

IMPACTS OF PRESCRIBED FIRE ON WATER USE EFFICIENCY AND
PHOTOSYNTHETIC CAPACITY IN UPLAND PINE AND OAK
FORESTS

by

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ABSTRACT OF THE THESIS

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A comparative analysis of the impacts of prescribed fire on an oak/pine and two pine dominated forest in the Northeastern US was conducted. Effects of prescribed fire on water use and photosynthetic capacity of overstory pines were estimated by sap-flux rates and photosynthetic measurements on *Pinus rigida* Mill. Study sites had two sap-flux plots, one experiencing prescribed fire and one control plot. Data were collected between 2011-2013. Control and burned plots were compared both before and after the fires. We found that photosynthetic capacity in terms of Rubisco-limited carboxylation rate (V_{Cmax}), carboxylation efficiency, and intrinsic water use efficiency were significantly greater in the burned vs. the control plot post-fire, while instantaneous internal to external CO_2 concentration was significantly lower. Furthermore, pines in the pine dominated stands were less affected than pines in the mixed oak/pine stand, as $\delta^{13}C$ and isotopic water use efficiency were significantly lower and water use efficiency and carboxylation efficiency were increased in the oak/pine stand post-fire compared to the control plot, but not in the pine dominated stands. Average daily sap-flux rates exhibited different patterns for each stand type due to differences in fuel consumption, increasing compared to control plots in pine dominated sites and decreasing in the oak/pine stand. Finally, when analyzed on the canopy scale, pines in pine-dominated forests were better suited to capitalize on available resources, as they were more sensitive to changes in vapor pressure deficit (VPD) in regards to transpiration, while pines in the oak/pine forest were unaffected in terms of stomatal responses to VPD. Therefore, prescribed fire affects physiological functioning and water use of pines, but many other factors can alter the degree to which these trees

are affected, because results are dependent on stand type and fuel consumption differences, making broad-scale generalizations on the effects of prescribed fire difficult.

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Introduction

Disturbance regimes can play key roles in shaping forest ecosystems and modifying the biotic processes that occur within them. Disturbances such as windthrow, fire, and pest infestations that lead to defoliation or mortality are all contributing factors in ecosystem dynamics (Lorente et al. 2013; Panayotov et al. 2011; Simard et al. 2011; Thomas et al. 2010). These disturbance regimes create canopy gaps, alter competitive relationships through changes in resource partitioning, modify species composition, and/or affect the health of individual trees, which in turn affect their biotic processes and can also modify the physical and chemical composition of the soil (Esser et al. 2002; Granged et al. 2011; Łaska 2001; Oliver and Larson 1990; Thomas et al. 2010). Therefore, studying effects of such disturbance regimes on different ecosystem types has become a necessary tool in understanding the use of natural resources of forests, along with forest management practices and forest health.

Fire plays a major role in many forest ecosystems around the globe. Some short-term studies of post-fire ecosystem responses have found both positive and negative changes in individual tree productivity (Reich et al. 2001; Renninger et al. 2013), as well as increases in growth following fire (Boerner et al. 1988; Gilbert et al. 2003). These changes in physiological responses can be attributed to a variety of factors. A possible mechanism in which productivity of over-story trees could be increased as a result of fire is through mortality of the understory. In many species, fire intensity and flame residence time are directly correlated to the amount of mortality caused by a specific fire (Bova and Dickinson 2005). Thus, for prescribed fires, which are generally low intensity fires, an

increase of resources may be available post-fire for overstory trees because these lower intensity fires generally cause mortality in understory shrubs, herbaceous species, and saplings (Peterson and Ryan 1986; Rozas et al. 2011; Ryan and Reinhardt 1988).

In addition to reduced competition, there are a variety of other secondary effects of fire that could affect tree growth and productivity. While prescribed fires are generally ground fires, they can sometimes reach relatively high intensities. These varying relative intensities can have differing effects on the ecosystem. For example, a low intensity fire could increase soil water repellency, while a high intensity fire could increase the soil's pH and affect its aggregate stability (Granged et al. 2011) which is dependent on chemical, physical, and biological factors (Mataix-Solera et al. 2011). Furthermore, many studies suggest that fire events can modify the amount of nutrients and composition in the soil by converting certain organic forms of phosphorus and nitrogen into an inorganic form that are more readily available to plants (Certini 2005; Covington and Sackett 1992; Gray and Dighton 2006; Gray and Dighton 2009).

The physical extent of a fire's effect on biological processes of individual trees can also extend belowground and include tree root-fungal interactions and belowground microbial processes. In addition to the negative effects that severe crown fires have on overstory tree production, low intensity ground fires, which begin to smolder and burn organic matter, could cause severe root damage, thus lowering the amount of water and nutrients the tree is capable of acquiring (Thomas et al. 2010). However, Clark et al (2010) found that most fires from 2004-2010 in the region of this study did not burn the organic horizon, where most shallow fine roots would be located. Finally, fire can have severe impacts on soil microbial communities. For example, following a fire, microbial

composition changes and biomass declines, and does not rebound for a number of years (Certini 2005; Mabuhay et al. 2003). Since microbes break down dead matter in the soil, releasing nutrients, a decline in microbial biomass could affect plant productivity, due to lower levels of available nutrients in the soil. Thus, less effective root systems due to physical damage from the fire, coupled with less nutrient availability due to decreased microbial decomposition processes could create a more nutrient poor soil.

