.89 $p < 0.0001$) (Table 4-12). $R_s$ models for both treatments identified $T_s$ and $M_s$ as significant terms while the 3YR model identified a significant negative relationship with distance (m) to the nearest palmetto. The ACMF season specific multiple linear regression models were slightly better at predicting $R_s$ rates during the growing season ($R^2$ = 0.93 - 0.94) than during the dormant season ($R^2$ = 0.81 - 0.83), although all models were significant ($p < 0.05$) (Table 4-13). Surprisingly, neither the 3YR nor the 40YR dormant season model of $R_s$ identified $T_s$ as a significant parameter, however both treatments identified significant negative relationships with precipitation (Table 4-13). The growing season ACMF multiple linear regression models identified significant relationships with $T_s$ and soil organic matter (%) (5 - 10 cm depth) in the 3YR treatment and $T_s$ and $M_s$ in the 40YR treatment (Table 4-13).

The amount of variation in $R_s$ rates explained by the Osceola study site all-season multiple linear regression models varied by treatment and ranged from ($R^2$ = 0.36 - 0.72) (Table 4-12). Similar to the linear and non-linear models, the mow+burn treatment model explained the least amount of the variation in $R_s$ ($R^2$ = 0.36 $p$ = 0.0006) while the control treatment model explained the greatest amount of the observed variation in $R_s$ rates ($R^2$ = 0.72 $p < 0.0001$) (Table 4-12). Soil temperature ($T_s$) explained the majority of $R_s$ rate variability in each of the Osceola all-season models with additional significant model terms ($M_s$, stand tree density, and stand basal area) significant in different treatments (Table 4-12). The Osceola season specific models explained more of the variation in $R_s$ rates during the cooler dormant season ($R^2$ = 0.85 - 0.93) than during the warmer growing season ($R^2$ = 0.53 - 0.85) (Table 4-13). During both the growing season and the dormant season the mow+burn treatment models explained the least amount of observed variation in $R_s$ ($R^2$ = 0.53 and $R^2$ = 0.85, respectively) while the control model explained the most in the dormant season ($R^2$ = 0.93) and the burn treatment model explained the most during the growing season ($R^2$ = 0.84) (Table 4-13). In the Osceola season specific multiple linear regression procedures model terms identified as significant during the forward step-wise process differed by treatment type and season. During the growing season $T_s$ was significant only in the control and mow models, while the other treatment models included $M_s$, monthly mean air temperature, precipitation, and distance to nearest palmetto (Table 4-13). During the dormant season $T_s$ explained the majority of the variation observed in $R_s$ rates in all models with subsequently added parameters explaining much less of the variation in $R_s$. The model parameters other than $T_s$ identified as significant (stand tree density, stand basal area, soil moisture content, and distance to nearest tree) provided evidence for the roles of additional drivers of $R_s$ beyond $T_s$ and $M_s$; although overall patterns in the relationships were not clear (Table 4-13).

**Temperature Response**

For each study site, treatment, and season, the β1 model estimates from Equation 4-2 were used to estimate $Q_{10}$ values using the $Q_{10}$ model (Equation 4-4) (Lundegardh, 1927) (Tables 4-9 and 4-11). $Q_{10}$ values are used to describe the incremental response of $R_s$ to a 10°C change in soil temperature (Lundegardh, 1927; Kobziar and Stephens, 2006). At the ACMF study site, in the all-seasons models, $Q_{10}$ values for the 3YR treatment ($Q_{10}$ = 2.14) were lower than the $Q_{10}$ values in the 40YR treatments the ($Q_{10}$ = 2.85) (Table 4-9). At the Osceola study site, estimated $Q_{10}$ values in the all-seasons models were highest in the control ($Q_{10}$ = 2.14) and lowest in the mow+burn treatment ($Q_{10}$ = 1.65) (Table 4-9). The $Q_{10}$ values in the season specific models at the ACMF study site and Osceola study site ranged from $Q_{10}$ =1.62 – 2.90 and $Q_{10}$ = 1.63 – 2.51 respectively (Table 4-11). At the ACMF site, $Q_{10}$ values tended to be slightly lower in the dormant season than the growing season, while at the Osceola study site, the opposite was observed, as $Q_{10}$ values in all treatment types and control were higher during the dormant season than the growing season.

**Estimated Carbon Flux**

Following Samuelson et al. (2004) total soil carbon (C) flux was estimated per hour for every 24-hour period and summed to compare total monthly and annual soil C fluxes per treatment at each study site. Soil carbon fluxes were estimated using treatment specific linear models (Table 4-8) of the relationship between soil $CO_2$ efflux rates (μmol $CO_2$ $m^{-2}$ $sec^{-1}$) and soil temperature (Table 4-11). Actual hourly 10 cm depth soil temperature measurements (°C) recorded at the Florida Automated Weather Network (FAWN) stations in Macclenny, Florida near the Osceola study site, and Putnam Hall, Florida near the ACMF study site were used as model inputs to predict flux rates. Model input soil temperatures for the Austin Cary Forest were recorded March 2010 – February 2011 while input soil temperatures for the Osceola study site were recorded February 2011 – January 2012. Predicted hourly soil $CO_2$ fluxes (μmol $CO_2$ $m^{-2}$ $sec^{-1}$) were then converted to hourly soil C fluxes (g C $m^{-2}$ $hr^{-1}$) and summed to estimate monthly and annual carbon fluxes per treatment and study site.

At the Osceola study site total estimated monthly soil carbon flux (g C $m^{-2}$ $month^{-1}$) varied monthly and seasonally. During the growing season, soil carbon flux was greatest in the control sites and lowest in the burn only treatments and mow+burn treatments (Figure 4-21). During the cooler dormant season months of December, January, and February, monthly total soil carbon flux in the control treatments reduced to lower than the other three treatment types (Figure 4-21). When soil carbon fluxes were totaled for the entire year, estimated annual soil C flux was greatest in the control units (1.89 kg C $m^{-2}$ $yr^{-1}$), and lowest in the mow+burn treatment (1.64 kg C $m^{-2}$ $yr^{-1}$), with the burn (1.69 kg C $m^{-2}$ $yr^{-1}$) and mow treatments falling in between (1.67 kg C $m^{-2}$ $yr^{-1}$) (Figure 4-22).

At the ACMF study site total estimated soil carbon flux varied both monthly and seasonally (Figure 4-23). During the growing season the estimated soil carbon flux was highest during the months of July and August with the greatest estimated C flux in the 40YR treatment (218.62 g C $m^{-2}$ $month^{-1}$ and 219.54 g C $m^{-2}$ $month^{-1}$ respectively) and the lowest C flux in the 3YR treatment (184.63 g C $m^{-2}$ $month^{-1}$ and 185.28 g C $m^{-2}$ $month^{-1}$ respectively). During the dormant season when overall soil carbon fluxes were at their lowest rates, the trend reversed, and the 3YR treatment had the greatest C fluxes (Figure 4-23). When estimated soil carbon fluxes for the entire year were summed, the 40YR prescribed fire interval resulted in a 7% higher soil carbon flux (1.61 kg C $m^{-2}$ $yr^{-1}$) than the 3YR treatment (1.51 kg C $m^{-2}$ $yr^{-1}$) (Figure 4-24).

## Discussion

The range of monthly mean soil $CO_2$ efflux rates (μmol $CO_2$ $m^{-2}$ $sec^{-1}$) recorded at the Osceola (1.16 - 8.73 μmol $CO_2$ $m^{-2}$ $sec^{-1}$) and ACMF (1.30 - 6.34 μmol $CO_2$ $m^{-2}$ $sec^{-1}$) study sites were similar but higher than those reported in many other published studies of $R_s$ rates. In a similar study of mechanical fuels mastication treatments, prescribed fire, and mechanical treatments followed by fire in a mixed conifer plantation in California, USA, Kobziar and Stephens (2006) reported growing season $R_s$ rates ranging from 2.37 - 4.55 µmol $CO_2$ $m^{-2}$ $sec^{-1}$. In another California study, Tang et al. (2005) also reported similar mean $R_s$ rates (3.26 - 3.78 µmol $CO_2$ $m^{-2}$ $sec^{-1}$) for thinned and un-thinned ponderosa pine plantations. The ranges of $R_s$ rates reported in the Osceola and ACMF study sites were also similar to those reported by Fang et al. (1998) and Ewel et al. (1987a) for mature slash pine plantations in north central Florida. The higher $R_s$ rates recorded in our studies relative to those mentioned previously from the western USA, were likely related to the relatively high mean annual temperatures, frequent precipitation, and long growing seasons in our sites.

**Effects of Prescribed Fire and Mechanical Fuels Mastication**

At the Osceola and ACMF study site neither mechanical fuels mastication, prescribed burning, nor mechanical fuels mastication followed by prescribed burning significantly altered overall mean soil $CO_2$ efflux rates relative to control (Osceola) or prolonged fire exclusion (ACMF). These results are similar to Kobziar (2007) who found that a single mechanical fuel mastication treatment had no significant effect on soil $CO_2$ efflux rates in a Sierra Nevada mixed conifer plantation in California, USA. In a similar western US study, Concilio et al. (2005) found no significant effect of prescribed burning on soil $CO_2$ efflux rates in the mixed conifer Teakettle Experimental Forest. In a related study of the effects of forest thinning on soil $CO_2$ efflux rates and soil conditions, Tang et al. (2005) also found no significant changes in overall mean soil $CO_2$ efflux rates following treatment. The lack of a treatment effect on $R_s$ rates at either of our study sites was surprising given the multiple effects that prescribed fire and mechanical fuels treatments can have on the autotrophic ($R_a$) and heterotrophic ($R_h$) sources of soil $CO_2$ efflux. Both mechanical fuel treatments and prescribed fire kill, consume, or damage live understory vegetation thereby reducing sources of root respiration ($R_a$). At the same time, such treatments provide heterotrophic soil microorganisms with fresh labile carbon in the form of dead plant roots, potentially increasing $R_h$ contributions to $R_s$. Surprisingly mechanical fuels mastication at the Osceola study site did not result in increased duff and litter depth compared to the control, burn, and mow+burn treatments (Table 4-2). Contrasting with those results were qualitative observations from the mowed sites that reported a distinct intact litter layer comprised of fractured vegetative material covering much of the forest floor (Figure 4-2). These results contrast with those of Kobziar (2007), who found increases in litter and duff depth following mechanical fuels mastication in a California, USA mixed-conifer pine plantation. Recent research by Kreye (2012) found that because the masticated material in pine flatwoods is predominantly foliar, rather than woody (as is the case in many of the western USA studies), its decay rate is much faster, its packing ratio higher, and its overall contribution to litter depth only temporarily significant.

At the ACMF study site, prolonged fire exclusion in the 40YR treatments resulted in significantly increased duff and litter depths compared to the frequently burned (3YR) treatments (Table 4-2). Similar to the ACMF 40YR treatments, Varner et al (2005) found that prolonged fire exclusion in southern pinelands resulted in deep duff and litter layer development while frequently burned sites similar to the 3YR treatments had little organic matter accumulation on the surface. Others have suggested that masticated plant material deposited on the forest floor and surface litter represents a potential source of labile carbon for heterotrophic soil microorganism metabolism and respiration ($R_h$) (Kobziar and Stephens, 2006; Ryu et al., 2009). Supporting this hypothesis are results from studies where litter and duff depths have been positively associated with soil $CO_2$ efflux rates (Concilio et al., 2005; Kobziar and Stephens, 2006). In addition experimental manipulations in multiple studies have found soil $CO_2$ efflux rates to increase significantly following litter additions (Bowden et al., 1993; Chemidlin Prévost-Bouré et al., 2010; Sulzman et al., 2012). In addition, a partitioning study of soil $CO_2$ efflux sources within a 29-year-old slash pine plantation in North Florida, Ewel et al. (1987b) reported that 48% of measured $R_s$ could be attributed to roots and microbial decomposition in the litter and humus horizons of the forest floor. In contrast, our results found little support for the association between litter depth and soil $CO_2$ efflux rates however this may have been the result of our data analysis dealing with plot level means instead of individual sample point means or our inability to differentiate between sources of $R_s$. Further study utilizing $^{13}C$ isotopic sampling may facilitate better understanding of the connectivity between natural surface litter layers accumulated over long fire-free periods and mechanically derived surface litter layers following mastication treatments and the sources of soil $CO_2$ efflux rates.

The lack of a detected $R_s$ response to the treatments could be due to the inability of the monthly sampling protocol employed in this study to capture short-term treatment responses. This is supported by a recent dissertation study of the Florida Everglades by Medvedeff (2012) that found a soil microbial response (in the form of altered $R_h$) was detectible only within two days of prescribed burning. The Medvedeff (2012) study reported that subsequent post-burn sampling of $R_h$ in burned and unburned sites weeks and months following treatment revealed no significant differences between treatments. Other studies including a $^{13}C$ isotope tracing experiment in a coniferous forest in northern Sweden, Ekblad and Hogberg (2001) and a $^{13}C$ tracing experiment in a 15-year-old loblolly pine plantation in North Carolina, USA (Andrews et al. 1999) have reported soil $CO_2$ efflux responses to treatments in as little as 1-4 days. We suggest, similar to Medvedeff (2012), that future $R_s$ sampling protocols employ more temporally intensive measurements in the period immediately following treatment while maintaining monthly long-term sampling to capture annual and seasonal variability. Quantifying short-lived responses may seem insignificant at the ecosystem level, but over broad spatial scales even transient $CO_2$ fluxes may be important for future landscape level carbon budgeting and modeling.

It is also possible that compensatory responses from $R_a$ and $R_h$ sources following treatment in our studies masked any detectible overall treatments effects on $R_s$ rates. Such a situation could occur if reduced understory vegetation in the frequently burned ACMF treatment and the burned and mowed treatments at the Osceola study site led to reduced $R_a$ contributions to $R_s$, while simultaneous increases in soil microbial consumption of the recently killed roots led to similar elevated $R_h$ contributions to $R_s$. Given that previous studies partitioning root and microbial sources of $CO_2$ efflux in slash pine plantations have shown the contributions of the two sources to be similar (Ewel et al., 1987b) this decrease and subsequent increase in the sources of $R_s$ could offset statistically detectible changes in $R_s$. Others who have investigated the effects of forest management practices on soil carbon dynamics have proposed similar explanations following studies where little or no treatment effects on $R_s$ rates were observed (Shan et al., 2002; Tang et al., 2005; Ryu et al., 2009).

Our results from the Osceola study site found that while prescribed burning and mechanical mastication treatments did not have a significant effect on soil $CO_2$ efflux rates, they did result in increased soil temperature relative to control sites. Similarly at the ACMF study site, while prolonged fire suppression in the 40YR treatment was shown not to affect mean total $R_s$ rates, it was shown to reduce soil moisture content relative to sites (3YR) managed with frequent prescribed fire. Previous studies of forest management practices have documented similar effects on soil conditions. In a study of a mixed-conifer forest in California, USA, Ryu et al. (2009) reported that prescribed burning and forest thinning treatments increased soil temperature and moisture content while simultaneously reducing soil $CO_2$ efflux rates. In another example, following a heavy thinning treatment in a ponderosa pine plantation in California, USA, Tang et al. (2005) found that thinning increased forest soil temperature and soil moisture while having no clear overall effect on mean $R_s$ rates. The elevated soil temperatures observed in all treated sites (burn, mow, mow+burn) relative to the control sites at the Osceola study site were likely due to the effect of prescribed fire and mechanical fuels mastication treatments on canopy cover and forest floor radiation exposure.

Other studies have shown that forest cover (Michelsen-Correa and Scull, 2005), forest management practices (Castro et al. 2000), and fire (Neary, 1999; Medvedeff, 2012) can significantly influence long-term soil temperatures among sites due to changes in canopy and vegetative cover. At the ACMF study site, the elevated soil moisture content observed in the frequently burned treatments (3YR) relative to the long unburned treatments (40YR) may have been due to changes in vegetative abundance and composition and the corresponding demands of such vegetation for soil water. At the ACMF study site, stand basal area ($m^2$ $ha^{-1}$), density (trees $ha^{-1}$), duff depth (cm), and litter depth (cm) were all significantly greater in the 40YR treatment than in the 3YR treatment (Table 4-2). In addition, though not quantified, observations from the ACMF sites suggested that palmetto height and density was much greater in the long unburned sites than in the frequently burned sites (Figure 4-3). These results are similar to those reported by Burger and Pritchett (1988) and Castro et al. (2000) following studies of the effects of silvicultural treatments that reduced site vegetation on soil moisture content in North Florida slash pine plantations.

**Soil $CO_2$ Efflux Response to Temperature Fluctuations**

Soil temperature was generally the strongest assessed driver of soil $CO_2$ efflux rates in our study at both study sites. When treatment types were ignored and all data per study site pooled in the Pearson's Correlation coefficient tests of all parameters, $T_s$ had the highest correlation with $R_s$ at both the Osceola (0.63) and ACMF (0.89) study sites (Tables 4-6 and 4-7). In the treatment specific all-season linear regression models, $T_s$ explained more variability in $R_s$ at the ACMF study site ($R^2$ = 0.83 - 0.85) than at the Osceola study site ($R^2$ = 0.33 - 0.58) (Table 4-8). Multiple regression models by treatment type at both study sites also identified soil temperature as explaining much of the variability in $R_s$ rates (Tables 4-12 and 4-12). These results are similar to three previously published studies of slash pine plantations in north central Florida, Clark et al. (2004) ($R^2$ = 0.49 - 0.78), Ewel et al. (1987a) ($R^2$ = 0.75), and Fang et al. (1998) ($R^2$ = 0.96) that all reported similar correlations between soil temperature and $R_s$ rates. At the Osceola study site, the burn and mow+burn treatments tended to reduce the amount of variability in $R_s$ rates explained by $T_s$ in linear and non-linear models in comparison to the control and mow treatments (Tables 4-8 and 4-9). This may have been due to reductions in the relative importance of temperature in governing $R_s$ production as plants and soil microorganisms responded to changes in microsite conditions and nutrient availability following fire (Medvedeff, 2012). Further study may show whether additional time since fire in the burned treatments leads to an increase in the amount of $R_s$ variability explained by $T_s$.

Positive correlations between soil $CO_2$ efflux rates and soil temperature have raised concerns regarding soil carbon fluxes under elevated temperatures due to global climate change (Rustad et al., 2000; Schlesinger and Andrews, 2000). Other factors associated with global climate change including elevated atmospheric $CO_2$ concentrations have also been associated with changes in soil $CO_2$ flux rates (Schlesinger and Andrews, 2000). Butnor et al. (2003) reported increased $R_s$ rates in loblolly pine stands in North Carolina, USA during a free air $CO_2$ enrichment (FACE) study, suggesting that increased atmospheric $CO_2$ concentrations may drive positive-feed-back cycles leading to soil carbon loss. In a similar study, Carney et al. (2007) reported increased belowground heterotrophic microorganism activity following $CO_2$ enrichment that led to increased $R_s$ rates and subsequent soil carbon losses. Our results and these suggest that research combining forest management practices with experimental in-situ $CO_2$ enrichment techniques may be exceptionally beneficial for predicting the effects of management practices on soil carbon fluxes and pools.

The estimated all-season $Q_{10}$ values of the soil $CO_2$ efflux response to changes in soil temperature across all of our study sites ranged from $Q_{10}$ = 2.14 - 2.85 at the ACMF study site and $Q_{10}$ = 1.65 - 2.14 at the Osceola study site (Table 4-9) (Lundegardh, 1927). These estimated values were similar to those reported by Fang et al. (1998) and

Clark et al. (2004) following studies of soil carbon dynamics in north Florida slash pine plantations. $Q_{10}$ values were also similar to root specific respiration measurements taken in a north Florida slash pine plantation by Cropper and Gholz (1991). The seasonal and overall estimated $Q_{10}$ values from our study imply that the sources of soil $CO_2$ efflux rates may have varied under the different treatment types. Previous research has suggested that heterotrophic soil microorganisms are likely to be more sensitive to changes in soil temperature than autotrophic sources of $R_s$ (Bhupinderpal-Singh et al., 2003). As $Q_{10}$ values are a measure of the temperature sensitively of soil $CO_2$ efflux rates, treatments with higher estimated $Q_{10}$ values would therefore be more likely to be driven by heterotrophic sources of $R_s$ than autotrophic sources. At the ACMF study site, $Q_{10}$ values for both the all-seasons models and season specific models were highest in the 40YR treatment and lowest in the 3YR treatment, suggesting that the frequent fire regime of the 3YR treatment resulted in reduced heterotrophic contributions to total $R_s$ as compared to prolonged fire exclusion. Supporting this are the results of previous research by Ewel et al. (1987b) from a long-unburned slash pine plantation (similar to our 40YR treatment) that reported that heterotrophic contributions to total $R_s$ (from the decomposition of forest floor litter) increased with stand age.

Similar to the ACMF study site, at the Osceola study site, estimated $Q_{10}$ values in the all-seasons models and in some of the season specific models were highest in the long unburned control treatment and lowest in the burn and mow+burn treatment. These results suggest that all treatments at the Osceola may have reduced $R_h$ sources of $R_s$ relative to the control, with the burn and mow+burn treatments having had the greatest reduction in $R_h$. These results are similar to a study of a mixed conifer forest in California, USA, where Ryu et al. (2009) suggested that $R_s$ rates in sites treated with prescribed fire were largely controlled by $R_a$ sources as $R_h$ sources had been reduced due to fire. The authors further suggested that $R_s$ production in sites treated with mechanical forest thinning was largely controlled by $R_h$ sources as $R_a$ sources had been reduced due to thinning (Ryu et al., 2009).

If the trends in the relative contributions of $R_h$ to $R_s$ suggested by the estimated $Q_{10}$ values are an accurate description of the partitioning of $R_s$ in our study areas, then our results suggest that either frequent prescribed fire (ACMF 3YR), or a single prescribed fire (Osceola burn), or a single prescribed fire following mechanical fuels mastication (Osceola mow+burn) can alter soil environmental conditions sufficient to reduce the contribution of heterotrophic soil microorganisms. However, utilizing $Q_{10}$ values as a partitioning method is not a well-established practice, and the results of Bhupinderpal-Singh et al., (2003) have been contradicted by other studies (Boone et al., 1998; Saiz et al., 2006). In some ways our results also question the strength of the $Q_{10}$ method for partitioning $R_s$ sources. For example, in both of our study sites in the treatments in which the $Q_{10}$ values suggested that the $R_h$ sources dominated $R_s$, vegetative quantitative (Table 4-2) and qualitative (Figure 4-2 and Figure 4-3) observations also suggested that $R_a$ sources might instead dominate total $R_s$. These results emphasize the importance of future non-invasive partitioning studies of the drivers of $R_s$ (Baggs, 2006).

At both the ACMF and Osceola study sites, seasonal differences in $Q_{10}$ values and the strength of the $T_s$ and $R_s$ relationship showed a distinct pattern. In all treatments at the Osceola study site during the dormant season $Q_{10}$ values and the fit of $R_s$ linear and non-linear models of the $R_s$ - $T_s$ relationships were higher than during the growing season. We suggest that the seasonal changes in the $Q_{10}$ values and $R_s$ models were indicative of treatment-independent phenological shifts in the relative contributions of $R_a$ and $R_h$ to $R_s$. Previous research from partitioning studies has shown that during periods of aboveground vegetative growth, $R_a$ contributions to $R_s$ can increase as plants allocate recent C photosynthate belowground, driving higher root maintenance, root growth, and mycorrihizal fungal respiration rates (Subke et al., 2006; Kuzyakov and Gavrichkova, 2010). In addition, previous research has also shown that during growing seasons, the $T_s$ and $R_s$ relationship can weaken as other variables such as soil moisture and available photosynthetically active radiation become more important in governing belowground C allocation by plants (Ekblad and Hogberg, 2001; Davidson et al., 2006; Wertin and Teskey, 2008).

Curiously, at the ACMF study site the seasonal trend in $Q_{10}$ values and the $R_s$ - temperature relationship were opposite that of the Osceola study site. More specifically, at the ACMF study site $Q_{10}$ values and the fit of $R_s$ – $T_s$ models were higher during the growing season than during the dormant season. It is not clear what could have led to this discrepancy in results between the two study sites and between the ACMF study site and existing literature. The influence of the building regional drought during both study periods may have played a role in altering the seasonal relationships between the biotic and abiotic drivers of $R_s$ as drought conditions were variable throughout both the ACMF and Osceola study periods. Both the results from the ACMF and the Osceola study sites support suggestions by others (Lee et al., 2003) that future models of soil

$CO_2$ efflux rates and soil carbon flux should account for site and treatment specific seasonal relationships between $R_s$ and soil temperature.

### Soil $CO_2$ Efflux Response to Soil Moisture and Precipitation

Other evidence from our study hinted at the possible influence of drought, precipitation, and soil moisture content on $R_s$ rates. At both the Osceola and ACMF study sites when treatments were ignored and all plot monthly means were pooled, $R_s$ and $M_s$ had negative Pearson's Correlation coefficients (-0.13 and -0.25, respectively), while at both study sites $R_s$ and monthly precipitation were positively correlated (0.35 and 0.24, respectively (Table 4-6 and Table 4-7). In addition, at both study sites, the amount of site vegetation (stand density, distance to nearest palmetto, and litter and duff depth) appeared to be negatively associated with $M_s$ and positively, though very weakly associated with $R_s$ (Table 4-6 and Table 4-7). These results suggest that the inverse relationships observed between $R_s$ rates and $M_s$ may not be causal, but rather indicative of the relationships between plants, soil moisture, and the sources of $R_s$. In both of our study areas, these results suggest that vegetative abundance within sample sites had a stronger effect on soil moisture content than on soil $CO_2$ efflux rates, as increased vegetative abundance was shown to be more strongly associated with decreased soil moisture content than increased soil $CO_2$ efflux rates. Site vegetation has been shown to strongly reduce soil moisture content in in many ecosystems including flatwoods forests due to the water demand of forest vegetation (Burger and Pritchett, 1988; Castro et al., 2000). Similarly, other studies have also shown that the amount of aboveground vegetation has been positively associated with soil $CO_2$ efflux rates, as belowground carbon allocation by plant roots leads to increases in $R_a$ and aboveground litter and organic matter leads to increases in $R_h$ (Luan et al., 2011). The positive correlation between monthly precipitation and $R_s$ and $M_s$ (0.24 and 0.40, respectively) at the ACMF and $R_s$ and $M_s$ (0.35) at the Osceola, suggests that in general, both soil moisture content and the $R_a$ and $R_h$ sources of soil $CO_2$ efflux likely responded positively to increased precipitation at both study sites. Our observed relationships between $R_s$, $M_s$, and monthly precipitation may explain why given that our study occurred during an extended regional drought, some aspects of our results conflict with previous studies.

**Effects of Treatment on Soil Carbon Flux**

Our monthly soil carbon flux (g C $m^{-2}$ $month^{-1}$) estimates showed little treatment induced monthly and seasonal variations in soil carbon emissions (Figures 4-21 and 4-23). In our study, both prescribed fire and mechanical fuels mastication treatments at the Osceola study site resulted in slightly reduced estimated total annual soil carbon fluxes (Figure 2-22). In addition, at the ACMF study site the frequently burned treatment was shown to slightly reduce estimated annual soil carbon fluxes relative to fire excluded treatment (Figure 2-24). Results from both sites are similar to estimated soil carbon fluxes (0.952 – 1.162 kg C $m^{-2}$ $yr^{-1)}$ following several years of continuous measurements reported by Clark et al. (2004) along a slash pine plantation chronosequence in north central Florida. Our results were also similar to the total estimated soil carbon flux reported for a 220-day measurement period in a 17-year-old loblolly pine stand (1.047 kg C $m^{-2}$) in North Carolina, USA (Butnor et al., 2003). As these results are only annual soil carbon flux calculations, the effects of prescribed fire and mechanical fuel mastication treatments on long-term soil carbon fluxes and possibly more importantly, total ecosystem carbon fluxes, will likely of great interest to resource managers and researchers.

## Conclusion

This study found that neither prescribed fire nor mechanical fuels mastication treatments significantly affected overall mean soil $CO_2$ efflux rates in mature flatwoods forests. Measured soil $CO_2$ efflux rates in all flatwoods sites varied seasonally and were largely correlated with soil temperature. Although this was not a specific partitioning study, our estimated $Q_{10}$ values support the findings of others who suggest that the contributions of heterotrophic and autotrophic sources of soil $CO_2$ efflux vary seasonally (Lee et al., 2003; Xu et al., 2011). Our results suggest that further study of the effect of prescribed fire and mechanical fuels mastication treatments that include intensive short-term and long-term pre- and post-treatment $^{13}C$ isotopic sampling may provide further information regarding the interactions between treatments and the sources of $R_s$. Future attempts to model soil carbon dynamics in these systems should account for the effects anthropogenic forest management activities on soil abiotic conditions and seasonal variations in the response of soil $CO_2$ efflux biotic and abiotic drivers.

Prescribed fire, mechanical fuels mastication, and mechanical fuels mastication followed by prescribed fire were found to significantly increase mean annual soil temperature within the Osceola National Forest flatwoods sites. Future research is needed to understand whether the changes in soil temperature will ultimately lead to altered decomposition rates and soil carbon fluxes. Our results however, found no evidence of elevated soil $CO_2$ fluxes within one-year of mastication treatment.

A management regime of frequent 3-year dormant season prescribed fire at the ACMF flatwoods study site was shown to increase monthly mean soil moisture content relative to a management regime of long-term fire suppression. Understanding the impacts of forest management practices on soil moisture content may be increasingly important in the future given the likelihood of prolonged droughts within many parts of the southeastern US due to the effects of global climate change (Karl et al., 2009; Liu et al., 2010).

Table 4-1. Parameters accessed for influence on soil $CO_2$ efflux rates at the Austin Cary Forest and Osceola National Forest, Florida, USA

| Parameter category | Plot variable | Abbreviation | Measured | Measurement location |
|---|---|---|---|---|
| Microclimate | Soil temperature | $T_s$ (°C) | 3x daily | Within 5 - 15 cm of collar |
| | Soil moisture content | $M_s$ ($m^3/m^3$) | 3x daily | Within 5 - 15 cm of collar |
| Vegetation | Basal area | BA ($m^2$ $ha^{-1}$) | Winter 2011 | 15 m radius circular plot from center collar |
| | Pine basal area | PBA ($m^2$ $ha^{-1}$) | Winter 2011 | 15 m radius circular plot from center collar |
| | Hardwood basal area | HWBA ($m^2$ $ha^{-1}$) | Winter 2011 | 15 m radius circular plot from center collar |
| | Stand density | TPH (trees $ha^{-1}$) | Winter 2011 | 15 m radius circular plot from center collar |
| | Distance to the nearest tree | Dnearest (m) | Winter 2011 | Linear distance from soil collar to nearest tree (DBH > 10 cm) |
| | Diameter of the nearest tree | DBH (cm) | Winter 2011 | DBH of the nearest tree measured in Dnearest |
| | Distance to the nearest palmetto | Dist Palm (m) | Winter 2011 | Linear distance from soil collar to center of nearest palmetto |
| Forest floor | Duff depth | Duff (cm) | Winter 2011 | Avg. of three measurements within 30 cm of collar |
| | Litter depth | Litter (cm) | Winter 2011 | Avg. of three measurements within 30 cm of collar |
| | Total duff and litter depth | DL (cm) | Winter 2011 | Avg. of three measurements within 30 cm of collar |
| | Soil organic matter | SOM (%) | Winter 2011 | Avg. of three samples per plot from measurements at 0 – 5 cm and 5 – 10 cm depths |
| | Soil total carbon | TC (%) | Winter 2011 | Avg. of three samples per plot from measurements at 0 – 5 cm and 5 – 10 cm depths |
| Weather | Total precipitation | Precip (cm) | Monthly | Osceola records were from the Olustee Remote Automated Weather Station (RAWS #OLSF1). ACMF records were from the Austin Cary Memorial Forest staff onsite rain gauge. |

Table 4-1. Continued

| | | | | |
|---|---|---|---|---|
| | Mean air temperature (2 m) | Temp (°C) | Monthly | Osceola records were from the Olustee Remote Automated Weather Station (RAWS #OLSF1). ACMF records were from the Austin Cary Memorial Forest AmeriFlux Tower. |
| | Palmer drought severity index | PDSI | Monthly | North central Florida regional estimate from NOAA-NCDC |

Table 4-2. Mean forest characteristics per treatment at the Austin Cary Forest and Osceola National Forest, Florida, USA.

| Site | Trt | BA ($m^2$ $ha^{-1}$) | TPH (Trees $ha^{-1}$) | Duff Depth (cm) | Litter Depth (cm) | SOM (0-5 cm) (%) | SOM (5-10 cm) (%) | TC (0-5 cm) (%) | TC (5-10 cm) (%) |
|---|---|---|---|---|---|---|---|---|---|
| ACMF | 3YR | 18.63 (2.43) b | 259.35 (32.67) b | 0.78 (0.76) b | 2.66 (0.91) b | 1.32 (0.50) a | 0.70 (0.42) a | 0.95 (0.61) a | 0.55 (1.02) a |
| ACMF | 40YR | 27.03 (3.12) a | 773.33 (198.22) a | 2.87 (1.15) a | 4.11 (1.02) a | 1.10 (0.31) a | 0.50 (0.15) a | 0.30 (0.12) a | 0.28 (0.81) a |
| Osceola | Burn | 21.63 (1.51) a | 457.40 (94.19) a | 4.18 (0.23) a | 1.57 (0.21) b | 2.18 (1.26) a | 0.74 (0.51) a | 1.62 (1.03) a | 0.36 (0.22) a |
| Osceola | Control | 25.08 (3.73) a | 542.27 (155.82) a | 4.48 (1.94) a | 4.50 (1.06) a | 2.53 (0.42) a | 0.89 (0.37) a | 2.86 (2.12) a | 0.45 (0.12) a |
| Osceola | Mow | 21.96 (6.14) a | 330.08 (216.55) a | 3.27 (2.47) a | 3.50 (0.51) a | 1.32 (0.43) a | 0.55 (0.21) a | 0.82 (0.26) a | 0.22 (0.14) a |
| Osceola | Mow+ Burn | 26.04 (2.89) a | 372.52 (94.19) a | 4.05 (0.44) a | 1.18 (0.54) b | 2.53 (1.01) a | 1.01 (0.48) a | 1.82 (0.80) a | 0.52 (0.23) a |

Data are means with SD in parentheses. BA is basal area, SOM is soil organic matter content, TC is total soil carbon content. Letters indicate significant differences (Student's t-test or Tukey's HSD $p < 0.05$) between treatments per site.

Table 4-3. Results of the repeated measures ANOVA for soil $CO_2$ efflux ($R_s$), soil temperature ($T_s$), and soil moisture content ($M_s$) means for the Austin Cary Memorial Forest and Osceola National Forest Florida, USA

| | | | $R_s$ | | | $T_s$ | | | $M_s$ | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Site | Analysis period | Source | df | F | P > F | df | F | P > F | df | F | P > F |
| ACMF | Total | Month | 11 | 63.08 | < 0.0001* | 9 | 900.65 | < 0.0001* | 11 | 45.57 | < 0.0001* |
| | | Treatment*Month | 11 | 2.43 | 0.0187* | 9 | 31.09 | < 0.0001* | 11 | 3.80 | 0.0008* |
| | | Treatment | 1 | 0.35 | 0.5888 | 1 | 5.74 | 0.0746 | 1 | 7.88 | 0.0484* |
| ACMF | Growing | Month | 7 | 71.87 | < 0.0001* | 6 | 1364.16 | < 0.0001* | 7 | 39.74 | < 0.0001* |
| | | Treatment*Month | 7 | 1.12 | 0.3768 | 6 | 39.34 | < 0.0001* | 7 | 2.64 | 0.0323* |
| | | Treatment | 1 | 0.68 | 0.4561 | 1 | 11.23 | 0.0286* | 1 | 8.64 | 0.0424* |
| ACMF | Dormant | Month | 3 | 33.21 | < 0.0001* | 2 | 313.13 | < 0.0001* | 3 | 38.91 | < 0.0001* |
| | | Treatment*Month | 3 | 1.71 | 0.2180 | 2 | 6.36 | 0.0223* | 3 | 1.42 | 0.2855 |
| | | Treatment | 1 | 11.15 | 0.0288* | 1 | 0.00 | 0.9789 | 1 | 2.56 | 0.1851 |
| Osceola | Total | Month | 11 | 35.69 | < 0.0001* | 9 | 321.78 | < 0.0001* | 11 | 22.57 | < 0.0001* |
| | | Treatment*Month | 33 | 0.66 | 0.9123 | 27 | 1.30 | 0.1932 | 33 | 1.88 | 0.0106* |
| | | Treatment | 3 | 0.86 | 0.4985 | 3 | 11.42 | 0.0029* | 3 | 2.33 | 0.1503 |
| Osceola | Growing | Month | 6 | 43.05 | < 0.0001* | 4 | 551.48 | < 0.0001* | 6 | 33.57 | < 0.0001* |
| | | Treatment*Month | 18 | 1.01 | 0.4666 | 12 | 1.72 | 0.1102 | 18 | 2.52 | 0.0059 |
| | | Treatment | 3 | 1.21 | 0.3658 | 3 | 31.37 | < 0.0001* | 3 | 3.02 | 0.0939 |
| Osceola | Dormant | Month | 4 | 35.42 | < 0.0001* | 4 | 242.75 | < 0.0001* | 4 | 13.35 | < 0.0001* |
| | | Treatment*Month | 12 | 0.20 | 0.9974 | 12 | 0.35 | 0.9715 | 12 | 0.34 | 0.9753 |
| | | Treatment | 3 | 0.54 | 0.6685 | 3 | 1.01 | 0.4355 | 3 | 1.30 | 0.3394 |

For each month, daily measurements per soil collar were averaged, and the nine soil collar means were then averaged to produce a plot-level mean value for each month. The effect of month, treatment, and treatment*month on plot-level means were tested for significance ($p < 0.05$).

Table 4-4. Overall means of soil temperature, moisture content, and soil $CO_2$ efflux rates per treatment and study site

| Site | Treatment | Mean $T_s$ (°C) | Mean $M_s$ ($m^3/m^3$) | Mean $R_s$ (μmol $CO_2$ $m^{-2}$ $sec^{-1}$) |
|---|---|---|---|---|
| ACMF | 3YR | 20.72 (3.57) a | 0.11 (0.08) a | 4.12 (1.27) a |
| ACMF | 40YR | 19.98 (2.69) a | 0.07 (0.05) b | 4.25 (1.24) a |
| Osceola | Burn | 19.71 (3.19) a | 0.12 (0.05) a | 3.44 (1.16) a |
| Osceola | Control | 19.14 (2.59) b | 0.09 (0.03) a | 3.83 (1.07) a |
| Osceola | Mow | 19.75 (3.02) a | 0.12 (0.05) a | 3.93 (1.22) a |
| Osceola | Mow+Burn | 19.92 (3.08) a | 0.14 (0.05) a | 3.89 (1.13) a |

Data are study period means with (SD) per study site and treatment type. Letters indicate significant differences (Student's t-test or Tukey's HSD $p < 0.05$) between treatments per site.

Table 4-5. Dormant and growing season mean soil temperature, mean moisture content, and mean soil $CO_2$ efflux rates per treatment at the Austin Cary Forest and Osceola National Forest, Florida, USA

| | | ---Dormant season--- | | | ---Growing season--- | | |
|---|---|---|---|---|---|---|---|
| Site | Treatment | Mean $T_s$ (°C) | Mean $M_s$ ($m^3/m^3$) | Mean $R_s$ (μmol $CO_2$ $m^{-2}$ $sec^{-1}$) | Mean $T_s$ (°C) | Mean $M_s$ ($m^3/m^3$) | Mean $R_s$ (μmol $CO_2$ $m^{-2}$ $sec^{-1}$) |
| ACMF | 3YR | 20.51 (1.44) a | 0.05 (0.03) a | 3.42 (0.51) b | 20.81 (4.19) a | 0.14 (0.08) a | 4.48 (1.40) a |
| ACMF | 40YR | 20.50 (1.45) a | 0.04 (0.02) a | 4.00 (0.67) a | 19.76 (3.08) b | 0.08 (0.05) b | 4.37 (1.44) a |
| Osceola | Burn | 18.32 (0.78) a | 0.12 (0.04) a | 3.28 (1.05) a | 21.12 (2.62) ab | 0.13 (0.05) a | 3.04 (0.90) a |
| Osceola | Control | 18.36 (0.78) a | 0.11 (0.03) a | 3.73 (1.24) a | 19.92 (2.19) c | 0.09 (0.03) a | 3.55 (0.82) a |
| Osceola | Mow | 18.64 (0.81) a | 0.11 (0.03) a | 3.61 (0.96) a | 20.78 (2.56) b | 0.15 (0.06) a | 3.54 (0.61) a |
| Osceola | Mow+Burn | 18.69 (0.78) a | 0.13 (0.04) a | 3.81 (1.18) a | 21.25 (2.70) a | 0.16 (0.06) a | 3.35 (0.70) a |

Data are means with (SD) per study location and treatment type. Means are for the entire study period per treatment type and site. Letters indicate significant differences (Student's t-test or Tukey's HSD $p < 0.05$) between treatments per site.