Due to the inherent nature of fire, and the many variables that can affect the extent, intensity, temperature, and combustion capabilities of a fire, it is important not to assume that all prescribed fires act uniformly. While meteorological conditions such as moisture and temperature are large drivers of fire behavior, total fuel loading and small-scale variations in fuel loading have shown to have an overriding effect (Anderson 1982; Thaxton and Platt 2006). In fact, it has been found that nearly 75% of fuel combustion can be inferred from pre-fire fuel loading conditions (Clark et al. 2013). Furthermore, not just the quantity, but the quality of fuel loading may play a vital role in fire ecology. Fuel loading, or the amount of combustible material along the forest floor, can be modeled via various parameters including total fuels in tons per hectare, partitioned into dead and live fuels and depth of fuel bed (the forest floor where the fuels accumulate) (Anderson 1982). However, different fuel types may not behave equally. Another determining factor is the diameter of the dead material as fuels with a larger diameter are less likely to combust (Cohen and Deeming 1985). A fire that burns mainly shrub stems can effectively reduce competition compared to a fire that more readily combusts forest floor materials, which would more effectively act as a fertilizer. Therefore, even in similar forest types, fires and their associated effects can vary due to large-scale meteorological

differences, microclimates, and fuel loading. Thus, it is important to study multiple fire events to better understand which physiological effects are generalizable across forest types and organic combustion, as opposed to effects that are more specific to an individual fire.

The New Jersey Pine Barrens is a unique ecosystem, located in the coastal plains of southern NJ. It is generally a *Pinus rigida* Mill. (pitch pine) and *Quercus spp.* (oak) dominated forest ecosystem, characterized by frequent disturbance regimes of both wildfire and prescribed burns (Scheller et al. 2011). These prescribed burns are conducted by the NJ Forest Fire Service (NJFFS), with a goal of burning over 8000 hectares annually. This is done within a designated burn block, which vary in size, but are usually many hectares. Given this unique situation, this study seeks to capitalize on the logistics of these fires, and monitor the effects that they have on overstory pines across multiple ecosystems. By measuring leaf-level photosynthesis rates at both control and burned plots before and after the fire, it can be determined if a reduction in competition or combustion of organic material could lead to an increase in photosynthetic responses of overstory pines. Thus, needle nutrient data will also be analyzed to account for changes in nutrient loading as a result of the fire. Also, by monitoring sap-flux and meteorological data at all of these sites both before and after the fires, the hypothesis that water use is increased due to increased productivity due to nutrient increases and/or competition reduction of the understory can also be tested. In our previous study, it was demonstrated that after an initial decrease in water-use following the fire, there was actually an increase persisting until the late summer (Renninger et al. 2013) Thus, by replicating this experiment across three fires at different stand types, this study aims to build upon our previous study to

assess whether or not these results are reproducible across the dominant forest types in this region.

Materials and Methods

Site Descriptions

Study sites were located in the Pinelands National Preserve, which is a forested coastal plain ecosystem, covering 450,000 hectares in central and southern New Jersey. The soils at each site are generally comprised of well drained, acidic, nutrient poor sands, with a characteristic low water holding and cation exchange capacity (Schäfer 2011). The topography is relatively flat, with a mean elevation of 33 m above sea level. Within each site, there were two sub-plots, one control plot and one burned plot. For the three years of study, 2011, 2012, and 2013, mean annual temperature was 13.0, 13.1, and 11.9 °C, with 1358, 997.2, and 1085.7 mm mean annual rainfall respectively. Due to the proximity of each coupled control and burned plot, the meteorological differences between plots for each respective site were assumed to be negligible.

The oak/pine site was located within the Rutgers Pinelands Research Field Station (also known as Silas Little Experimental Forest, SL), in Pemberton, NJ, USA. The SL control plot was located at N 39° 55'0", W 74° 36'0" and its associated burned plot was located 350 m to the west within a NJFFS burn block. This study site was composed of a mixed oak/pine forest, with an oak understory. The species composition was comprised of *Quercus prinus* L. (chestnut oak), *Quercus velutina* Lam. (black oak), *Quercus alba* L. (white oak) and *Pinus rigida* Mill (pitch pine, Table 1). The first pine dominated site was located in the Brendan T. Byrne State Forest (BTB), in New Lisbon, NJ, USA (39° 53'

27.66 ° N 74° 34' 46.63" W). The BTB burned plot was located 250 m northwest of the BTB control plot, within a NJFFS burn block. This study site is a pitch pine dominated forest with some overstory oaks and scrub oak understory (Table1). The second pine dominated site was located near the Cedar Bridge Fire Tower (CB), in Lacey Township, NJ, USA (N 39° 84' 21' W° 74 37' 77.92'). The control plot for CB was located 800 m south-southeast of the CB burned plot, which was within a NJFFS burn block. This study site was a pure pitch-pine stand, with a scrub oak understory. Table 1 shows species composition, stand density, and tree sizes, along with the measurement plot size for each of the plots and the date each site was burned.

Meteorological Data

Each site was equipped with meteorological instruments that were connected to Campbell Scientific data loggers (Campbell Scientific Inc, Logan, UT, USA), in which half hourly averages or totals, based on the instrument, were calculated and stored. Soil moisture, was measured with four 0-30 cm CS616 Water Content Reflectometers (Campbell Scientific Inc), placed at the four cardinal directions from the center of each plot. At the two pine dominated control plots, soil temperature was also measured using four 107 temperature probes (Campbell Scientific Inc). At both the oak/pine SL control plot and pine dominated BTB control plot, a Licor LI190SB quantum sensor (Licor Inc Bioscience, Lincoln, NE, USA) was used to measure photosynthetic photon flux density in the understory (PPFD, $\mu\text{mol m}^{-2} \text{s}^{-1}$) below the canopy. Throughfall was collected at each control plot using a Texas Electronics TE525M tipping rain gauge (Dallas, TX, USA) and starting in March 2013, four 5" ClearVU Rain and Sprinkler Gauges (Taylor Precision Group, LLC, Oakbrook, IL, USA) were installed at each of the two CB plots,

and four were installed in June of 2013 at each SL plot. The tops were then fitted so that the gauges were as level as possible. Each control plot also measured relative humidity (%) and air temperature in °C in the canopy (HMP45C, Vaisala Inc, Helsinki, Finland). These measurements were then used to calculate saturated vapor pressure (SVP) and vapor pressure deficit (VPD). SVP (in kPa) was calculated using the air temperature data, while VPD was calculated according to an equation derived from Goff and Gratch (1946).