Table 4-6. Pearson's Correlation coefficients between soil $CO_2$ efflux ($R_s$), soil temperature ($T_s$), soil moisture content ($M_s$) and field conditions for the Osceola National Forest

| Variable | $R_s$ (µmol $CO_2$ $m^{-2}$ $sec^{-1}$) | $T_s$ (°C) | $M_s$ ($m^3/m^3$) |
|---|---|---|---|
| $R_s$ (µmol $CO_2$ $m^{-2}$ $sec^{-1}$) | 1.00 | 0.63 | -0.13 |
| $T_s$ (°C) | 0.63 | 1.00 | 0.09 |
| $M_s$ ($m^3/m^3$) | -0.13 | 0.09 | 1.00 |
| Dist nearest tree (m) | -0.06 | -0.04 | -0.14 |
| DBH nearest (cm) | -0.09 | 0.03 | 0.23 |
| Stand density (tree $ha^{-1}$) | 0.00 | -0.03 | -0.15 |
| Basal area ($m^2$ $ha^{-1}$) | 0.11 | 0.02 | 0.03 |
| Dist nearest palmetto (m) | -0.18 | 0.04 | 0.22 |
| Duff depth (cm) | 0.08 | -0.01 | -0.12 |
| Litter depth (cm) | 0.06 | -0.09 | -0.27 |
| Duff+litter depth (cm) | 0.09 | -0.06 | -0.26 |
| Monthly temp (°C) | 0.52 | 0.77 | -0.18 |
| Monthly precip (cm) | 0.35 | 0.28 | -0.06 |
| Organic matter 0-5 cm (%) | -0.01 | -0.04 | -0.23 |
| Organic matter 5-10 cm (%) | -0.05 | -0.03 | -0.12 |

Correlations are of monthly mean plot measurements with treatments ignored and all treatment x plot x month means pooled. $R_s$ is soil $CO_2$ efflux rate (µmol $CO_2$ $m^{-2}$ $sec^{-1}$), $T_s$ is soil temperature (°C), $M_s$ is soil volumetric moisture content ($m^3/m^3$). Plot vegetative and meteorological variables are described further in Table 4-1.

Table 4-7. Pearson's Correlation coefficients between soil $CO_2$ efflux ($R_s$), soil temperature ($T_s$), soil moisture content ($M_s$) and field conditions for the Austin Cary Forest

| Variable | $R_s$ (µmol $CO_2$ $m^{-2}$ $sec^{-1}$) | $T_s$ (°C) | $M_s$ ($m^3/m^3$) |
|---|---|---|---|
| $R_s$ (µmol $CO_2$ $m^{-2}$ $sec^{-1}$) | 1.00 | 0.89 | -0.25 |
| $T_s$ (°C) | 0.89 | 1.00 | -0.51 |
| $M_s$ ($m^3/m^3$) | -0.25 | -0.50 | 1.00 |
| Dist nearest tree (m) | -0.02 | 0.10 | 0.27 |
| DBH nearest (cm) | 0.00 | 0.12 | 0.19 |
| Stand density (tree $ha^{-1}$) | 0.01 | -0.13 | -0.25 |
| Basal area ($m^2$ $ha^{-1}$) | -0.03 | -0.09 | -0.23 |
| Dist nearest palmetto (m) | 0.00 | -0.01 | -0.15 |
| Duff depth (cm) | 0.02 | -0.13 | -0.28 |
| Litter depth (cm) | 0.05 | -0.11 | -0.38 |
| Duff+litter depth (cm) | 0.03 | -0.13 | -0.33 |
| Monthly temp (°C) | 0.82 | 0.80 | -0.01 |
| Monthly precip (cm) | 0.24 | 0.02 | 0.40 |
| Organic matter 0-5 cm (%) | -0.07 | 0.07 | 0.16 |
| Organic matter 5-10 cm (%) | -0.11 | 0.07 | 0.26 |

Correlations are of monthly mean plot measurements with treatments ignored and all treatment x plot x month means pooled. $R_s$ is soil $CO_2$ efflux rate (µmol $CO_2$ $m^{-2}$ $sec^{-1}$), $T_s$ is soil temperature (°C), $M_s$ is soil volumetric moisture content ($m^3/m^3$). Plot vegetative and meteorological variables are described further in Table 4-1.

Table 4-8. Results of simple linear regression models of soil $CO_2$ efflux rates and field conditions by study area and treatment

| Site | Treatment | Variable | Model and estimates | $R^2$ | F | p |
|---|---|---|---|---|---|---|
| ACMF | 3YR | $T_s$ | $R_s = -2.178 + 0.304*T_s$ | 0.83 | 136.20 | < 0.0001 |
| ACMF | 3YR | Temp | $R_s = -1.067 + 0.262*Temp$ | 0.74 | 93.63 | < 0.0001 |
| ACMF | 3YR | $M_s$ | $R_s = 4.486 – 3.224*M_s$ | 0.04 | 1.33 | 0.2565 |
| ACMF | 3YR | Precip | $R_s = 3.490 + 0.079*Precip$ | 0.08 | 2.82 | 0.1026 |
| 40YR | 40YR | $T_s$ | $R_s = -4.430 + 0.431*T_s$ | 0.85 | 161.31 | < 0.0001 |
| 40YR | 40YR | Temp | $R_s = -0.339 + 0.229*Temp$ | 0.62 | 56.17 | < 0.0001 |
| 40YR | 40YR | $M_s$ | $R_s = 4.858 – 8.748*M_s$ | 0.12 | 4.66 | 0.0380 |
| 40YR | 40YR | Precip | $R_s = 3.800 + 0.055*Precip$ | 0.04 | 1.48 | 0.2315 |
| Osceola | Burn | $T_s$ | $R_s = -0.297 + 0.175*T_s$ | 0.33 | 13.96 | 0.0008 |
| Osceola | Burn | Temp | $R_s = 1.124 + 0.117*Temp$ | 0.27 | 12.61 | 0.0011 |
| Osceola | Burn | $M_s$ | $R_s = 4.451 – 8.533*M_s$ | 0.12 | 4.49 | 0.0415 |
| Osceola | Burn | Precip | $R_s = 2.272 – 0.157*Precip$ | 0.14 | 5.61 | 0.0237 |
| Osceola | Burn | TPH | $R_s = 6.442 – 0.007*TPH$ | 0.20 | 8.30 | 0.0068 |
| Osceola | Burn | BA | $R_s = 11.625 – 0.378*BA$ | 0.17 | 6.85 | 0.0131 |
| Osceola | Burn | Litter | $R_s = 7.712 – 2.722*Litter$ | 0.17 | 7.13 | 0.0116 |
| Osceola | Burn | Duff+Litter | $R_s = 12.911 – 1.647*Duff+litter$ | 0.18 | 7.26 | 0.0109 |
| Osceola | Burn | Dist Palmetto | $R_s = 4.824 – 1.355*Dist\ palmetto$ | 0.18 | 7.39 | 0.0103 |
| Osceola | Control | $T_s$ | $R_s = -2.009 + 0.295*T_s$ | 0.55 | 33.76 | < 0.0001 |
| Osceola | Control | Temp | $R_s = 1.802 + 0.103*Temp$ | 0.24 | 10.45 | 0.0028 |
| Osceola | Control | $M_s$ | $R_s = 3.100 + 7.711*M_s$ | 0.04 | 1.53 | 0.2249 |
| Osceola | Control | Precip | $R_s = 2.790 + 0.141*Precip$ | 0.13 | 5.07 | 0.0311 |
| Osceola | Mow | $T_s$ | $R_s = -0.459 + 0.204*T_s$ | 0.58 | 37.59 | < 0.0001 |
| Osceola | Mow | Temp | $R_s = 1.164 + 0.140*Temp$ | 0.34 | 17.73 | 0.0002 |
| Osceola | Mow | $M_s$ | $R_s =4.406 – 3.886*M_s$ | 0.03 | 0.94 | 0.3391 |
| Osceola | Mow | Precip | $R_s = 2.610 + 0.177*Precip$ | 0.16 | 6.49 | 0.0155 |

Table 4-8. Continued

| | | | | | | |
|---|---|---|---|---|---|---|
| Osceola | Mow+Burn | $T_s$ | $R_s = -0.226 + 0.191*T_s$ | 0.36 | 15.09 | 0.0006 |
| Osceola | Mow+Burn | Temp | $R_s = 1.770 + 0.107*Temp$ | 0.24 | 10.66 | 0.0026 |
| Osceola | Mow+Burn | $M_s$ | $R_s = 4.375 – 3.537*M_s$ | 0.02 | 0.78 | 0.3830 |
| Osceola | Mow+Burn | Precip | $R_s = 3.014 + 0.116*Precip$ | 0.08 | 2.84 | 0.1013 |

For variable descriptions see Table 4-1.

Table 4-9. Results of nonlinear models of soil $CO_2$ efflux rates using soil temperature as a predictor

| Site | Treatment | Model | $Q_{10}$ | $R^2$ | p |
|---|---|---|---|---|---|
| ACMF | 3YR | $R_s = 0.8248\ e^{0.0761*Ts}$ | 2.14 | 0.80 | < 0.001 |
| ACMF | 40YR | $R_s = 0.4977\ e^{0.1049*Ts}$ | 2.85 | 0.82 | < 0.001 |
| Osceola | Burn | $R_s = 1.1183\ e^{0.0520*Ts}$ | 1.68 | 0.32 | 0.001 |
| Osceola | Control | $R_s = 0.8319\ e^{0.0761*Ts}$ | 2.14 | 0.53 | < 0.001 |
| Osceola | Mow | $R_s = 1.2199\ e^{0.0539*Ts}$ | 1.71 | 0.56 | < 0.001 |
| Osceola | Mow+Burn | $R_s = 1.3091\ e^{0.0500*}$ | 1.65 | 0.35 | 0.001 |

Models developed using Equation 4-3 are of monthly mean soil $CO_2$ efflux rate ($R_s$) (µmol $CO_2$ $m^{-2}$ $sec^{-1}$) responses to soil temperature ($T_s$). Coefficients were estimated using statistical software JMP 9.0. $Q_{10}$ was calculated using Equation 4-4 (Lundegardh, 1927).

Table 4-10. Results of simple linear regression models of soil $CO_2$ efflux rates and field conditions by study area, treatment, and season

| Site | Treatment | Season | Variable | Model | $R^2$ | F | p |
|---|---|---|---|---|---|---|---|
| ACMF | 3YR | Dormant | $T_s$ | $R_s = -0.042 + 0.180*T_s$ | 0.50 | 7.03 | 0.0328 |
| ACMF | 3YR | Dormant | Temp | $R_s$ = 1.073 + 0.140*Temp | 0.82 | 48.25 | < 0.0001 |
| ACMF | 3YR | Dormant | $M_s$ | $R_s = 4.334 – 16.630*M_s$ | 0.74 | 28.43 | 0.0003 |
| ACMF | 3YR | Dormant | Precip | $R_s$ = 3.970 – 0.106*Precip | 0.81 | 43.27 | < 0.0001 |
| ACMF | 3YR | Growing | $T_s$ | $R_s = -2.057 + 0.307*T_s$ | 0.89 | 155.30 | < 0.0001 |
| ACMF | 3YR | Growing | Temp | $R_s$ = -2.473 + 0.326*Temp | 0.75 | 64.58 | < 0.0001 |
| ACMF | 3YR | Growing | $M_s$ | $R_s = 5.869 – 9.594*M_s$ | 0.29 | 8.37 | 0.0087 |
| ACMF | 3YR | Growing | Precip | $R_s$ = 3.330 + 0.123*Precip | 0.12 | 2.78 | 0.1102 |
| ACMF | 40YR | Dormant | $T_s$ | $R_s = -2.830 + 0.342*T_s$ | 0.53 | 8.04 | 0.0252 |
| ACMF | 40YR | Dormant | Temp | $R_s$ = 1.504 + 0.148*Temp | 0.55 | 12.33 | 0.0056 |
| ACMF | 40YR | Dormant | $M_s$ | $R_s = 4.797 – 19.870*M_s$ | 0.50 | 9.95 | 0.0103 |
| ACMF | 40YR | Dormant | Precip | $R_s$ = 4.671 – 0.131*Precip | 0.73 | 26.94 | 0.0004 |
| ACMF | 40YR | Growing | $T_s$ | $R_s = -4.650 + 0.448*T_s$ | 0.90 | 174.62 | < 0.0001 |
| ACMF | 40YR | Growing | Temp | $R_s$ = -2.966 + 0.340*Temp | 0.81 | 93.00 | < 0.0001 |
| ACMF | 40YR | Growing | $M_s$ | $R_s = 5.377 – 11.898*M_s$ | 0.19 | 5.06 | 0.0348 |
| ACMF | 40YR | Growing | Precip | $R_s$ = 2.970 + 0.145*Precip | 0.17 | 4.37 | 0.0483 |
| Osceola | Burn | Dormant | $T_s$ | $R_s = -1.782 + 0.276*T_s$ | 0.69 | 28.57 | 0.0001 |
| Osceola | Burn | Dormant | Temp | $R_s$ = -1.127 + 0.292*Temp | 0.35 | 6.94 | 0.0206 |
| Osceola | Burn | Dormant | $M_s$ | $R_s =2.282 + 8.766*M_s$ | 0.11 | 1.53 | 0.2387 |
| Osceola | Burn | Growing | $T_s$ | $R_s = -0.941 + 0.1886*T_s$ | 0.30 | 5.65 | 0.0335 |
| Osceola | Burn | Growing | Temp | $R_s$ = -1.922 + 0.237*Temp | 0.54 | 22.70 | 0.0001 |
| Osceola | Burn | Growing | $M_s$ | $R_s = 5.480 – 15.862*M_s$ | 0.44 | 14.81 | 0.0011 |
| Osceola | Burn | Growing | TPH | $R_s$ = 6.703 – 0.007*TPH | 0.19 | 4.54 | 0.0464 |
| Osceola | Burn | Growing | BA | $R_s$ = 12.984 – 0.436*BA | 0.20 | 4.71 | 0.0427 |
| Osceola | Burn | Growing | Litter+duff | $R_s$ = 14.980 – 1.994*Litter+Duff | 0.23 | 5.67 | 0.0279 |

Table 4-10. Continued

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Osceola | Control | Dormant | $T_s$ | $R_s = -3.293 + 0.382*T_s$ | 0.74 | 37.69 | < 0.0001 |
| Osceola | Control | Dormant | Temp | $R_s = -1.844 + 0.368*Temp$ | 0.40 | 8.71 | 0.0112 |
| Osceola | Control | Dormant | $M_s$ | $R_s = 0.506 + 30.079*M_s$ | 0.65 | 15.36 | 0.0018 |
| Osceola | Control | Growing | $T_s$ | $R_s = -1.716 + 0.264*T_s$ | 0.51 | 13.31 | 0.0030 |
| Osceola | Control | Growing | Temp | $R_s = -0.564 + 0.195*Temp$ | 0.63 | 30.77 | < 0.0001 |
| Osceola | Control | Growing | $M_s$ | $R_s = 4.857 – 11.225*M_s$ | 0.09 | 1.73 | 0.2056 |
| Osceola | Control | Growing | Precip | $R_s = 1.875 + 0.228*Precip$ | 0.34 | 9.22 | 0.0071 |
| Osceola | Mow | Dormant | $T_s$ | $R_s = -1.623 + 0.281*T_s$ | 0.79 | 44.89 | < 0.0001 |
| Osceola | Mow | Dormant | Temp | $R_s = -1.303 + 0.325*Temp$ | 0.51 | 13.79 | 0.0026 |
| Osceola | Mow | Dormant | $M_s$ | $R_s =1.590 + 17.881*M_s$ | 0.34 | 6.79 | 0.0218 |
| Osceola | Mow | Growing | $T_s$ | $R_s = -0.289 + 0.184*T_s$ | 0.60 | 19.27 | 0.0007 |
| Osceola | Mow | Growing | Temp | $R_s = -1.282 + 0.235*Temp$ | 0.44 | 15.23 | 0.0010 |
| Osceola | Mow | Growing | $M_s$ | $R_s = 5.329 – 9.022*M_s$ | 0.17 | 3.40 | 0.0630 |
| Osceola | Mow+Burn | Dormant | $T_s$ | $R_s = -2.369 + 0.330*T_s$ | 0.70 | 30.64 | < 0.0001 |
| Osceola | Mow+Burn | Dormant | Temp | $R_s = -1.263 + 0.335*Temp$ | 0.37 | 7.63 | 0.0161 |
| Osceola | Mow+Burn | Dormant | $M_s$ | $R_s = 0.653 + 23.468*M_s$ | 0.67 | 26.22 | 0.0002 |
| Osceola | Mow+Burn | Growing | $T_s$ | $R_s = -0.746 + 0.193*T_s$ | 0.55 | 14.71 | 0.0024 |
| Osceola | Mow+Burn | Growing | Temp | $R_s = -1.430 + 0.231*Temp$ | 0.66 | 34.25 | < 0.0001 |
| Osceola | Mow+Burn | Growing | $M_s$ | $R_s = 6.048 – 14.954*M_s$ | 0.53 | 20.24 | 0.0003 |
| Osceola | Mow+Burn | Growing | Precip | $R_s = 1.730 + 0.241*Precip$ | 0.21 | 4.82 | 0.0415 |

For variable descriptions see Table 4-1 (this chapter).

Table 4-11. Results of season specific nonlinear models of the relationships between soil $CO_2$ efflux rates and soil temperature at the Austin Cary Forest and Osceola National Forest, Florida, USA

| Site | Treatment | Season | Model | $Q_{10}$ | $R^2$ | p |
|---|---|---|---|---|---|---|
| ACMF | 3YR | Dormant | $R_s = 1.3539\ e^{0.0482*Ts}$ | 1.62 | 0.49 | 0.0346 |
| ACMF | 3YR | Growing | $R_s = 0.9207\ e^{0.0726*Ts}$ | 2.07 | 0.84 | < 0.0001 |
| ACMF | 40YR | Dormant | $R_s = 0.8178\ e^{0.0792*Ts}$ | 2.21 | 0.51 | 0.0302 |
| ACMF | 40YR | Growing | $R_s = 0.4889\ e^{0.1065*Ts}$ | 2.90 | 0.86 | < 0.0001 |
| Osceola | Burn | Dormant | $R_s = 0.8308\ e^{0.0737*Ts}$ | 2.09 | 0.64 | 0.0004 |
| Osceola | Burn | Growing | $R_s = 0.8731\ e^{0.0586*Ts}$ | 1.80 | 0.30 | 0.0352 |
| Osceola | Control | Dormant | $R_s = 0.6686\ e^{0.0920*Ts}$ | 2.51 | 0.70 | < 0.0001 |
| Osceola | Control | Growing | $R_s = 0.8671\ e^{0.0702*Ts}$ | 2.02 | 0.50 | 0.0034 |
| Osceola | Mow | Dormant | $R_s = 0.9375\ e^{0.0713*Ts}$ | 2.04 | 0.76 | < 0.0001 |
| Osceola | Mow | Growing | $R_s = 1.2696\ e^{0.0489*Ts}$ | 1.63 | 0.58 | 0.0010 |
| Osceola | Mow+Burn | Dormant | $R_s = 0.8687\ e^{0.0777*Ts}$ | 2.17 | 0.67 | 0.0002 |
| Osceola | Mow+Burn | Growing | $R_s = 1.0365\ e^{0.0548*Ts}$ | 1.73 | 0.55 | 0.0025 |

Models developed using Equation 4-3 are of monthly mean soil $CO_2$ efflux rate ($R_s$) (µmol $CO_2$ $m^{-2}$ $sec^{-1}$) responses to soil temperature ($T_s$). Data are presented by treatment type, study site, and season. Dormant season defined as October – February and growing season defined as March - September. Coefficients were estimated using statistical software JMP 9.0. $Q_{10}$ was calculated using Equation 4-4 (Lundegardh, 1927).