Understory and Forest Floor Consumption

Fuel consumption data were derived from subtraction of post-fire biomass loadings from pre-fire, collected from 1 m²-clip plots. At all three NJFFS burn blocks, in which the burned plots for all three sap-flux sites were located, 20 1 m² clip plots were randomly selected. Inside each clip plot, fuels were collected and separated into these two main categories: forest floor and shrubs. The forest floor materials were comprised of fine fuels, reproductive parts such as acorns and pinecones, and coarse wood fuels. Understory vegetation was comprised solely of standing dormant shrub stems since no live foliage was present during the dormant season. The categories were separated, dried at 70°C for a minimum of 72 hours, and then weighed. By comparing the fuel loading before and after the fire, the amount of fuels consumed in each fuel class was determined. Thus, using total consumption values, quantitative data were determined, while analysis of individual fuel categories allowed for qualitative assessment.

Leaf Nutrient and Isotope Analysis

Needles from the same branch as the needle samples measured for photosynthesis were analyzed for internal concentrations of nitrogen, phosphorus, potassium and magnesium. This was done to quantitatively determine if overstory trees were able to acquire more nutrients from soils following prescribed fire. Furthermore, groups of senesced oak and pine leaves were collected from tree branches and forest floor (when sufficient amounts were not available on the branches), in the winter of 2014 to determine the different nutrient loadings of litter on the forest floor and the amount of nutrient translocation during leaf senescence. Three batches of each dominant oak species (*Q. prinus*, *Q. velutina*, *Q. coccinea*, and *Q. alba*) and the one pine species were collected for each SL burned and control plots, while three batches of pine needles were collected at both CB burned and control plots, totaling 12 pine samples and 24 oak samples. Nutrient contents were determined by the University of Massachusetts, Amherst, Soil and Plant Tissue Testing Laboratory (Amherst, MA, USA). Preparation of the samples included cleaning the samples of dead matter and wood. The samples were then air dried for at least 24 hours, and then shipped to the lab for analysis. Furthermore, the leaves measured for photosynthesis were sent to University of California, Stable Isotope Facility (Davis, CA, USA) for carbon and nitrogen isotopic analysis. In some cases, extra samples from the same branch were added, so that there would be enough matter for analysis. Samples were dried in an oven, ground to powder via a Spex Certiprep 80000 Mixer/Mill (Metuchen, NJ, USA), weighed into tin capsules and sent out to the lab for analysis. Nitrogen and carbon concentrations (C% and N% respectively) were determined as well as carbon isotopic data, which were used to calculate intrinsic water use efficiency, the

ratio between external and internal concentrations of CO₂ (C_i/C_a), the discrimination factor ($\Delta\text{‰}$) and $\delta^{13}\text{C}$ of the needle ($\delta^{13}\text{C}$).

Photosynthesis Data

Along with meteorological and sap-flux data, photosynthetic parameters were collected and compared using analysis of variance both before and after the fires. This was done by extracting parameters from light response-net assimilation, as well as net assimilation to leaf internal CO₂ concentration ($A-C_i$) curves, using a Licor 6400 XT Infrared Gas Analyzer (Licor Inc Bioscience). The $A-C_i$ curves are measures of photosynthetic rates under a range of CO₂ concentrations within the leaf at saturating light levels ($1500 \mu\text{mol m}^{-2} \text{s}^{-1}$). Light response curves are measures of photosynthetic rates under a range of light intensities at ambient CO₂ concentration (set at 400 ppm). Measurements were taken during each growing season, as well as before and after each fire. To obtain each measurement, branches were cut from the tree using a pole pruner (Jameson LLC, Clover SC, USA). The branches were then re-cut under water to ensure water flow resumed. Finally, after the measurements were complete, the leaf material within the chamber was stored in sealed plastic bags until they were scanned via an Epson Perfection V30 flatbed scanner (Epson, Long Beach, CA, USA). By using Image J (Scion Image, Frederick, MD, USA), areas were determined using threshold analysis, and a 1 cm^2 reference square. The leaf area estimates within the chamber were then used to correct the measurements of the LICOR 6400.

Deriving Parameters from Photosynthesis Data

After collection of the photosynthetic data, photosynthetic parameters were inferred from the curves that are described and defined in Table 2 (Farquhar et al. 1980). From the light response curves, maximum assimilation, quantum yield, light compensation point and dark respiration rate were calculated using Sigma Plot version 11.0 (Systat Software Inc, Chicago IL, USA). For the A-Ci curves, the same methods as the light curve were used, extracting maximum assimilation, carboxylation efficiency, and CO₂ compensation point. However, in conjunction with the parameters extracted via linear curve fitting, maximum Rubisco-limited carboxylation rates (V_{Cmax}), maximum electron transport-limited carboxylation rates (J_{max}), and carboxylation rates limited by triose phosphate utilization (TPU) were also obtained using non-linear regressions (Farquhar et al. 1980; Harley and Sharkey 1991; Sharkey 1985) that were optimized via a best fit in attempt to minimize the least sums of squares between modeled and measured data. Measurements were made under a range of temperature conditions; thus, V_{Cmax} and J_{max} were corrected to a standard temperature of 25 °C via equations derived from Campbell and Norman (1998) and Bernacchi et al (2003) respectively. Finally, instantaneous, leaf-level parameters including stomatal conductance, transpiration, water use efficiency, and internal to ambient CO₂ concentrations (C_i/C_a) were extracted from photosynthesis measurements taken at saturating light conditions (PPFD >1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$) and ambient CO₂ chamber conditions (400 ppm).

Sap-Flux Measurements

To quantify the amount of water used by overstory pines, the Thermal Dissipation (TD) method was used (Granier 1987). Individual pines were selected to be a

representative sample of the size distribution of the stand, while accounting for a large enough diameter at breast height (1.35 m above ground, DBH in cm) to accommodate the sensor lengths. At all sites, *P. rigida* individuals with a DBH greater than 10 cm were fitted with 2 cm long sensors (Table 1), individuals larger than 30 cm in DBH were fitted with two 2 cm long sensors one at the 0-2cm sapwood depth range and another at the 2-4cm range to account for radial variation of sap-flux (Phillips et al. 1996).

The TD sap-flux sensors were placed approximately at 1.3-1.5 m from the ground at azimuthal locations of 0°. The heated sensors were placed on average 10 cm above the reference sensors, to minimize influence of a temperature gradient along the trunk of the tree. The installation of the TD sensors is outlined by Renninger and Schäfer (2012). Sap-flux sensors were connected to AM16/32 multiplexers and relayed to dataloggers (Campbell Scientific Inc.). The dataloggers collected data every 30 seconds and 30 minute averages were stored. The raw, differential voltage data were then converted to sap-flux rates (J_s ; $\text{kg m}^{-2} \text{s}^{-1}$) using a calibration equation originally devised by Granier (1987):

$$J = 0.119 \times \left(\left(\frac{\Delta T_{\max}}{\Delta T} \right) - 1 \right)^{1.23} \quad \text{Eq. (1)}$$

Where ΔT_{\max} is the greatest recorded difference between the heated and reference TD probes (ie. when there was no water moving) such as when VPD is less than 0.5 kPa for more than 2 hours, PPFD is approximately 0, temperature is not too low ($> -5^\circ \text{C}$) to avoid frozen stems, and ΔT is the difference in temperature during sap-flux movement.

Calculating Sapwood Depths

In order to scale sap-flux to whole tree and canopy transpiration, sapwood area is required. Thus, by analyzing 10 pitch-pine core samples taken in 2011 using an increment borer (Haglof Incorporated, Sweden), linear regressions were devised to find relationships between diameter at breast height (1.3 m above the ground, DBH) and sapwood area (A_{SW}) sapwood depth (D_{SW}) heartwood depth (D_{HW}), and heartwood area (A_{HW}). The equations used to calculate these biometric parameters can be found in Table 3. Two separate relationships were devised and separated by diameter class. For individuals with a DBH lower than 5.4 cm, it was assumed that the entire wood area was sapwood. To determine bark depth (D_{BK}), a section of the bark for 20 trees was carved out, and the D_{BK} was manually measured to the nearest 0.1 mm using a ruler. For the trees with a DBH lower than 5.4 cm, a D_{BK} of 0.35 cm was assumed, as the linear relationship held true for the larger trees, and reached a minimum D_{BK} around 0.35 cm.

Scaling Up Sap-Flux

In order to account for radial patterns in sap-flux rates in *Pinus* species that are non-porous, the ratio of inner sensor sap-flux rates (see Table 1) to outer sensor sap-flux rates were taken. It was found that on average, inner sapwood was moving water at 0.55 ($\text{g H}_2\text{O m}^{-2} \text{ sapwood area s}^{-1}$) times the rate of the outer sensors, similar to the 0.6 rate found in other studies (Phillips et al. 1996; Renninger et al. 2013). By coupling sap-flux rates with stand level biometric data such as tree density, A_{SW} , and leaf area index (LAI in m^2 leaf area per m^2 ground area), half hourly individual sap flux rates were averaged across the sites, and scaled up to the canopy leaf level transpiration (E_L). Since DBH and stand densities were measured every dormant season, the values associated with the

beginning and end of each sap-flux year were used to account for gradual changes in A_{sw} throughout the growing season, via a growth dynamic (Schäfer 2011). LAI was calculated using biometric equations developed by Whitaker and Woodwell (1968) for pitch pine. Use of an allometric relationships was justified by the rain gauge data, as the SL burned and control plots were equal and the CB control plot had only slightly higher throughfall than its burned plot, suggesting similar LAIs. However, since Whitaker and Woodwell (1968) calculated LAI by leaf perimeter, a correction factor between needle perimeter and a 2-dimensional plane was determined by measuring the perimeter of 18 pine needles across the 6 plots (3 in each site) with a metric Vernier caliper (Scherr Tumico, Minnesota, USA). It was determined that the ratio of the 2-dimensional projection to the whole perimeter area for *P. rigida* was 0.352. A growth dynamic for loblolly pine, time shifted to match the regions seasonality was applied to the LAI to account for changing leaf areas over time (Kinerson et al. 1974).