Table 4-12. Step-wise multiple linear regression models by study site and treatment predicting soil $CO_2$ efflux rates from field parameters

| Site | Treatment | Equation | RMSE | $R^2$ | F | p |
|---|---|---|---|---|---|---|
| ACMF | 3YR | $R_s = -1.595 + 0.338*T_s + 2.659*M_s - 2.824*$Dist palmetto | 0.40 | 0.90 | 75.47 | < 0.0001 |
| ACMF | 40YR | $R_s = -6.782 + 0.526*T_s\ 7.034*M_s$ | 0.43 | 0.89 | 108.36 | < 0.0001 |
| Osceola | Burn | $R_s = 2.402 + 0.175*T_s - 0.006*TPH$ | 0.67 | 0.56 | 17.05 | < 0.0001 |
| Osceola | Control | $R_s = -4.837 + 0.285*T_s - 11.714*M_s + 0.075*BA$ | 0.58 | 0.72 | 22.07 | < 0.0001 |
| Osceola | Mow | $R_s = -1.281 + 0.200*T_s + 0.042*BA$ | 0.50 | 0.65 | 24.16 | < 0.0001 |
| Osceola | Mow+Burn | $R_s = -0.226 + 0.191*T_s$ | 0.80 | 0.36 | 15.09 | 0.0006 |

Models developed using a forward step-wise procedure with parameter inclusion and retention $p < 0.05$. For input parameter descriptions see Table 4-2.

Table 4-13. Step-wise multiple linear regression models by study site, treatment, and season predicting soil $CO_2$ efflux rates from field parameters

| Site | Treatment | Season | Equation | RMSE | $R^2$ | F | p |
|---|---|---|---|---|---|---|---|
| ACMF | 3YR | Dormant | $R_s$ = 3.970 – 0.106*Precip | 0.23 | 0.81 | 43.27 | < 0.0001 |
| ACMF | 3YR | Growing | $R_s$ = -1.584 + 0.308*$T_s$ – 0.689*OM (5-10 cm) | 0.35 | 0.94 | 143.21 | < 0.0001 |
| ACMF | 40YR | Dormant | $R_s$ = 4.124 – 0.130*Precip + 0.693*Dist palmetto | 0.30 | 0.83 | 22.61 | 0.0003 |
| ACMF | 40YR | Growing | $R_s$ = -7.093 + 0.542*$T_s$ + 7.249*$M_s$ | 0.40 | 0.93 | 122.39 | < 0.0001 |
| Osceola | Burn | Dormant | $R_s$ = 0.917 + 0.270*$T_s$ – 0.006*TPH | 0.41 | 0.87 | 40.05 | < 0.0001 |
| Osceola | Burn | Growing | $R_s$ = -1.349 + 0.213*Temp + 0.169*Precip – 1.517*Dist palmetto | 0.53 | 0.84 | 30.57 | < 0.0001 |
| Osceola | Control | Dormant | $R_s$ =-18.120 + 0.240*$T_s$ + 14.331*$M_s$ + 0.319*BA + 3.141*Dist tree | 0.38 | 0.93 | 34.35 | < 0.0001 |
| Osceola | Control | Growing | $R_s$ = -2.839 + 0.259*$T_s$ + 0.146*$M_s$ | 0.46 | 0.72 | 15.74 | 0.0004 |
| Osceola | Mow | Dormant | $R_s$ = -1.966 + 0.269*$T_s$ + 0.002*TPH | 0.36 | 0.89 | 44.69 | < 0.0001 |
| Osceola | Mow | Growing | $R_s$ = -0.289 + 0.184*$T_s$ | 0.40 | 0.60 | 19.27 | 0.0007 |
| Osceola | Mow +Burn | Dormant | $R_s$ = 27.779 + 0.332*$T_s$ - 0.906*DBH | 0.49 | 0.85 | 33.55 | < 0.0001 |
| Osceola | Mow +Burn | Growing | $R_s$ =6.048 – 14.954*$M_s$ | 0.79 | 0.53 | 20.24 | 0.0003 |

Models developed using a forward step-wise procedure with parameter inclusion and retention p < 0.05. For input parameter descriptions see Table 4-2. Dormant season is October – February, Growing season is March – September.

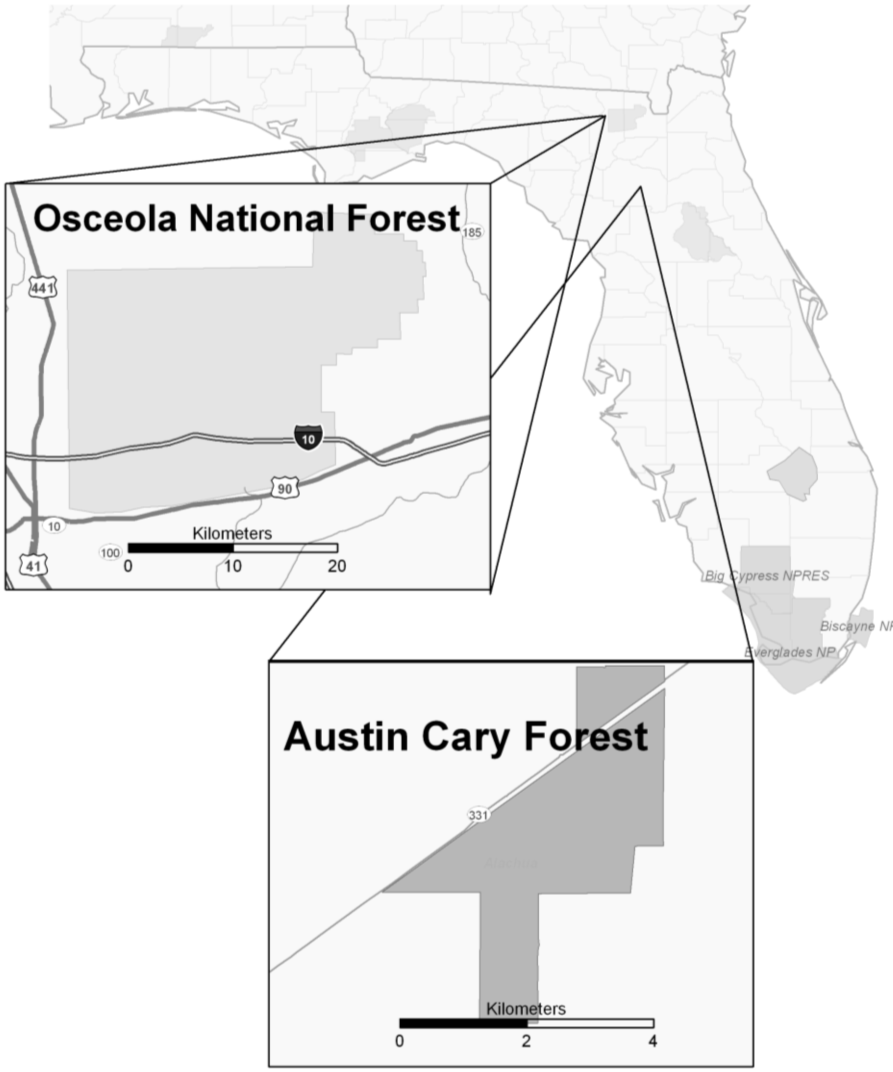


Figure 4-1. Map of the study areas at the Osceola National Forest near Lake City, Florida and Austin Cary Forest near Gainesville, Florida, USA. Map produced by David Godwin.

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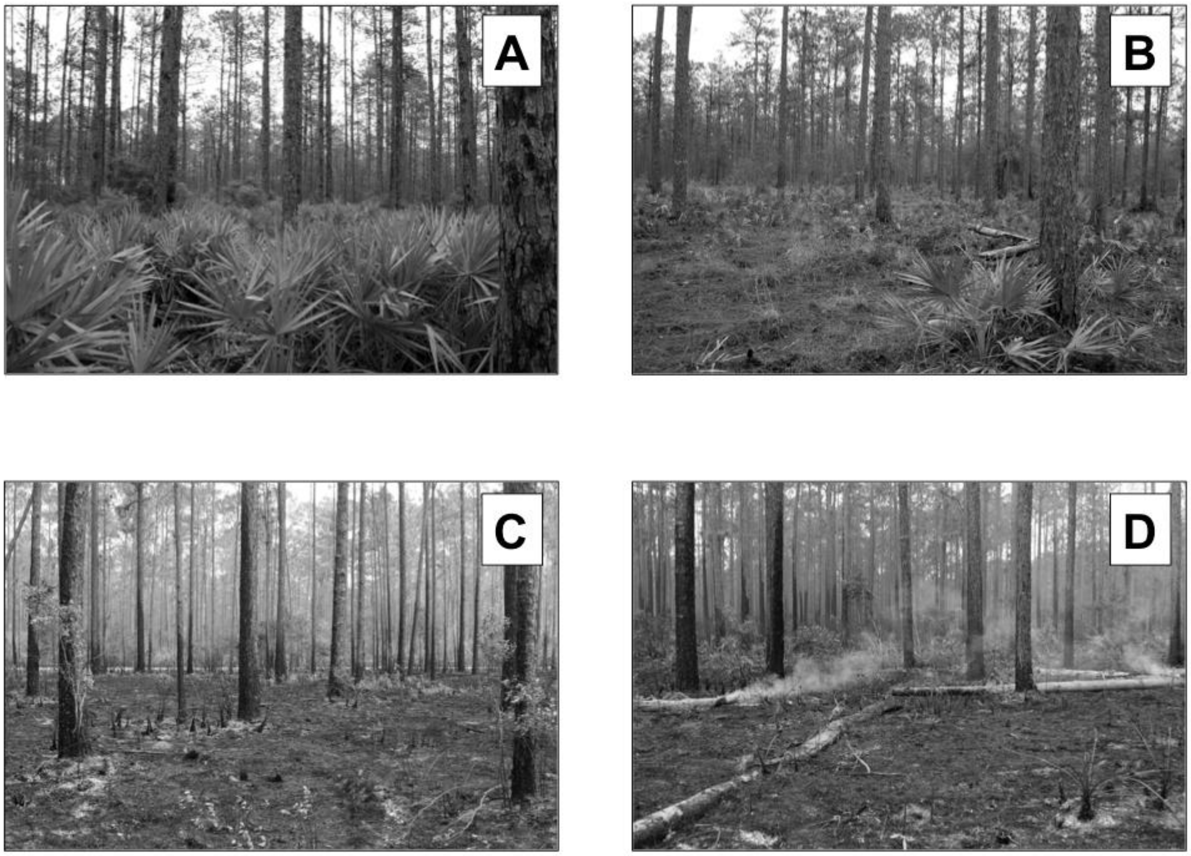


Figure 4-2. Examples of the four pine flatwoods forest management types sampled in the Osceola National Forest study site near Lake City, Florida, USA: (A) Unburned control, (B) mow only, (C) burn only, and (D) mow+burn. Mow only understory vegetation regrowth shown is approximately two months following mechanical treatment. Burn only and mow+burn photos depict conditions one day post prescribed burn. Prior to mowing and prescribed fire treatments, conditions within all sites were similar to control units. Photographs courtesy of David Godwin.


Figure 4-3. Pine flatwoods forest management types represented in the study at the Austin Cary Memorial Forest, Gainesville, Florida, USA. The prescribed fire sites (A) were burned on a 3-year winter burn rotation while the fire excluded sites (B) were unburned for >40 years. Photographs courtesy of David Godwin.

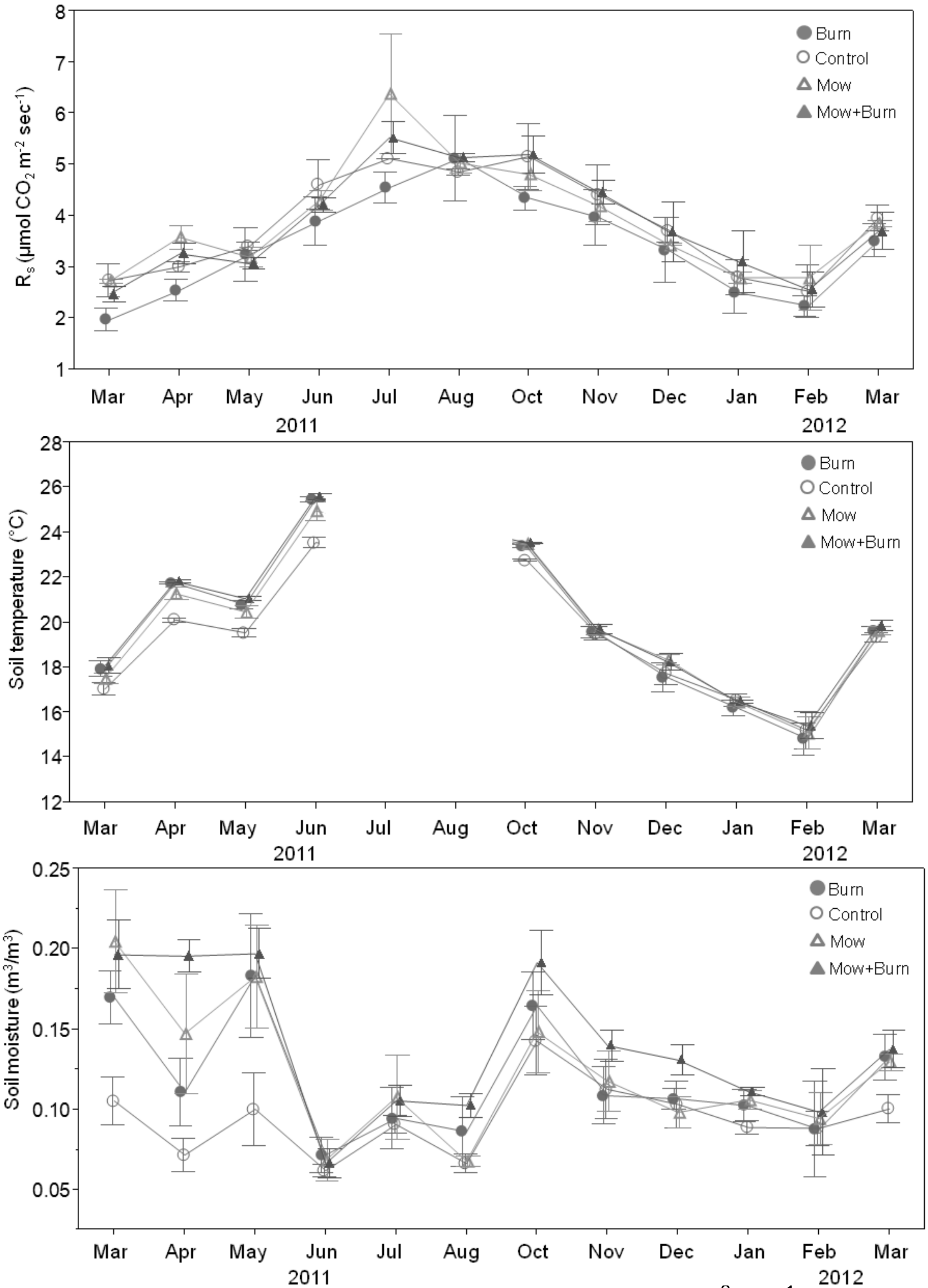


Figure 4-4. Monthly mean soil $CO_2$ efflux rates ($R_s$) (µmol $CO_2$ $m^{-2}$ $sec^{-1}$), soil temperature ($T_s$) (°C), and soil moisture content ($M_s$) (m3/m3) per treatment at the Osceola National Forest near Lake City, Florida, USA. Due to equipment problems $T_s$ was not recorded during the months of July and August 2011.

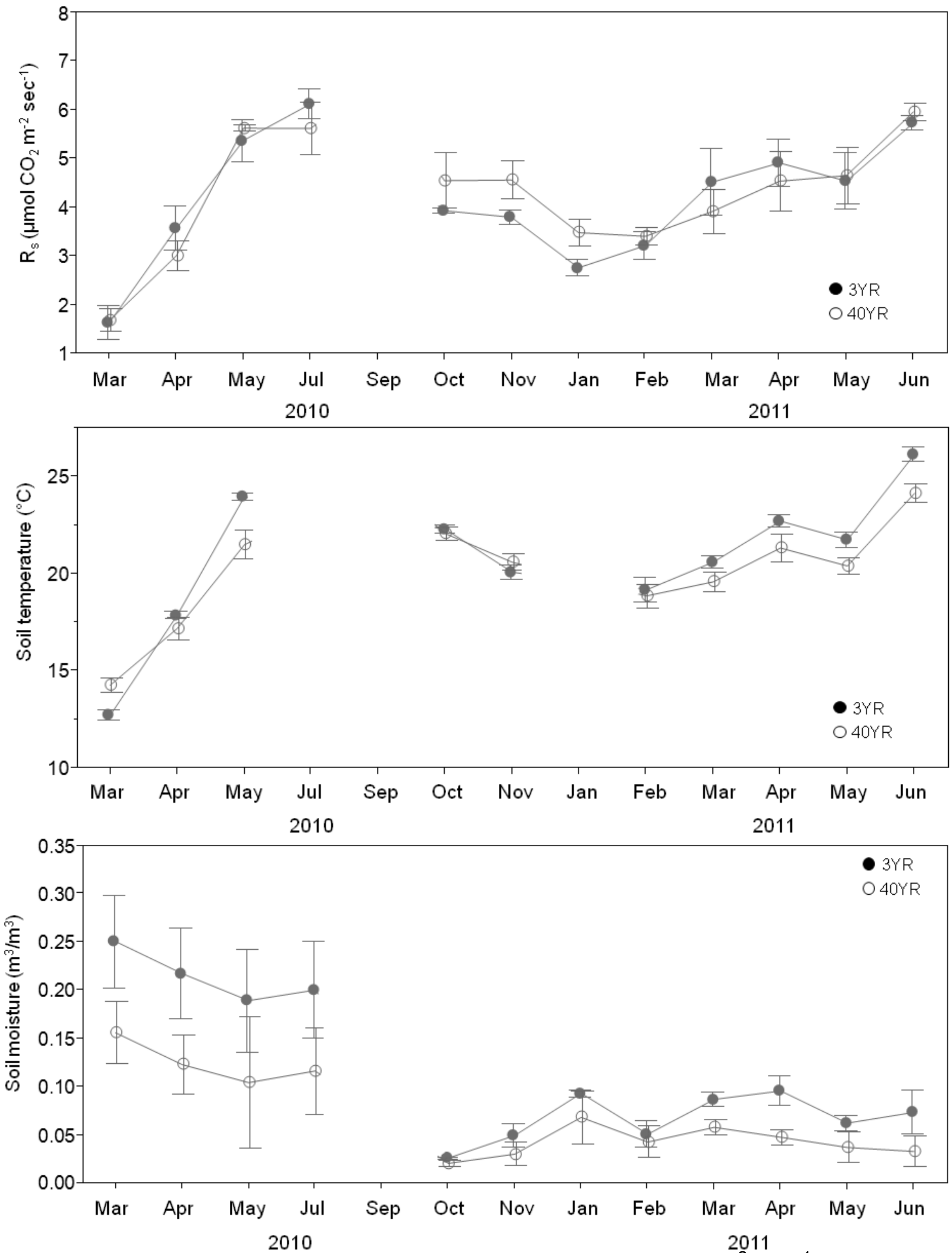


Figure 4-5. Monthly mean soil $CO_2$ efflux rates ($R_s$) (µmol CO2 $m^{-2}$ $sec^{-1}$), soil temperature ($T_s$) (°C), and soil moisture content ($M_s$) ($m^3/m^3$) per treatment at the Austin Cary Forest near Gainesville, Florida, USA. Due to equipment problems $T_s$ was not recorded during the months of July 2010 and January 2011.