Canopy stomatal conductance (G_{si}) was calculated as follows:

$$G_{si} (mmol) = \frac{N \times E_L \times G_V \times T_A}{VPD \times R} \quad (\text{Eq. 2})$$

Where N is the molar weight of water (18 g/mol), E_L is canopy transpiration per unit leaf area, G_V is the universal gas constant scaled for water vapor ($0.461 \text{ m}^3 \text{ kPa kg}^{-1} \text{ K}^{-1}$), T_A is air temperature in Kelvin, VPD is vapor pressure deficit ($VPD > 0.6 \text{ kPa}$) and R is the molar volume of an ideal gas (22.4 L). This equation assumes that the canopy is well-coupled to the atmosphere and that storage was negligible to overall sap-flux, or VPD was time lagged appropriately (Granier and Loustau 1994; Köstner et al. 1992). For the oak/pine forest (SL) it is assumed to be well coupled as a study showed the middle of the canopy was only 3% different in vapor pressure deficit than the top of the canopy

(Renninger et al. 2014). The pine dominated forests (CB and BTB), as coniferous forests, have been shown to be well coupled in past studies as well (Phillips et al. 1996).

Once canopy stomatal conductance (G_{si}) for the pines was calculated, the response of G_{si} was plotted against the natural logarithm of VPD, by separating the data into bins of $250 \mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetically photon flux density (PPFD) (Schäfer et al. 2000). Then, after applying boundary line analysis to select the optimal data, which justification and benefits are outlined in Vanderkein et al. (2012), the relationship between the intercept and slope for G_{si} at saturated PPFD levels (G_{sisat}) (mean of light levels $>1600 \mu\text{mol photon m}^{-2} \text{s}^{-1}$) was selected to compare the burned plots to control plots, as this is an adequate indicator of how canopy stomatal conductance responds to VPD under optimum environmental conditions (Oren et al. 1999; Schäfer et al. 2000).

Statistical Analysis

Using analysis of variance (ANOVA) in Matlab version R2012b (Mathworks, Natick, MA), a baseline was set using pre-fire photosynthetic and sap-flux data to quantitatively check the magnitude of difference, if any, there was between corresponding burned and control plots. Once the differences of the control and burned plot was obtained pre-fire, it was then possible to evaluate what effects the fires had on the burned plots without any inherent natural difference between the control and burned plots convoluting the results post-fire. A P -value of 0.05 was assumed to be significant. Furthermore, for photosynthetic parameter analysis, all time points post-fire for all three fires were pooled together, regardless of year, to increase the statistical power of the data set. For further analysis, separation of the pine dominated sites and the oak/pine site was applied. To quantify whether the individual fires had an effect on sap flux rates for their

respective stands, a repeated measures ANOVA was conducted, grouping daily sap flux rates for each corresponding burned and control plot's individual trees by day, to test for differences within the month for the year of the respective fires.

Results

Understory and Forest Floor Consumption

Consumption data differed in quality and quantity for each fire. At BTB, 363.6 g m⁻² of shrub biomass and 325.5 g m⁻² of forest floor litter was consumed by the fire in 2011. In 2012, the SL fire consumed only 42.8 g m⁻² shrub stems and 464.5 g m⁻² of forest floor. Finally, in the 2013 CB fire, 285.3 g m⁻² of shrubs were consumed, while 1057.2 g m⁻² of litter was consumed. While CB had the highest total consumption, (95% higher than the BTB fire and 160% higher than the SL fire), it actually had 22% less shrub consumption than the BTB fire. Finally, SL had the least amount of shrub consumption, as it only had 12% of the shrub biomass that was consumed in the BTB fire and 15% of the CB fire.

Needle Nutrient Analysis

Following the fire at the CB stand, only potassium (K) significantly increased in the burned plot, being nearly 1/3 higher compared to the control plot post-fire. All other nutrients analyzed either increased in the control plot, such as Mg and Zn, or had no significant change. By the first summer growing season following fire, there were no signs of higher concentrations of K in the leaves collected from the burned plot at CB. At SL, the opposite effect was observed with regards to K with no differences observed immediately prior or after the fire, but significant differences in the first summer growing

season after fire with the burned plot having 25% higher K than the control plot. At SL, an increase in Mn concentrations was also noted following the fire, and lasted until the first summer growing season after fire. Furthermore, while there was no difference in Fe concentration either pre- or post-fire, it was a fifth higher in the control plot the first summer after the fire at SL.

The nutrient analysis of the senesced needles and leaves gave insight into the effects of overstory species composition nutrient loading on the forest floor for the three sites. Almost all nutrients analyzed had higher concentration by % weight in the oak leaves when compared to pine needles (Table 4). Nitrogen, phosphorous, calcium, manganese and boron were all around 50% higher in oak leaves, while potassium, copper, and iron were about 70% higher in oak leaves (Table 4).

Photosynthetic Parameters

The pre-fire conditions of the physiological responses of the overstory pines in all stands were analyzed separately from all of the post-fire parameters to establish a baseline for pooling all of the control plots as compared to the burned plots. It was found that for almost all of the estimated parameters, there was no difference (P -value > 0.05) between the burned and control plots pre-fire. Thus, any significant differences between the burned and control plots calculated post-fire could be attributed to the effects of the fire. However, the carboxylation efficiency and light compensation point were different in the control and burned plots. Furthermore, after this routine analysis, a deeper look into the data including forest type and time revealed that forest type was a significant factor, and was, thus, included in further analysis.

Light Response Curves

The burned and control plots did not differ in maximum assimilation, quantum yield, or dark respiration rate, both before and after the fire, while light compensation point was significantly higher at the control plot both before and after the fire (Table 5). However, pre-fire, light compensation point was nearly 5 times the burned plot compared to the control plot, while following the fire it was only about 50% greater than the control plot, indicating an increase as result of the fire. Furthermore, when forest type was included in the ANOVA, the interaction showed that this relationship was stronger in the oak/pine stand (Figure 1). While the burned plot and control plots were different pre-fire (roughly 5 fold for both pine dominated and oak/pine stands), the burned plots had slight increases in light compensation point, while the control plots had decreases in light compensation point following fire (Figure 1). However the pine dominated stands' control plots were still about 1.5 times higher than the burned plots post fire, while the oak/pine control plot was not different than its' burned plot post-fire (Figure 1), showing a clear increase as a result of the fire.