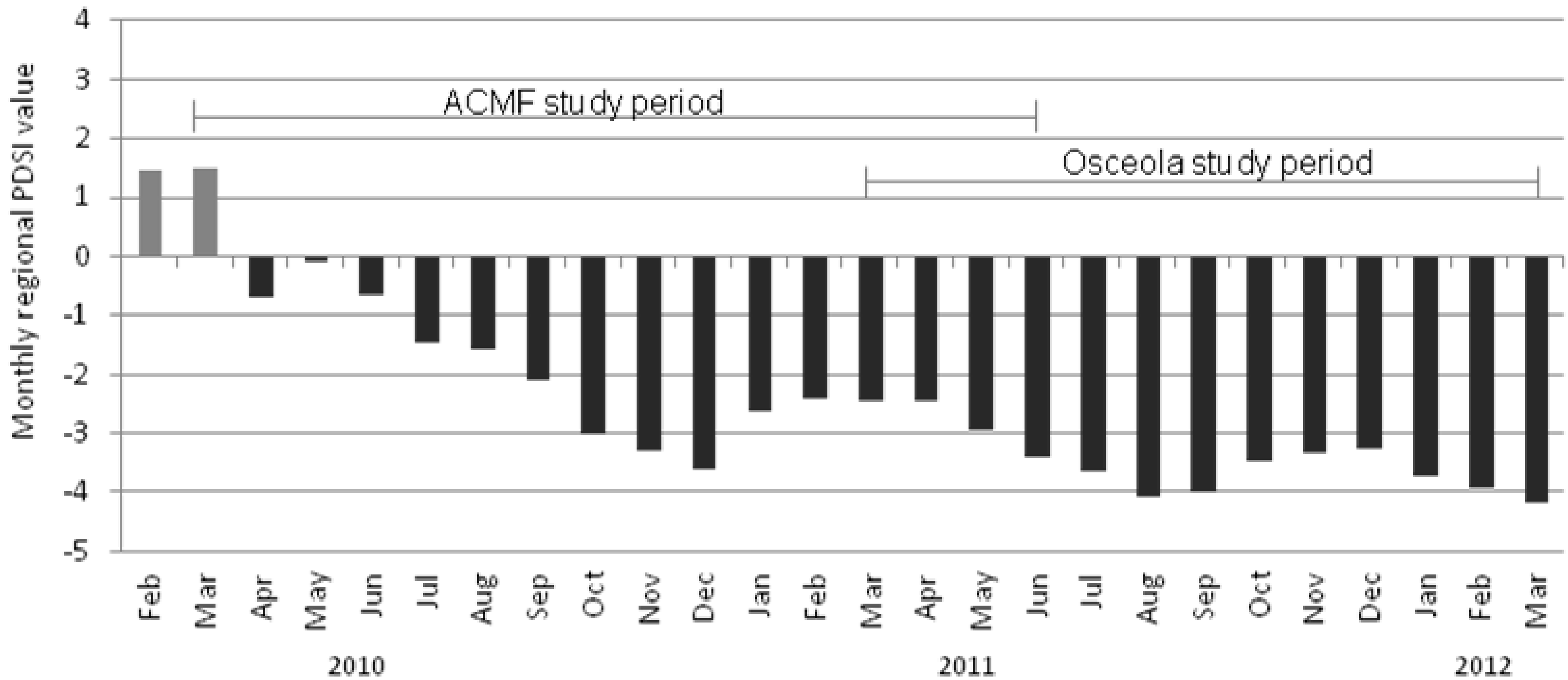


Figure 4-6. Monthly Palmer Drought Severity Index values for the region containing the Austin Cary Forest and the Osceola National Forest study areas. Data are from the National Oceanic and Atmospheric Administration (NOAA) National Climatic Data Center (NCDC). All scores below zero represent increasing levels of regional drought severity.

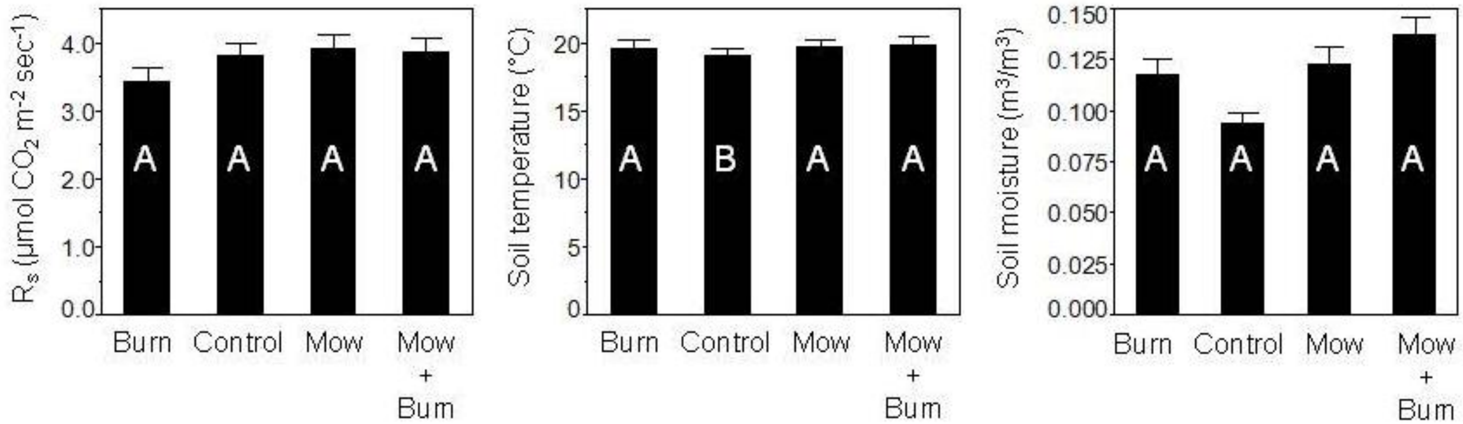


Figure 4-7. Treatment means of soil $CO_2$ efflux rates ($R_s$) (µmol $CO_2$ m$^{-2}$ sec$^{-1}$), soil temperature ($T_s$) (°C) and soil volumetric moisture content ($M_s$) (m$^3$/m$^3$) for the Osceola National Forest during the sampling period of March 2011 - March 2012. Letters indicate significant differences between treatments (Tukey's HSD $p < 0.05$).

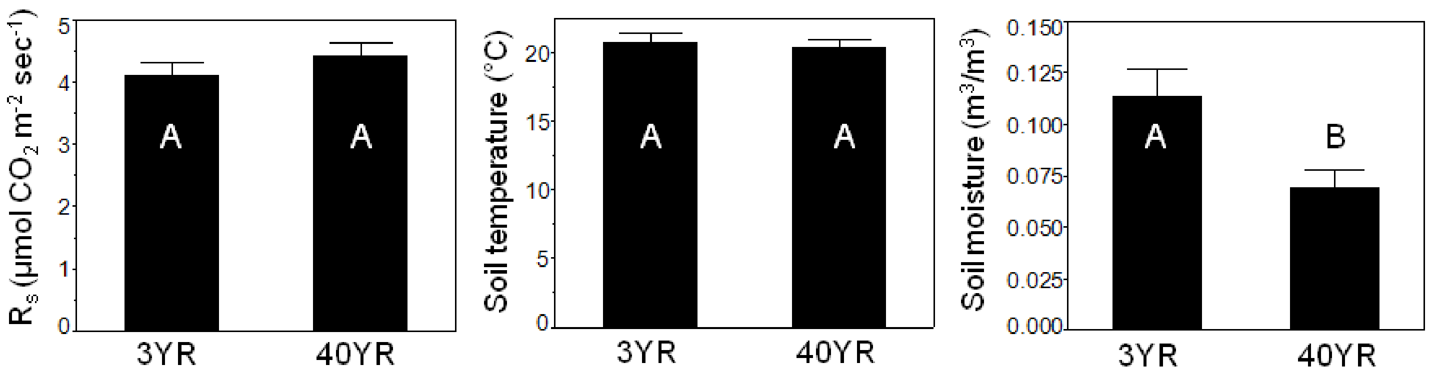


Figure 4-8. Treatment means of soil $CO_2$ efflux rates ($R_s$) (µmol $CO_2$ m$^{-2}$ sec$^{-1}$), soil temperature ($T_s$) (°C) and soil volumetric moisture content ($M_s$) (m$^3$/m$^3$) for the Austin Cary Forest during the sampling period of February 2010 - June 2011. Letters indicate significant differences between treatments (Student's t-test $p < 0.05$).

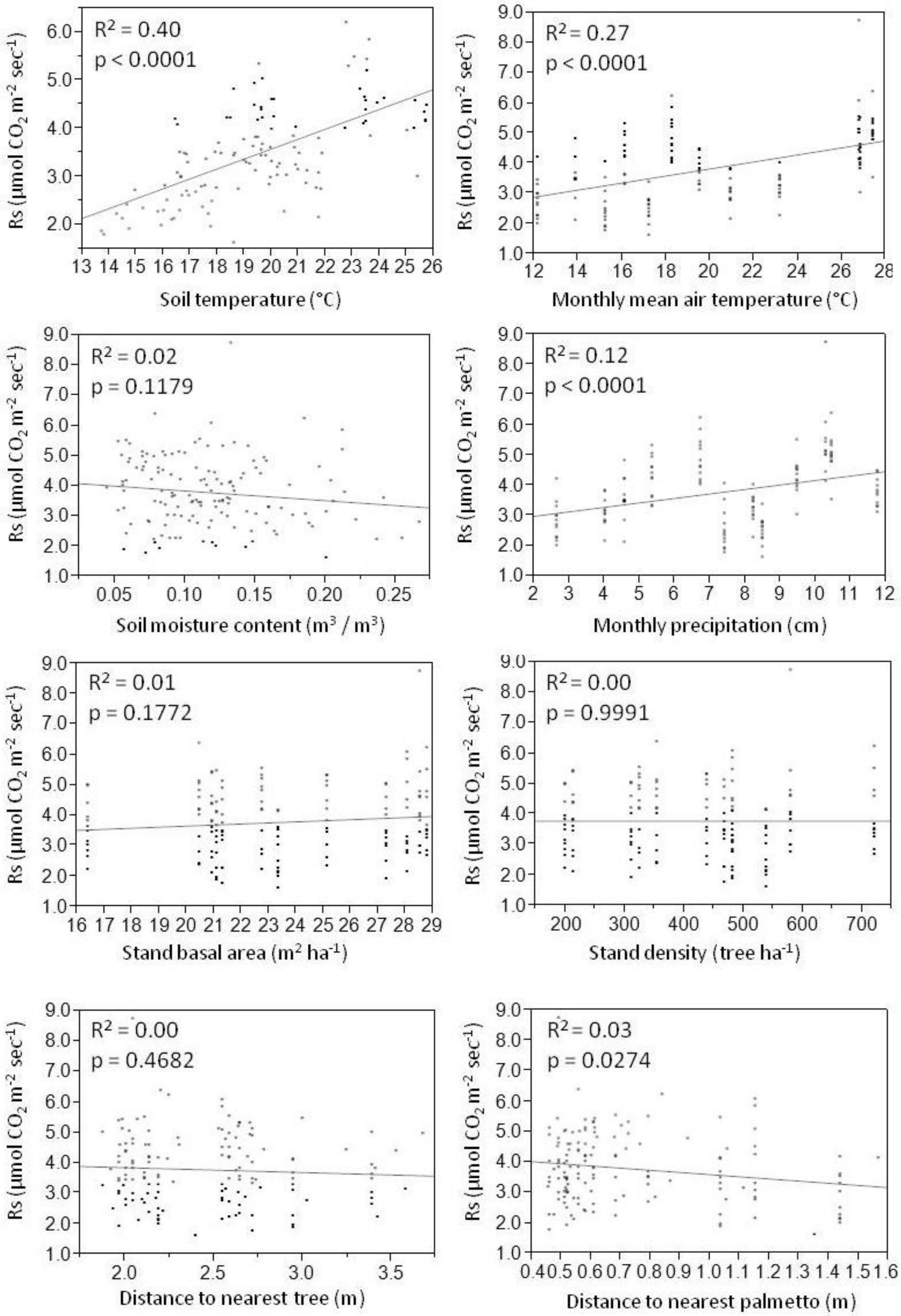


Figure 4-9. Linear regressions of the relationships between mean soil $CO_2$ efflux rates ($R_s$) (μmol $CO_2$ $m^{-2}$ $sec^{-1}$) and mean: soil temperature (°C), monthly mean air temperature (°C), soil moisture content ($m^3/m^3$), monthly total precipitation (cm), basal area ($m^2$ $ha^{-1}$), stand density (tree $ha^{-1}$), distance to nearest tree (m), and distance to nearest palmetto (m) for the Osceola National Forest. Each point represents entire study period means per sample plot with all treatments combined.

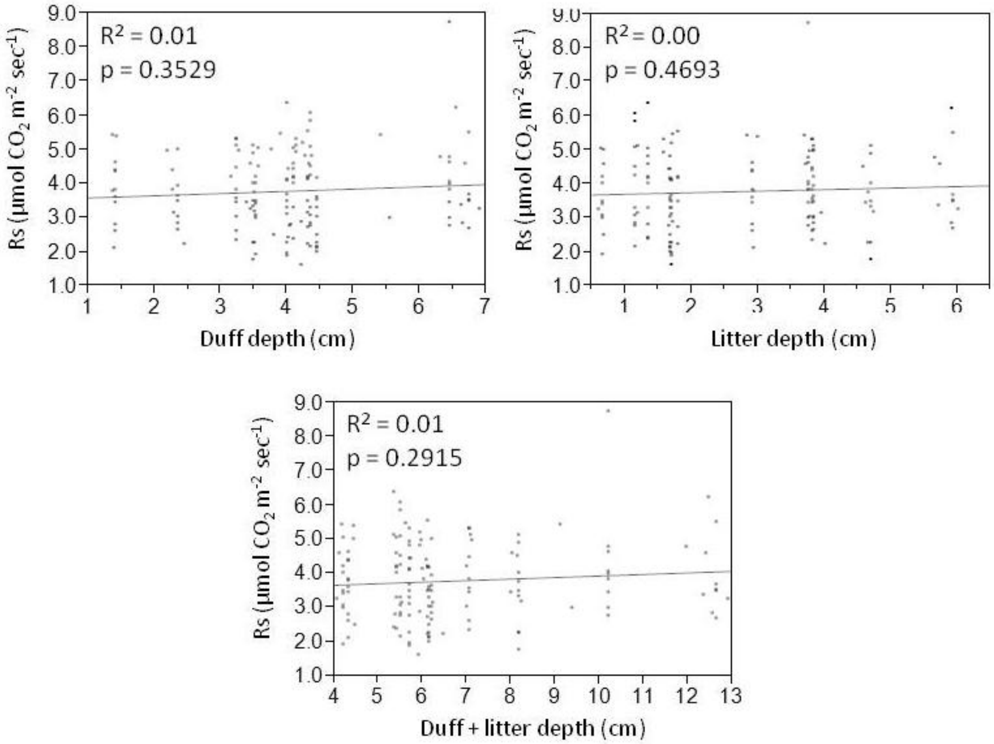


Figure 4-10. Linear regression of the relationships between mean soil $CO_2$ efflux rates ($R_s$) (μmol $CO_2$ $m^{-2}$ $sec^{-1}$) and mean: duff depth (cm), litter depth (cm), and litter+duff depth (cm) for the Osceola National Forest. Each point represents entire study period means per sample plot with all treatments combined.

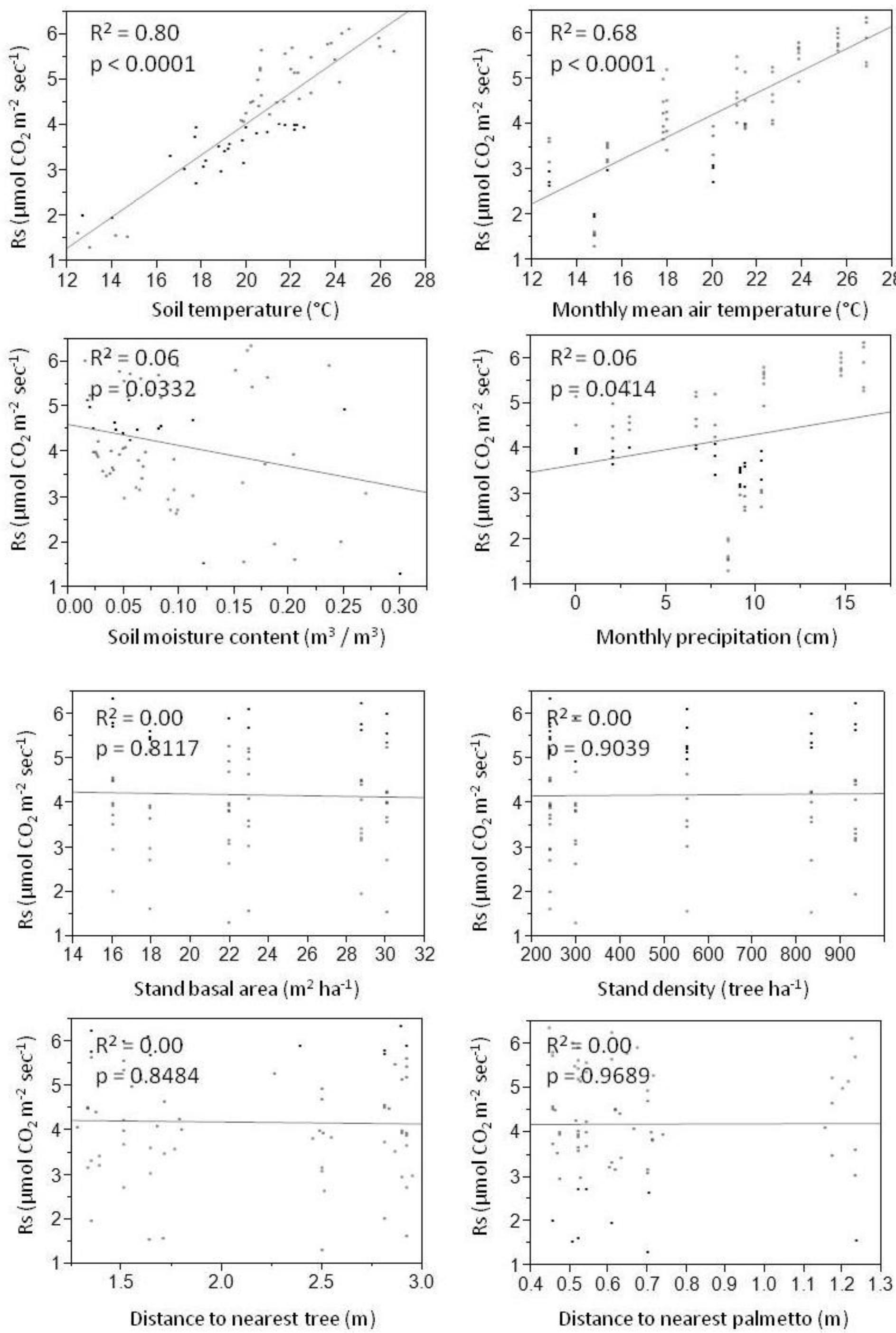


Figure 4-11. Linear regression of the relationships between mean soil $CO_2$ efflux rates ($R_s$) (µmol $CO_2$ $m^{-2}$ $sec^{-1}$) and mean: soil temperature (°C), mean monthly air temperature (°C), soil moisture content ($m^3/m^3$), total monthly precipitation (cm), basal area ($m^2$ $ha^{-1}$), stand density (tree $ha^{-1}$), distance to nearest tree (m), and distance to nearest palmetto (m) for the Austin Cary Forest. Each point represents entire study period means per sample plot with all treatments combined.