A-Ci Curves

V_{Cmax} and Rubisco-limited assimilation of the overstory pines in all of the stands were significantly increased following the fire (Table 6). Values between the burned and control plots were statistically similar pre-fire, and diverged between all burned and control plots at all times post-fire. In fact, while V_{Cmax} and Rubisco-limited assimilation were the same for burned and control plots pre-fire, they were 16% and 25% higher in the burned plots post-fire (Table 6). Furthermore, carboxylation efficiency was different between the burned and control plots pre-fire, being nearly 80% higher in the control

plots, while after the fire they were similar, showing a possible increase in the burned plots as a result of the fire (Table 6). Upon further investigation, it was found that only the pine dominated stands were different pre-fire and then similar post-fire, while the oak/pine stands were similar in the pre-fire period and different post-fire (Figure 1). The carboxylation efficiency in the control plot was nearly double the burned plot in the pine stands pre-fire, while post-fire they were not different. The oak/pine stand showed no difference between burned and control plots pre-fire, but was significantly higher in the burned plot (over two fold) post-fire despite a large variance in the data.

Instantaneous Gas Exchange Parameters

In terms of instantaneous leaf-level gas exchange parameters derived from photosynthetic measurements at saturated light and ambient CO₂ levels, both instantaneous leaf-level C_i/C_a and intrinsic water use efficiency were affected by the fire (Table 7). While pre-fire conditions for all of the instantaneous leaf-level parameters were not significantly different, C_i/C_a was roughly 15% higher in the control plot post-fire, while water use efficiency was about 25% higher in the burned plot post fire. When forest types were examined separately, water use efficiency was affected by the fire only in the oak/pine stand (Figure 1). Water use efficiency was similar between burned and control pre-fire, and 50% greater in the burned plot post fire when compared to the control plot.

Isotope Analysis

Across forest type there were no significant differences between burned and control plots either before or after the fire for any isotopically derived parameter (Table

8). However, when considering forest type as a contributing factor, $\delta^{13}\text{C}$, isotopic water use efficiency, and C_i/C_a were significantly different in the oak/pine stand but not in either pine dominated stand (Figure 2). Since these parameters were not significantly different pre-fire, clear divergence of all three parameters post-fire, with $\delta^{13}\text{C}$ and isotopic water use efficiency decreasing and C_i/C_a increasing, an effect of the fire on these parameters is shown (Figure 2).

Sap-Flux

Due to similar meteorological data throughout the study years, environmental differences on overall sap-flux for different years were deemed insignificant (Figure 3). While all values are not identical, in fact BTB seemed to have slightly higher soil moisture and lower VPD (Figure 3), they are within range of each other and could thus be deemed comparable without any meteorological difference driving statistical significance. Temperature range (approximately -10 to 30 °C) and seasonality matches throughout all study sites, while VPD is between 0 and 4 kPa, and soil moisture content is generally between 5 and 20 %. The BTB fire of 2011 had no statistically significant influence on the amount of water being transpired per unit sapwood area (Figure 3a) as evidenced by a lack of change in daily sap flux totals for the burned plot compared to the control plot. Although the two plots showed no statistically significant difference between the burned and control plot pre-fire, and that persisted for over a year, steady increases were shown in the burned plot when compared to the control plot for the first few months after the fire (Figure 3a). The fire in the SL oak/pine forest of 2012 showed a more complex pattern, as the burned and control plots were statistically different pre-fire and post-fire, persisting until August, while due to power outages and equipment failure

there was not sufficient data for the last few months (Figure 3b). However, for the data obtained, quantifications of the difference can be obtained. It was found that pre-fire, the pines in the burned plot were only transporting water at roughly 2/3 the rate of the control plot per unit sapwood area. However, the few months after the fire (April, May, and June), the burned plot pines were transpiring only half the water as the control plot (Figure 3b). Finally, in the three months following June, the burned plot was only moving a little more than one third the volume of water when compared to the control plot, although only July was statistically significant (Figure 3b). Thus, as the growing season progressed, the pines in the burned plot were moving increasingly less water when compared to the control plot. For the fire at CB, in 2013, a clearly statistically significant increase of rates at the fire site when compared to the control site is demonstrated post-fire. In fact, pre-fire and a few days following the fire in March there was no difference in sap-flux rates between the burned and control plots (Figure 3c). However, in the four months following the month of the fire, the sap-flux rates at the burned plot were significantly higher than the pines in the control plot by 280, 260, 190, and 180 % respectively (Fig. 3c). All months following July were not significantly different.