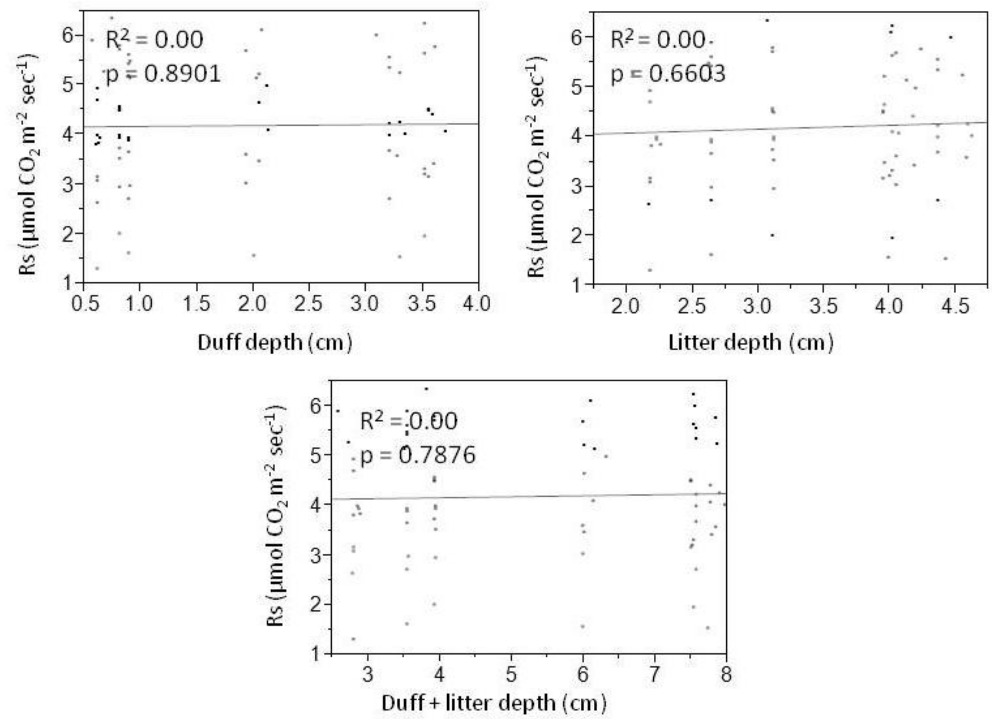


Figure 4-12. Linear regression of the relationships between mean soil $CO_2$ efflux rates ($R_s$) (µmol $CO_2$ $m^{-2}$ $sec^{-1}$) and mean: duff depth (cm), litter depth (cm), and litter+duff depth (cm) for the Austin Cary Forest. Each point represents entire study period means per sample plot with all treatments combined.

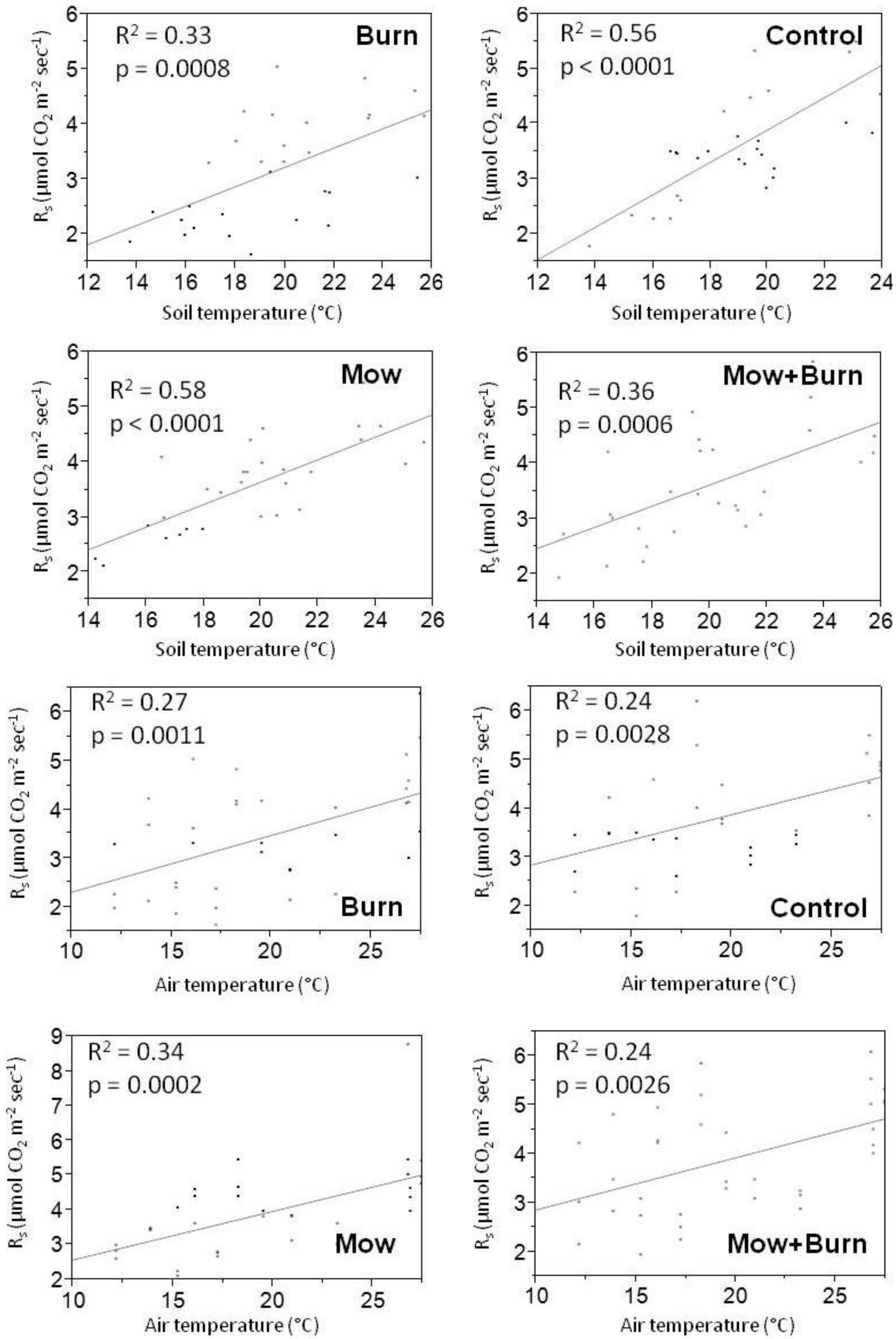


Figure 4-13. Linear regression of the relationships between monthly mean soil $CO_2$ efflux rates ($R_s$) (µmol $CO_2$ $m^{-2}$ $sec^{-1}$) and soil temperature ($T_s$) (°C) (top four plots) as well as $R_s$ and monthly mean air temperature (M Temp) (°C) (bottom four plots) for treatments at the Osceola National Forest. Each point represents monthly mean values per sample plot.

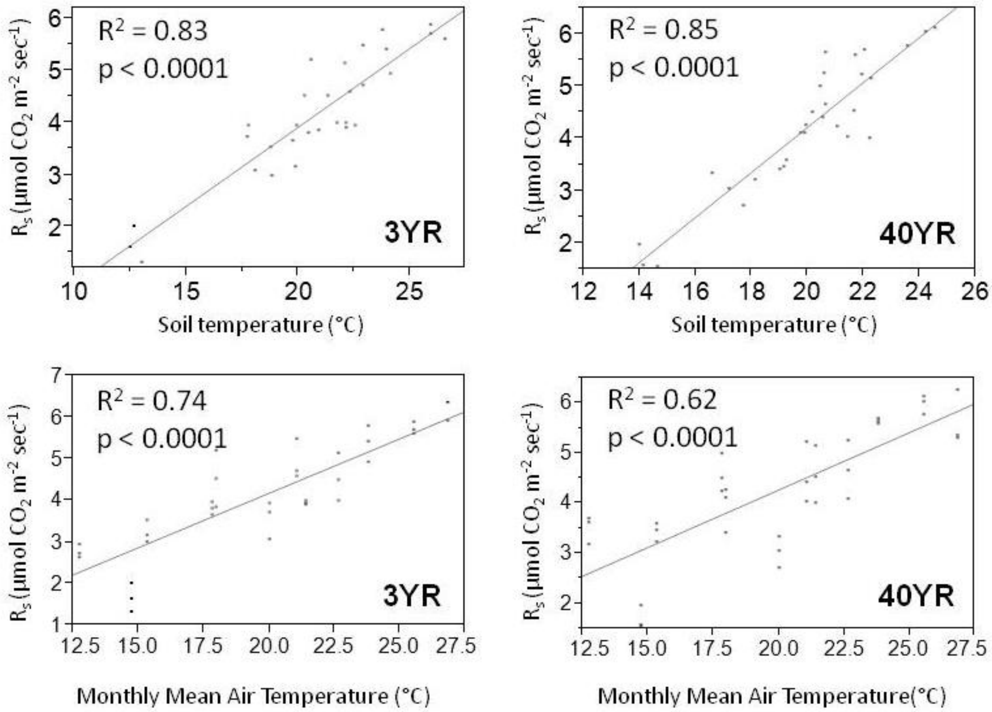


Figure 4-14. Linear regression of the relationships between monthly mean soil $CO_2$ efflux rates ($R_s$) (µmol $CO_2$ $m^{-2}$ $sec^{-1}$) and soil temperature ($T_s$) (°C) (top two plots) as well as $R_s$ and monthly mean air temperature (M Temp) (°C) (bottom to plots) for treatments at the Austin Cary Forest. Each point represents monthly mean values per sample plot.

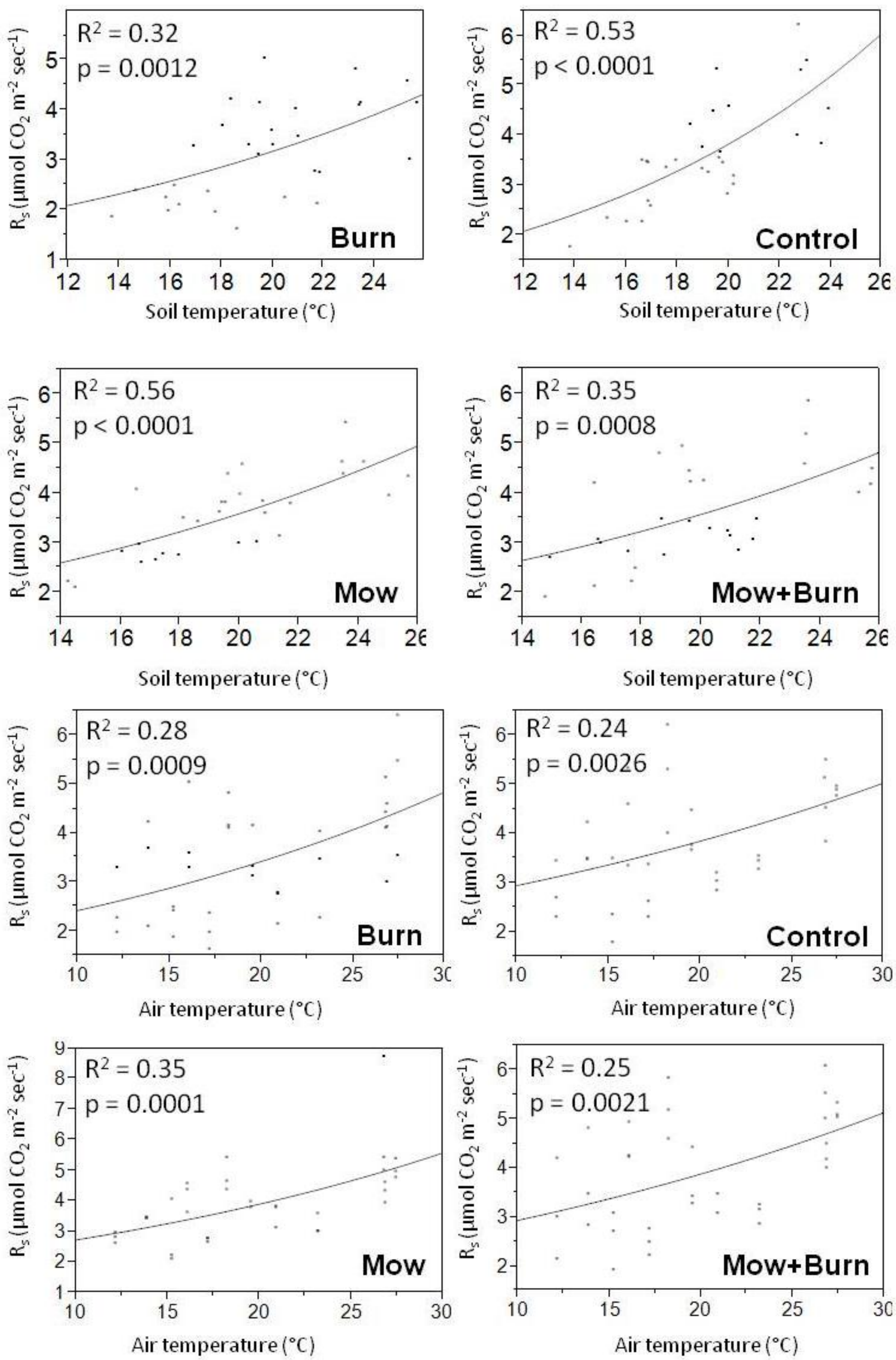


Figure 4-15. Non-linear regression of the relationships between monthly mean soil $CO_2$ efflux rates ($R_s$) (µmol $CO_2$ $m^{-2}$ $sec^{-1}$) and soil temperature ($T_s$) (°C) (top four plots) as well as $R_s$ and monthly mean air temperature (M Temp) (°C) (bottom four plots) for treatments at the Osceola National Forest. Each point represents monthly mean values per sample plot.

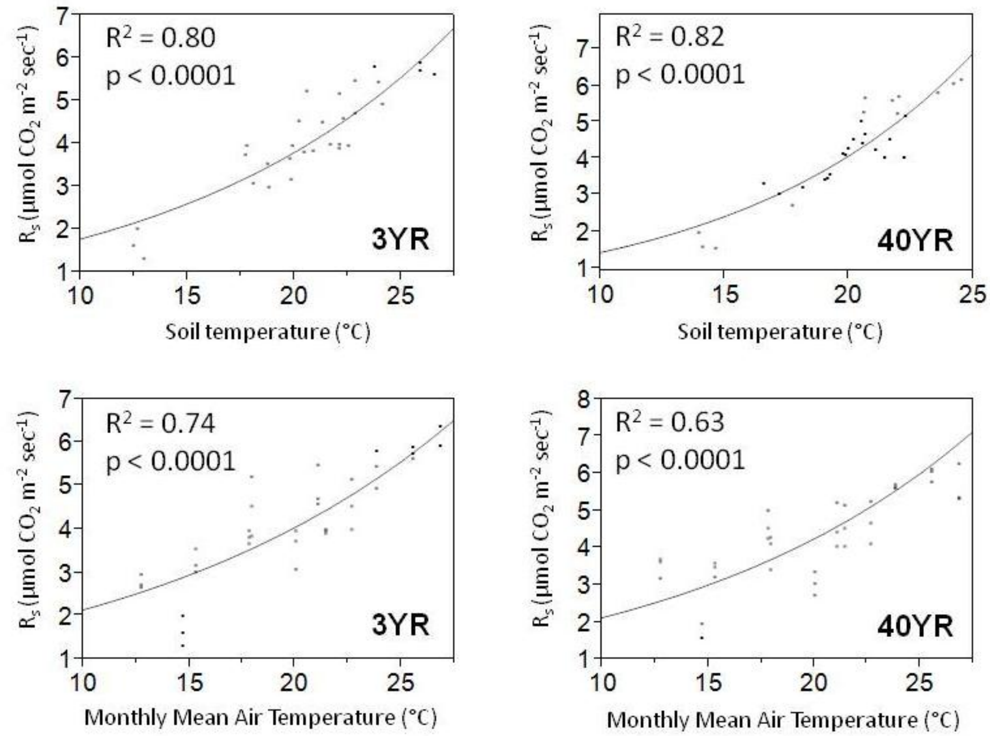


Figure 4-16. Non-linear regression of the relationships between monthly mean soil $CO_2$ efflux rates ($R_s$) (µmol $CO_2$ $m^{-2}$ $sec^{-1}$) and soil temperature ($T_s$) (°C) (top two plots) as well as $R_s$ and monthly mean air temperature (M Temp) (°C) (bottom two plots) for treatments at the Austin Cary Forest. Each point represents monthly mean values per sample plot.

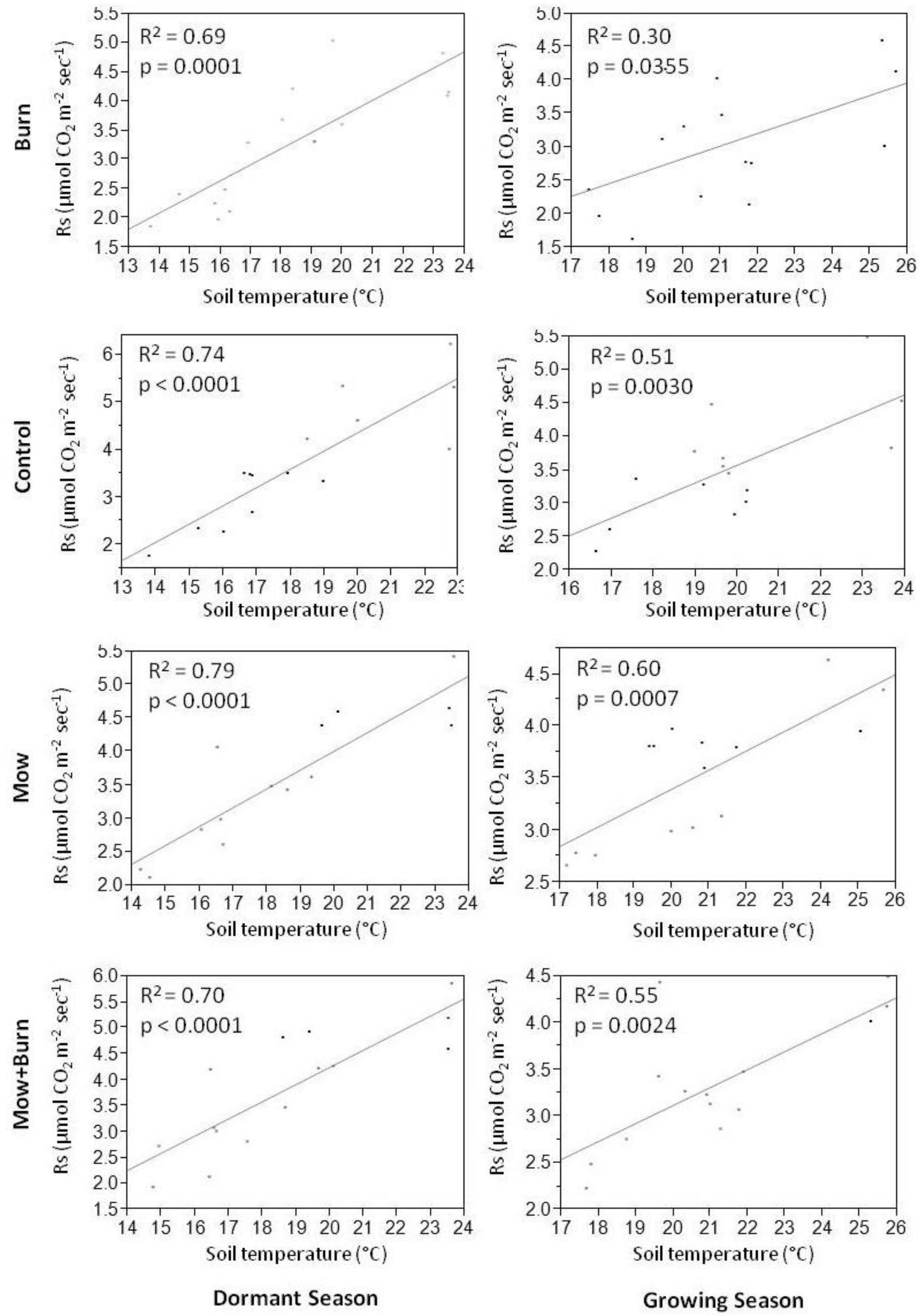


Figure 4-17. Seasonal (dormant and growing) linear regressions of the relationships between monthly mean soil $CO_2$ efflux rates ($R_s$) (µmol $CO_2$ $m^{-2}$ $sec^{-1}$) and soil temperature ($T_s$) (°C) for treatments at the Osceola National Forest. Each point represents monthly mean values per sample plot.