Canopy Stomatal Conductance Response to Environmental

Parameters

By evaluating the response of G_{si} in pitch pine to the natural logarithm of VPD by separate PPFD levels, the slope and intercepts from the linear regressions of the higher PPFD values were used to infer the sensitivity of stomata to VPD, which is an indicator of how efficiently the stomata can act to prevent cavitation, with a ratio of 0.60 being the optimal range (Oren et al. 1999). This method allows for assessment of differences in

canopy stomatal conductance under similar VPD and light under the most optimal conditions. Thus by graphing all burned and control plots, the degree of deviation from the optimal line could be observed to assess what level of impact these fires were having on the canopy level stomatal conductance (Figure 4). Furthermore, since the meteorological parameters for the three years were not drastically different, optimizing the data were further justified (Figure 3). At CB, the fire of 2013 resulted in the burned plot being closer to the optimal range of 0.6, with a mean ratio of 0.49, while the control plot only had a mean ratio of 0.17 (Figure 4). The other pine dominated site (BTB 2011) showed similar results, where the mean ratio was 0.51 at the burned plot, and only 0.30 at the control plot (Figure 4). The only ratio that was not significantly different the year of the fire was the oak/pine site (SL 2012), which had a mean ratio of 0.35 at the burned plot and 0.37 at the control plot (Figure 4). Finally, it was shown that throughout the year of the fire, the CB burned plot had a higher soil volumetric water content than CB control plot (Figure 5A). At the SL site, the opposite trend occurred, where the control plot's soil had higher soil water content throughout the year of the fire compared to the burned plot (Figure 5B).

Discussion

Effects of Prescribed Fire on Photosynthetic Capacity

A primary goal of this study was to assess the physiological responses of overstory trees to prescribed fire. By measuring the same physiological parameters pre- and post-fire at three stands, our results indicate that relatively low intensity prescribed fires can cause substantial changes in photosynthetic parameters. Previous studies

focusing on one fire event have found responses that both support and contrast the findings in this study. In an Australian savanna, Cernusak et al. (2006) demonstrated an increase in stomatal conductance and C_i/C_a in burned plots, but no change in photosynthetic assimilation rates. When the results from all three fires were pooled in our study, we observed no change in photosynthetic assimilation rates; however, a decrease for C_i/C_a , and no change in stomatal conductance occurred. In contrast, a study in a Wisconsin mixed-oak forest showed an increase of photosynthetic rates following one fire instance across four different species of trees, with each species showing a slightly different response (Reich et al. 1990). Despite these two experiments (Cernusak et al. 2006; Reich et al. 1990) not being performed on the same species as this experiment, it effectively displays the variation found among the physiological responses of trees following a fire and the need for multiple fire events to draw meaningful conclusions about these inherent effects.

Due to a lack of comprehensive studies with such a large amount of parameters analyzed on pines across multiple fire events, it is difficult to compare our results for many of these experimental findings with other studies. Despite this, comparisons of observed values to literature values can be used to confirm the results. Across all three fires, pre-fire burned and control and post-fire control V_{Cmax} values were consistent with literature values. The range of 40-60 $\mu\text{mol m}^{-2} \text{s}^{-1}$ agree with rates found in maritime pine (*Pinus pinaste*) (Porté and Loustau 1998) and ponderosa pine (*Pinus ponderosa*) (Misson et al. 2006). Only burned plots post-fire exceed these values, where V_{Cmax} averaged 70 $\mu\text{mol m}^{-2} \text{s}^{-1}$, which was significantly higher than the control plots post-fire. A possible explanation for this could be an increase of available nutrients post fire. However, in the

needle nutrients results, in which concentrations were analyzed pre and post fire due to lack of biomass weights, no differences were found in any significant nutrient loadings.

Another interesting finding of this study was the affect that these fires had on the water use efficiencies of the trees. Prescribed fire was found to increase the instantaneous measurements of water use efficiency and intrinsic water use efficiency but resulted in a decrease in the long-term isotopic water use efficiency of overstory pines in our study. Before each fire, intrinsic water use efficiency was equivalent in all three control and burned plots, and were significantly higher at all times post-fire in the burned plots, while water use efficiency was only statistically higher in the pines at the oak/pine stand. This could be partially due to the differences in the fuel combustion quality, as oak leaves were found to have much more nutrients than pine leaves. The long-term isotopic data indicated a decrease in isotopic water use efficiency over time, although, it is a long-term average and may not have been indicative of the fire's true effects. However, a more negative $\delta^{13}\text{C}$ following the fire indicates less water stress and is consistent with the findings in a study of the effects of fire on Scots pine (*Pinus sylvestris* L.) (Beghin et al. 2011). By burning of the forest floor, it is very likely that nitrogen was released or made more readily available (Beghin et al. 2011) for the surviving overstory pines, allowing them to be more productive. The ability for the overstory pines to efficiently use water could potentially improve the forests resistance to drought and forms of stress, as the higher the water use efficiency, the less water needed to assimilate a given amount of carbon (photosynthesis). However, no increase in Nitrogen was found in needles post fire. A study on the effects of fire on ponderosa pine found that water relations were improved in unscorched needles of burned trees, leading to higher photosynthetic rates

(Wallin et al. 2003). Therefore, under stressful conditions such as drought or other disturbances that limit water use, fire can serve as a buffer for decreased productivity and stress. This is demonstrated in a study on soil compaction, where areas that were burned actually saw increases in net photosynthesis following a soil compaction disturbance. It is thus presumed that the vegetation in these areas were able to compensate for the negative effects of soil compaction due to the effects of fire, as the areas that were not burned saw a decrease in photosynthetic capacity (Freeman et al. 2004).