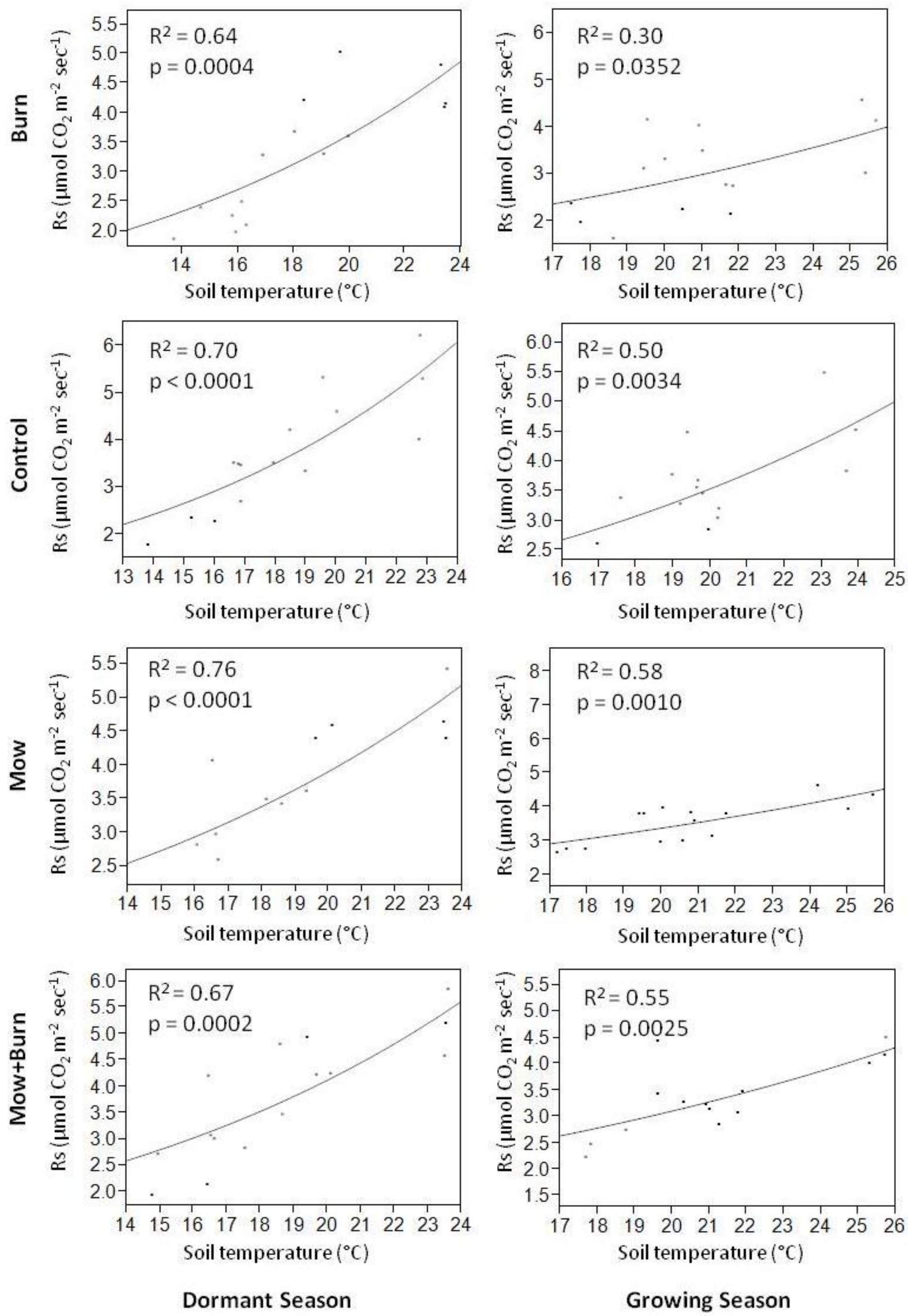


Figure 4-18. Seasonal (dormant and growing) non-linear regressions of the relationships between monthly mean soil $CO_2$ efflux rates ($R_s$) (µmol $CO_2$ $m^{-2}$ $sec^{-1}$) and soil temperature ($T_s$) (°C) per treatment at the Osceola National Forest. Each point represents monthly mean values per sample plot.

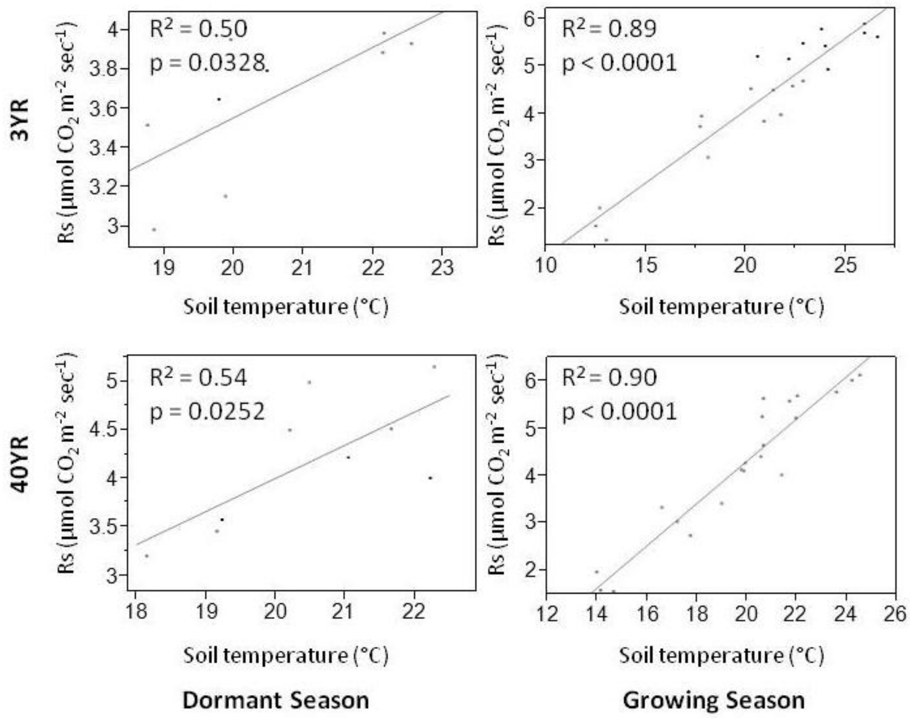


Figure 4-19. Seasonal (dormant and growing) linear regressions of the relationships between monthly mean soil $CO_2$ efflux rates ($R_s$) (µmol $CO_2$ $m^{-2}$ $sec^{-1}$) and soil temperature ($T_s$) (°C) per treatment at the Austin Cary Forest. Each point represents monthly mean values per sample plot.

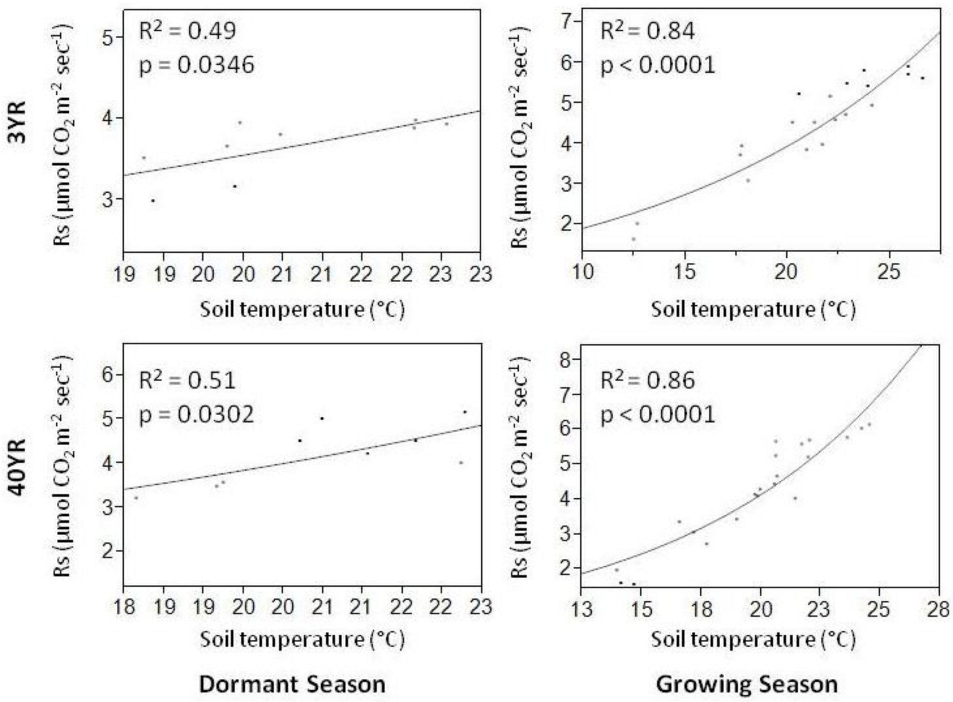


Figure 4-20. Seasonal (dormant and growing) non-linear regressions of the relationships between monthly mean soil $CO_2$ efflux rates ($R_s$) (μmol $CO_2$ $m^{-2}$ $sec^{-1}$) and soil temperature ($T_s$) (°C) per treatment at the Austin Cary Forest. Each point represents monthly mean values per sample plot.

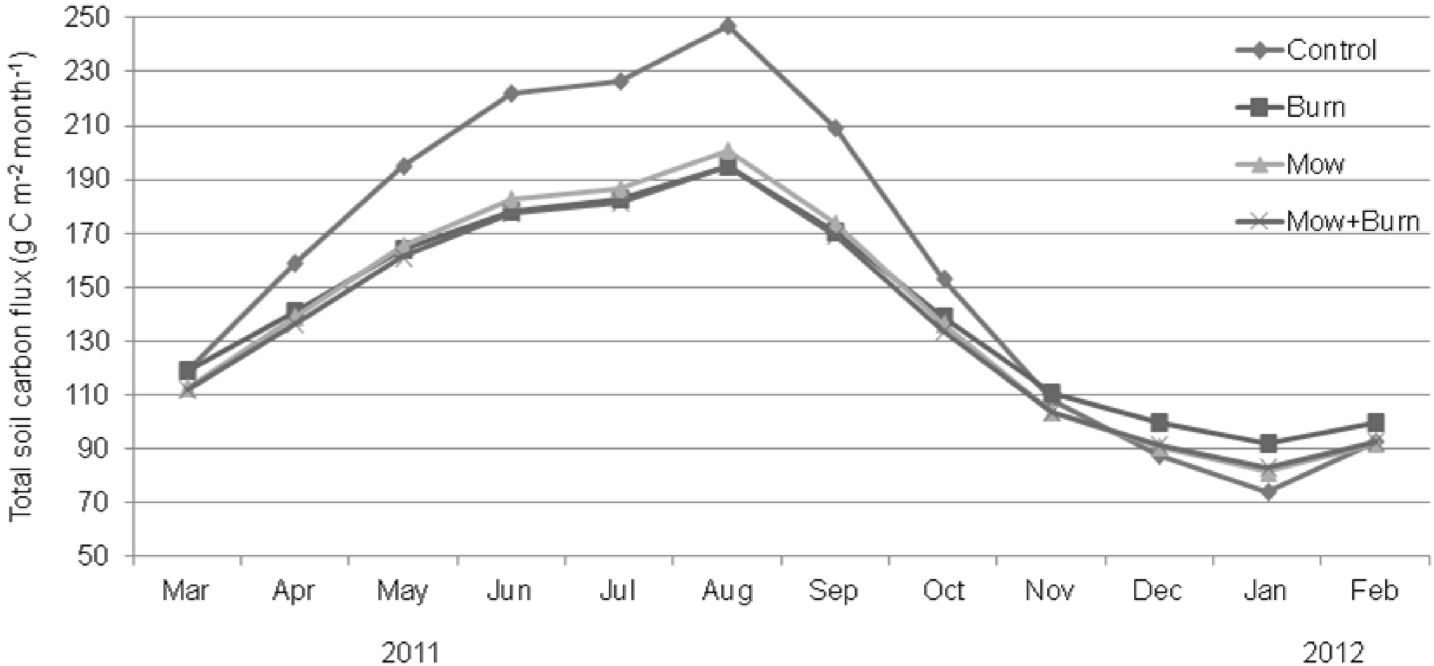


Figure 4-21. Predicted monthly total soil carbon flux (g C $m^{-2}$ $month^{-1}$) for the four treatments at the Osceola National Forest near Lake City, Florida, USA for the period March 2011 – February 2012. Flux values were predicted using treatment specific linear models of soil $CO_2$ efflux response to changes in soil temperature. Model input hourly mean 10 cm depth soil temperature for the period of March 2011 - February 2012 was recorded at the nearby Macclenny, Florida Automated Weather Network (FAWN) station.

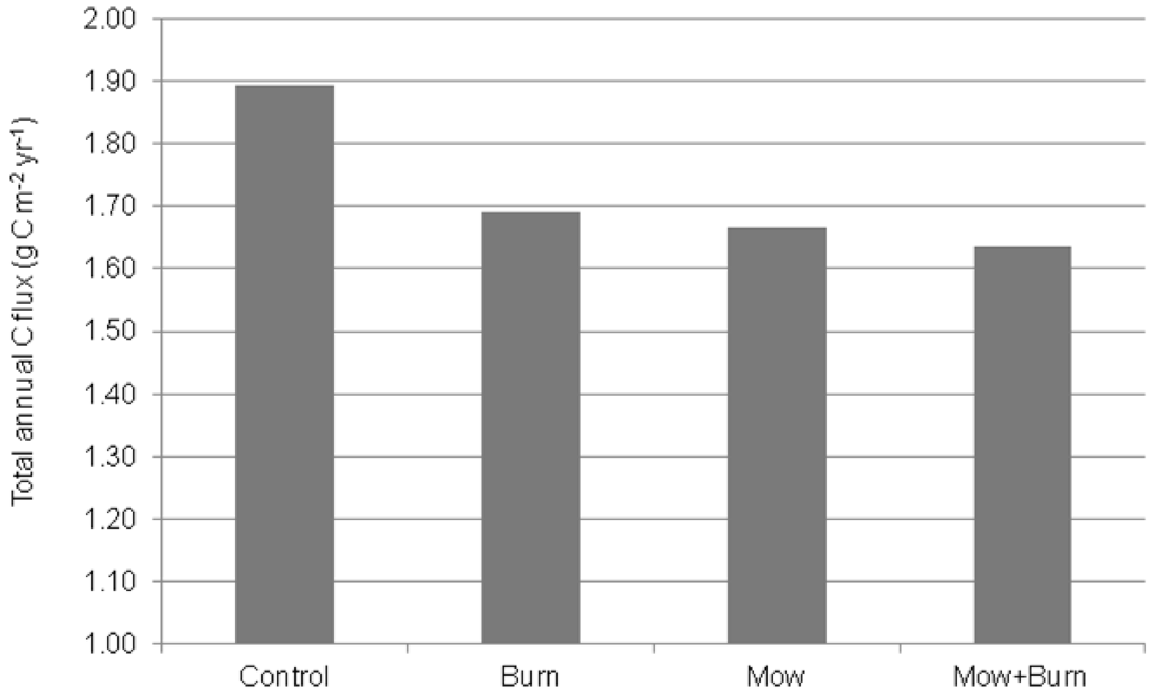


Figure 4-22. Predicted annual total soil carbon flux (kg C $m^{-2}$ $yr^{-1}$) for the four treatments at the Osceola National Forest near Lake City, Florida, USA for the period of March 2011 – February 2012. Flux values were predicted using treatment specific linear models of soil $CO_2$ efflux response to changes in 10 cm soil temperature. Model input hourly mean soil temperature was recorded at the nearby Macclenny, Florida Automated Weather Network (FAWN) station.

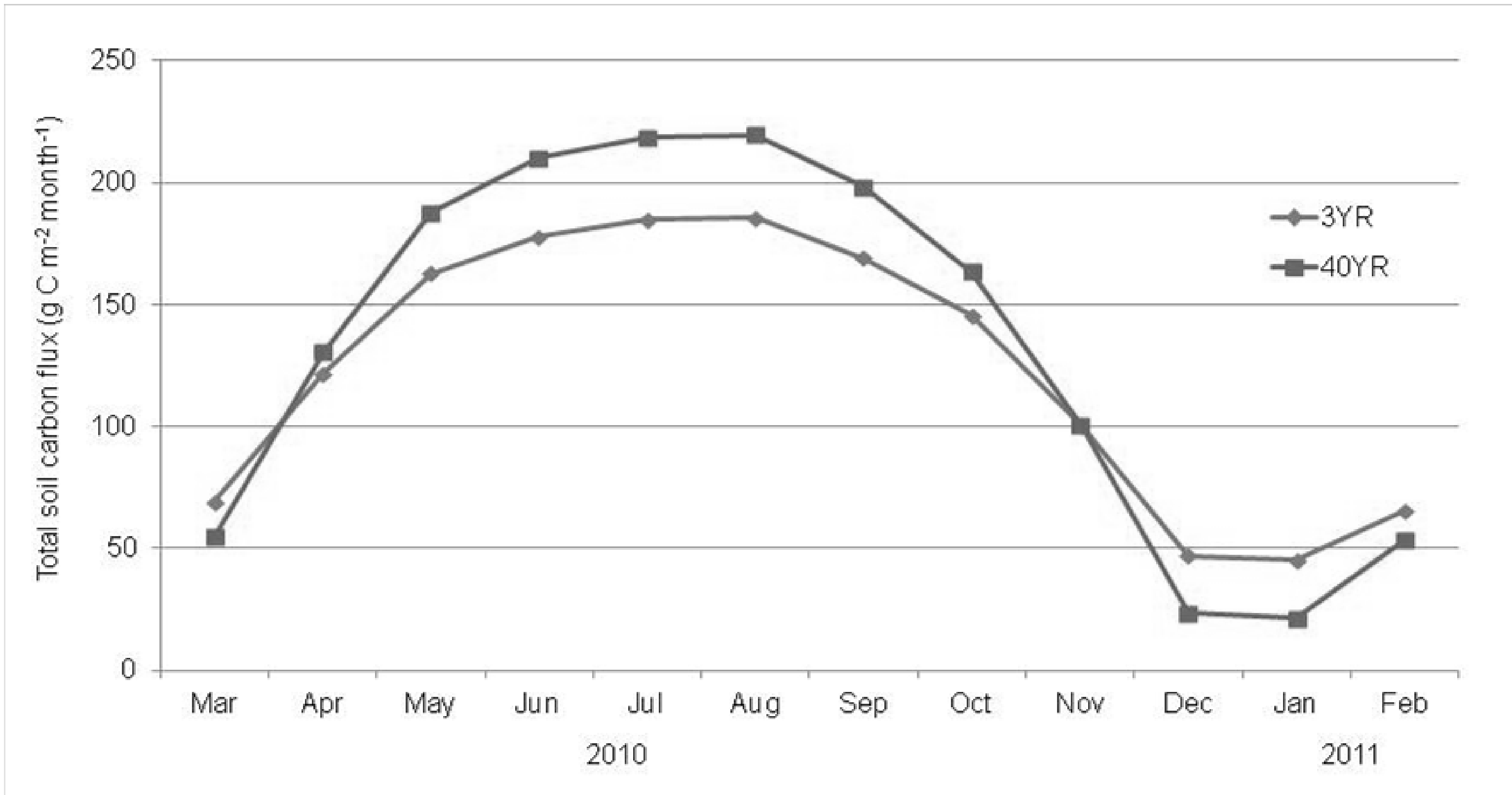


Figure 4-23. Predicted monthly total soil carbon flux (g C $m^{-2}$ $month^{-1}$) for the two prescribed fire treatments at the Austin Cary Forest, Gainesville, Florida, USA for the period of March 2010 – February 2011. Flux values were predicted using treatment specific linear models of soil $CO_2$ efflux response to changes in soil temperature. Model input hourly mean 10 cm depth soil temperature recorded at the Putnam Hall, Florida, FAWNS station.

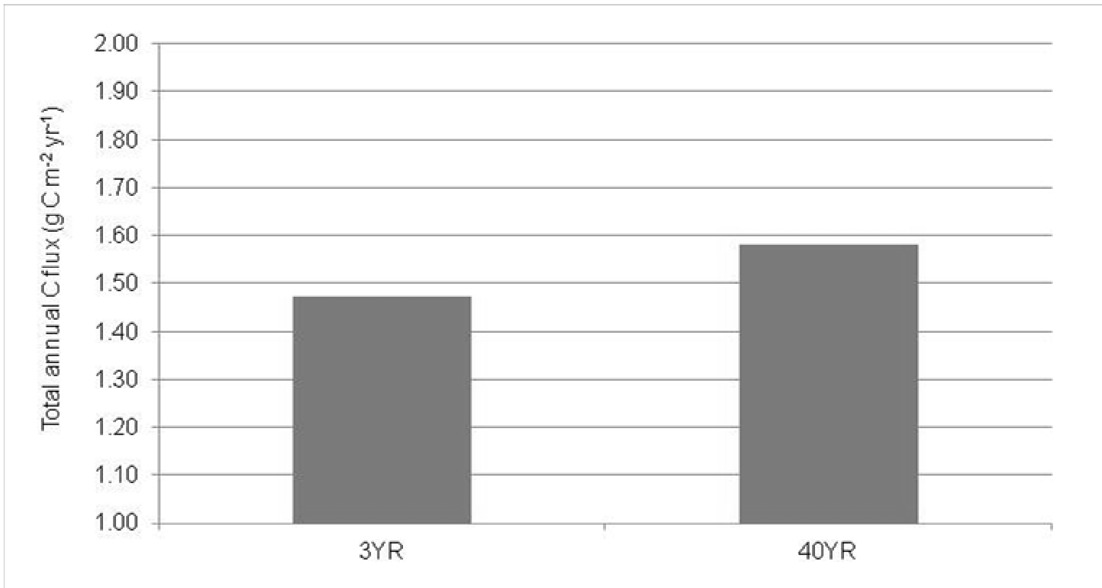


Figure 4-24. Predicted annual total soil carbon flux (kg C $m^{-2}$ $yr^{-1}$) for the period of March 2010 – February 2011 for two prescribed fire treatments at the Austin Cary Forest near Gainesville, Florida, USA. Flux values were predicted using treatment specific linear models of soil $CO_2$ efflux response to changes in 10 cm soil temperature. Model input hourly mean soil temperature recorded at the Putnam Hall, Florida Automated Weather Network (FAWN) station.

CHAPTER 5
SUMMARY AND SYNTHESIS

## Summary

The results of the studies presented here expand the understanding of the influence of prescribed fire and mechanical fuels mastication treatments on soil $CO_2$ efflux rates in Florida old-field and flatwoods forests.

In Chapter 2, the results of a nearly two year study of soil $CO_2$ efflux rates at Tall Timbers Research Station found differences in rates among three different prescribed fire management regimes. It was found that prolonged management regimes utilizing frequent prescribed fire in loblolly pine - shortleaf pine old-field forests drive large shifts in forest structure and composition that result in reduced monthly mean soil $CO_2$ efflux rates as compared to a management regime of prolonged fire exclusion. Average monthly mean soil $CO_2$ efflux rates in the annually burned forests were approximately 37% lower than those in the long-unburned forests. In addition, estimated annual soil carbon fluxes based on the response of monthly diurnal soil $CO_2$ efflux rates to changes in soil temperature, found that total annual soil carbon efflux was lower in the annually (1069 g $m^{-2}$ $y^{-1}$) and biennially (1268 g $m^{-2}$ $y^{-1}$) burned forests than in the unburned forest (1688 g $m^{-2}$ $y^{-1}$).

In Chapter 3, a seven month litter manipulation experiment in a loblolly pine - shortleaf pine old-field forest supported the conclusions of Chapter 2: frequent prescribed burning reduces soil $CO_2$ efflux rates relative to fire exclusion, with annual burning resulting in lower soil $CO_2$ efflux rates than biennial burning. In addition, soil $CO_2$ efflux rates in frequently burned old-field forests respond positively to one-time elevated litter inputs, with higher rates persisting for at least several months following litter additions. Soil $CO_2$ efflux rates in the same forests do not appear sensitive to short-term reductions in leaf litter inputs, although longer-term studies may yet identify seasonal relationships between litter inputs and soil $CO_2$ efflux rates. The results of this study indicate that prolonged prescribed fire management regimes result in changes in the importance of aboveground litter inputs on the heterotrophic sources of soil $CO_2$ efflux, with frequently-burned sites, rather than long fire excluded sites, much more sensitive to increases in litterfall.

In Chapter 4, a study in two mature flatwoods forests found that neither prescribed fire nor mechanical fuels mastication treatments, nor mechanical fuels mastication followed by prescribed fire significantly influenced mean soil $CO_2$ efflux rates. Prescribed fire and mechanical fuels mastication treatments at the Osceola National Forest study site were found to significantly increase monthly mean soil temperature. At the Austin Cary study site, a management regime of prescribed fire was shown to increase soil moisture content relative to a management regime of fire exclusion. These results, while indicating no direct influences on soil $CO_2$ efflux rates, suggest that prolonged periods of continuous management may affect soil carbon dynamics through persistent changes in the abiotic conditions that influence heterotrophic and autotrophic sources of soil carbon efflux. Further research is needed to understand the long-term implications of increased soil temperature in these systems, particularly in sites where mechanical fuels mastication treatments have occurred, as the fate and duration of the ecosystem effects of masticated fuel treatments are not well known.

In Chapters 2, 3, and 4, soil $CO_2$ efflux rates were generally strongly positively correlated with soil temperature and monthly mean ambient air temperature. These results are consistent with many previous studies of soil $CO_2$ efflux rates in multiple ecosystems (Raich and Schlesinger, 1992; Ryan and Law, 2005; Luo and Zhou, 2006). Given this correlation and the magnitude of total global soil carbon emissions (75 Pg C $yr^{-1}$), our results provide evidence of a need for continued research regarding the influence of changing global temperatures on soil $CO_2$ efflux rates.

Chapters 2, 3, and 4 all provided some non-conclusive evidence suggesting that seasonal variations, as well as prescribed fire and mechanical fuels mastication treatments, may influence the relative contributions of heterotrophic and autotrophic sources of soil $CO_2$ efflux. To better predict the effects of global climate change on soil $CO_2$ efflux rates, more research is needed to understand how autotrophic and heterotrophic sources of $CO_2$ respond to forest management practices, as well as to changes in elevated atmospheric $CO_2$ concentrations, temperature, moisture regimes, and forest vegetation. Our results suggest that future studies would benefit from both short and long-term sampling intervals that capture the daily, monthly, and seasonal variability in soil $CO_2$ efflux rates. In addition, cost-effective methods that allow for the partitioning of the components of heterotrophic and autotrophic sources of soil $CO_2$ efflux *in-situ* without disturbing site biotic or abiotic factors are greatly needed.

The research presented in these studies provides evidence suggesting that future models of southeastern US forest soil $CO_2$ efflux rates account for forest-type specific responses to management practices. In Chapters 2 and 3, a management regime of frequent prescribed fire in old-field forests resulted in conditions that supported lower soil $CO_2$ efflux rates and soil carbon emissions. In contrast, in Chapter 4, a prolonged prescribed fire management program at the Austin Cary flatwoods site did not significantly influence soil $CO_2$ efflux rates. While these studies provide insight into management influences on soil $CO_2$ efflux rates, it is important to remember that soil $CO_2$ efflux is only one component of the complex forest carbon cycle (Wardle et al., 2004). Additional research that assesses direct carbon emissions from prescribed fires, as well subsequent post-burn vegetative responses is needed to fully understand the implications of long-term prescribed fire and mechanical fuels mastication management programs on total ecosystem carbon dynamics and budgets.

## Synthesis

In the studies reported here it was predicted that a frequent prescribed fire management regime would result in reduced soil respiration rates relative to a management regime of fire exclusion. This hypothesis was based primarily on previous research describing the influence of prescribed fire on forest biomass, composition, and litter pools (Glitzenstein et al., 2012; Lavoie et al., 2010; Reid et al., 2012) and previous research describing the importance of those and similar factors in driving the autotrophic and heterotrophic sources of soil respiration rates (Ryan and Law, 2005; Kuzyakov, 2006; Lou and Zhou, 2006; Sulzman et al., 2012). The research of those authors and others was used to develop a conceptual model that identified a wide range of biotic and abiotic factors known to influence autotrophic, heterotrophic, and total soil respiration rates (Figure 5-1). As soil respiration is the sum of heterotrophic respiration from soil microbial metabolism and autotrophic respiration from live root and rhizosphere fungi activity, it was hypothesized that changes in aboveground vegetative characteristics caused by prescribed fire would have significant impacts on total measured soil respiration rates. In addition, it was hypothesized that mechanical fuels mastication treatments, due to their impact on aboveground vegetative biomass, structure, and forest floor characteristics, would also reduce soil respiration rates relative to untreated sites. To test these hypotheses, studies were established in loblolly pine - shortleaf pine old-field sites and longleaf pine - slash pine flatwoods sites managed with prescribed fire and mechanical fuels mastication (flatwoods only).

Following over three and a half years of measurement at multiple study sites, relationships were identified between soil respiration rates and forest management methods, vegetative characteristics, and abiotic conditions. To illustrate the influence of prescribed fire on soil respiration rates, a more specific conceptual model was developed based on the results of the studies reported here (Figure 5-2). The research reported here demonstrated that in the old-field forests, a forest management regime utilizing frequent prescribed fire, when maintained for an extended period of time, can result in significant shifts in ecosystem structure and composition as compared to a management regime of fire exclusion. It was determined that prescribed fire frequency can alter certain site biotic characteristics resulting in lower soil respiration rates. The results of these studies found that increasing prescribed fire frequency drives lower total aboveground living biomass, hardwood abundance relative to conifer abundance, and duff and litter accumulation (Figure 5-2). Reductions in aboveground living biomass were generally associated with lower soil respiration rates, likely due to lower autotrophic and heterotrophic soil respiration. Reductions in hardwood vegetative abundance were also generally associated with lower soil respiration rates. This was likely due to reductions in the quantity of deciduous hardwood leaf litter relative to conifer litter. Hardwood litter typically has higher nutrient content than conifer litter and the quality of leaf litter has been shown to positively influence heterotrophic soil respiration rates in previous studies (Luo and Zhou, 2006). Reductions in forest floor duff and litter accumulation likely resulted in lower heterotrophic soil respiration rates, as overall soil respiration rates were found in frequently burned sites to respond positively to increases in aboveground litter inputs. As none of the studies reported here attempted to explicitly partition the sources of soil respiration, we can only infer the specific responses of autotrophic and heterotrophic sources of respiration based on the results of the litter manipulations and previous studies in the literature.

The studies reported here also documented the importance of season, weather, and management activities on soil temperature and moisture content (Figure 5-2). Prescribed fire frequency and mechanical fuels mastication treatments were shown to influence soil temperature and soil moisture, largely due to changes associated with forest vegetative cover and forest floor exposure. While soil temperature and to a much lesser extent soil moisture, were shown to influence temporal variations in soil respiration rates, they did not explain differences in soil respiration rates among management regimes. This suggests that while soil temperature and soil moisture content are important factors influencing photosynthesis and belowground carbon allocation by plants and enzymatic activity by soil microbes, it is the effect of management activities on biotic characteristics that drives differences in overall soil respiration rates between different sites.

In contrast to the initial hypothesis, the results did not find mechanical fuels mastication treatments and prescribed fire frequency to reduce soil respiration rates in flatwoods sites. It is possible that in the flatwoods sites neither prescribed fire nor mechanical fuels mastication treatment frequency or management regime tenure were sufficient to drive changes in site biotic or abiotic characteristics that would result in changes in total soil respiration rates.  It is also possible that treatments in the flatwoods sites may have induced compensatory shifts in the response of autotrophic and heterotrophic sources of soil respiration that masked changes in overall soil respiration rates.

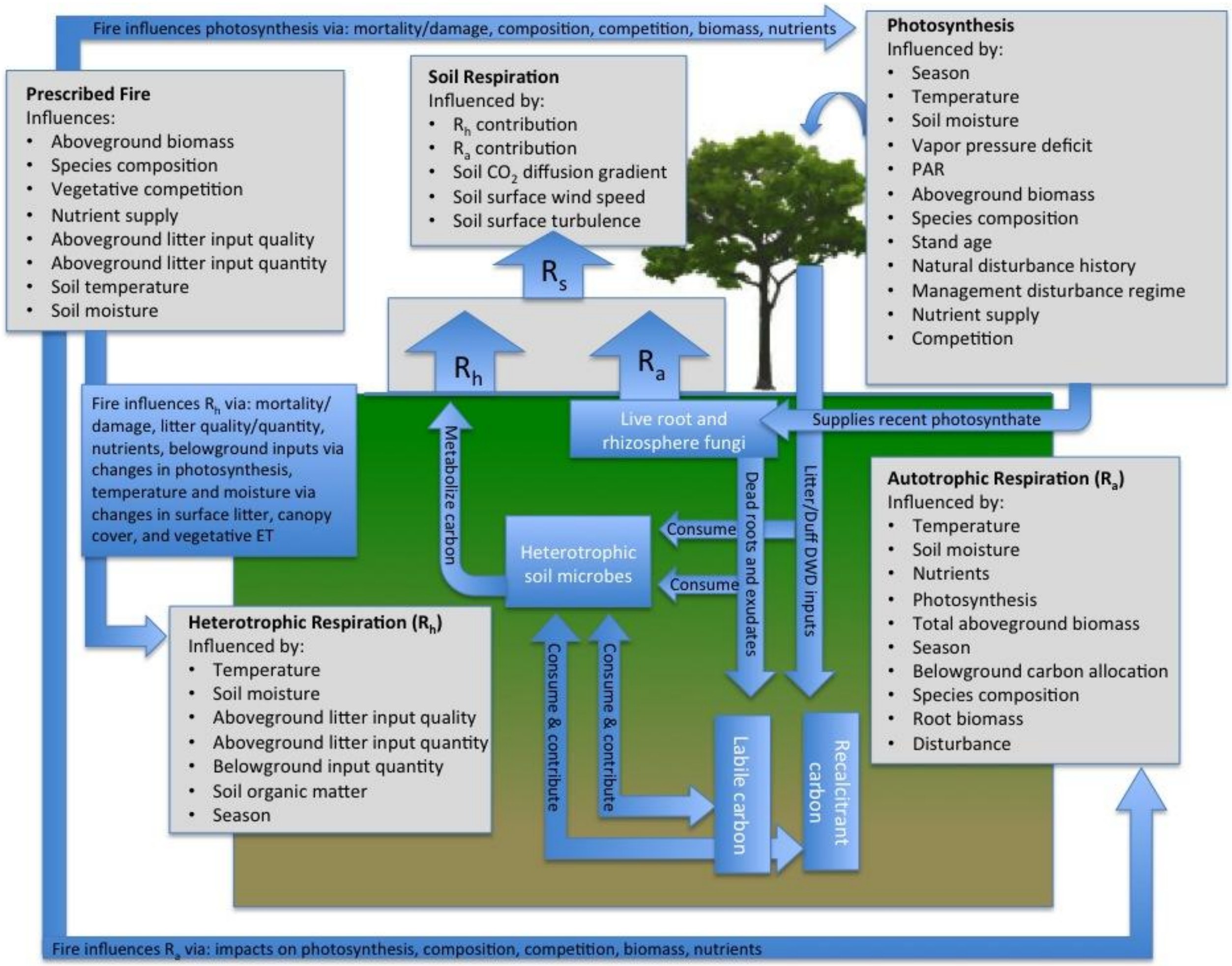


Figure 5-1. Conceptual model of the sources and drivers of soil respiration rates in forested ecosystems managed with prescribed fire. Depicted drivers and sources were determined through a survey of previously published research. Illustration by David Godwin.

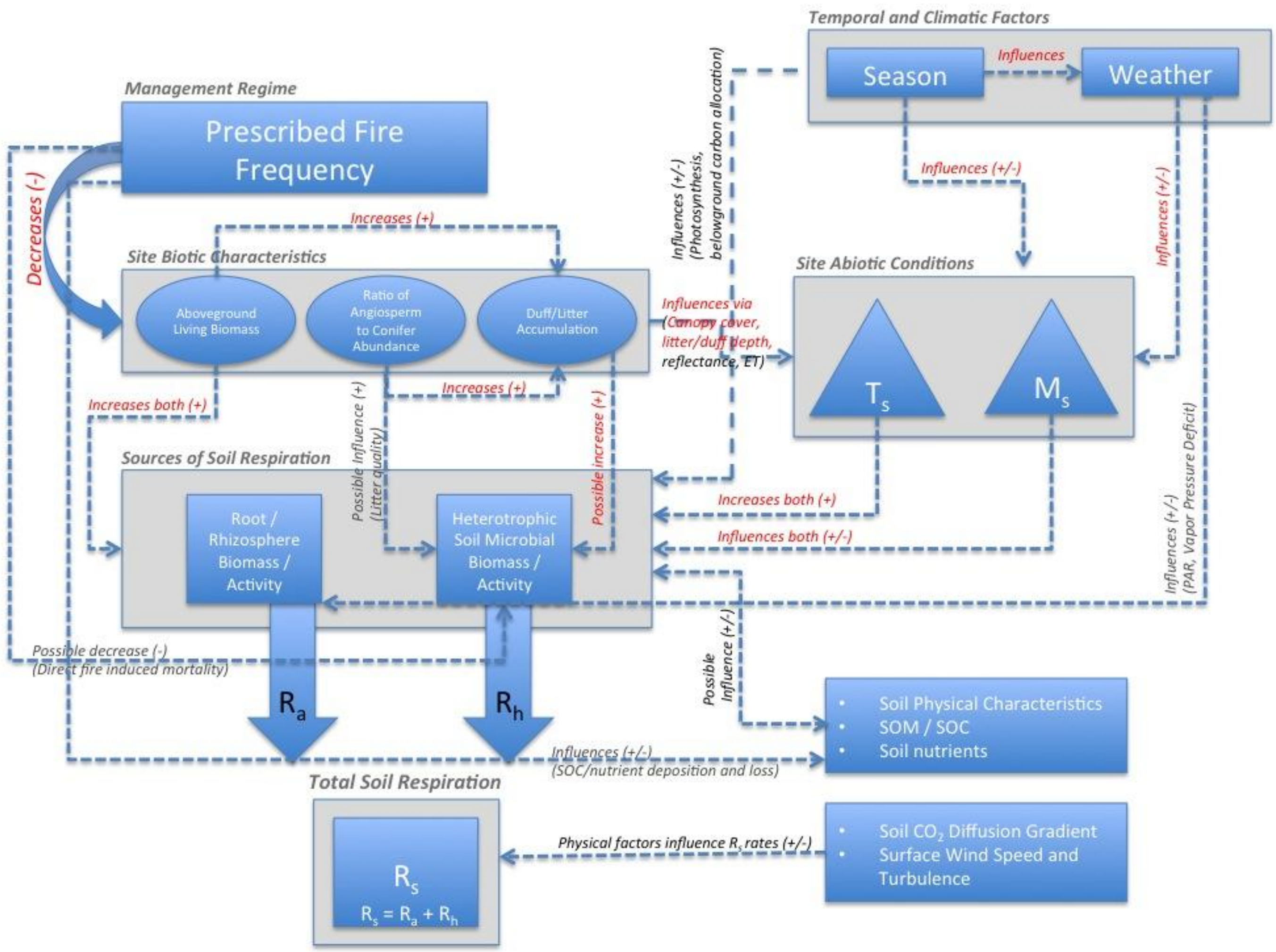


Figure 5-2. Conceptual model of the influence of prescribed fire frequency and seasonal and environmental factors on soil respiration rates. Red italicized text indicates relationships among factors that were quantified in the studies reported in this document. Black italicized text indicates possible relationships that were supported by the results of previous studies in the literature. Illustration by David Godwin.

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# BIOGRAPHICAL SKETCH

David Robert Godwin grew up in Tallahassee, Florida. A life-long naturalist with a keen appreciation for maps, he earned his Bachelor of Science in geography from Florida State University in 2003. After discovering an interest in forest management and fire ecology while working on public wildlife management areas, he started graduate school in 2007 and in 2008 completed a Master of Science degree from the School of Forest Resources and Conservation at the University of Florida. He began his doctorate in 2009 under the tutelage of Dr. Leda Kobziar at University of Florida and successfully defended his dissertation in 2012.

David is married to Katie (Kight) Godwin of Orange Park and St. Augustine, Florida. Their delightful son Benjamin was born in Jacksonville, Florida in 2012. They currently reside in St. Augustine, Florida.