Effects on Sap-Flux

A second goal of this study was to quantify the effects of prescribed fire on sap-flux rates in overstory pines. This built upon a previous study by (Renninger et al. 2013). By analyzing the data using a stronger statistical tool and additionally analyzing two other fires in different stands, it could be tested whether the results of this study held true across multiple stand types and fire events. It was found that not only did the forest type affect the response of pitch pine to prescribed fire, but the inherent differences between the consumption of each fire could have potentially affected the response as well. Thus, by assessing the biomass consumed by the fire, a possible explanation for the different responses can be determined. A previous study showed the effect of prescribed fire that occurred in this stand in 2008, where Clark et al. (2012) reported a 25% reduction in overall evapotranspiration due to loss of both understory and overstory leaf area in the flux footprint area. The fire of 2013 at pine dominated CB had the highest consumption, with nearly $1400 \text{ g biomass m}^{-2} \text{ m}^2$, approx. 80% of which was fine litter and wood on the forest floor. Thus, it is not surprising that the clearest effect in terms of temporary increase of water-use was observed in this stand, as the burned plot had significantly

higher sap-flux rates in the few months following the fire, before it became equivalent with its control plot again. The increase found in this study could largely be due to damage to the understory shrubs by the consumption of nearly 300 g of biomass, in conjunction with increases in photosynthetic capabilities noted above. The transient increase in sap-flux rates could be attributed to delayed shrub growth in the understory following a resurgence of greater growth later in the growing season. The fire did effectively reduce shrub growth early in the season, but the stimulated growth, which is common after a fire (Ahlgren and Ahlgren 1960), could have been responsible for the loss of increased rates, explaining why water use equaled the control plot by August of the same year.

At the pine dominated BTB stand, there was no significant difference in average daily transpiration per m^2 A_{SW} between the control and the burned plot following the fire, which is consistent with results found in a study of scorched long-leaf pine stand (Clinton et al. 2011). However, a general trend of the burned site having increased water movement was observed following the fire. While this fire did have the least amount of forest floor consumption (325 g m^{-2}), total consumption was intermediate (690 g m^{-2}). With a relatively large burning of the aboveground biomass, it is possible that reduction in competition in the understory could have occurred.

Finally, the most intricate results of the three stands were the oak/pine SL stand. That is, because pre-fire rates of the overstory pines were significantly different pre-fire, with the control plot having higher rates. However, a gradual decline in rates post-fire was noted at the burned plot, as it gradually moved less water when compared to the control plot. At this plot, a minimal amount of shrub stems were combusted

(approximately 43 g m^{-2}), while an intermediate amount of the forest floor was consumed (465 g m^{-2}). Due to a lack of shrubs consumed, and despite the moderate amount of forest floor litter consumed, which could make the needles more productive, sap-flux rates did not increase, but were in fact decreasing. This could be a result of very little competition being removed via understory shrub consumption, coupled with an increase in productivity of the surrounding oaks and some possible root damage (Busse et al. 2000; Smith et al. 2004). Previous studies have shown oaks and other hardwoods to increase photosynthetic capacity (Boerner et al. 1988) and transpiration (Reich et al. 1990) post-fire, indicating that the overstory and understory oaks may have been capitalizing on the extra resources, outcompeting the overstory pines. This could have resulted in decreased rates in the burned plot post-fire, as no needle scorch was observed.

Effects on Canopy Stomatal Response to Environmental Parameters

Canopy level data indicated that both pine-dominated stands were more suited to capitalize on available nutrients as a result of the fire via their stomatal response to VPD. Despite all of the relationships falling below the 0.60 optimization line, which is consistent with a study conducted on dwarf pitch pine in the Long Island Pine Barrens (Vanderklein et al. 2012), the burned plots in the pine-dominated stands were significantly closer to the 0.60 line than pines in the control plots. This indicates that the pines in the burned plot in pine dominated stands would be transpiring more than their control plot counterplots on given day due to their heightened coupling with VPD, which is consistent with the sap-flux rate data. A possible explanation could be a higher availability of water due to lessened competition from the understory, although it is hard to determine, as CB control plot actually had higher soil moisture on average than CB

burned plot the year of the fire; however, this could be a result of the overstory pines using more water. Thus, this would indicate that utilization of nutrients are a limiting factor, as the pines in the pine dominated control plot were transpiring less even though they had more available water.

In contrast to the pine-dominated stands, pines in the burned and control plots at the oak/pine stand showed no differences in their response to VPD. The burned plot had higher soil moisture levels than the control plot, but no difference in throughfall depths. The SL burned plot's similarity in the control plot's sensitivity to VPD suggests that there could have been more water available due to lessened competition. However, the overstory pines were limited by some other factor, possibly competition from highly productive oaks as a result of the fire.

Conclusion

This comprehensive study suggests that fire did indeed affect water use in overstory pines, although forest type and quality/quantity of combustion played a large role in how they were affected. Certain leaf-level photosynthetic parameters, such as $V_{C_{max}}$ and intrinsic water use efficiency were increased as a result of the fire, regardless of forest type, possibly due to release of nutrients from the litter during the fire. However, due to litter quality and nutrients, it was found that other photosynthetic parameters, such as light compensation point, water use efficiency, and carboxylation efficiency were increased in the overstory pines in the oak/pine stand but not in the pine dominated stands. Also, it was found that at the pine dominated stands, sap-flux rates were increased as a result of the fire, where the stand with the highest understory combustion showed the clearest statistically significant trend. However, at the oak/pine stand, a decrease in sap-

flux rates was noted, despite a reduction in competition from the understory. This can be potentially attributed to the increase in productivity of co-dominant oaks in the stand. Furthermore, it was evident that the pines in the pine dominated stand were more sensitive to changes in VPD on the canopy level and could thus transpire more water under a given condition than their control plot counterparts, indicating that they were better suited to utilize available nutrients. Therefore, while relatively low-intensity prescribed fires did increase some photosynthetic parameters of overstory pines and effectively reduce competition, the degree to which individual trees were able to capitalize upon these increases relies heavily on the composition of the surrounding stand.

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Appendix

Table 1. Stand species composition and density of the six sites.

Site	Species Composition (%)	Mean DBH (cm)	<i>P. rigida</i> sensored	Plot Size (hectares)	Date Burned
CB Burned (2013)	<i>P. rigida</i> 96.2 <i>Q. coccinea</i> 3.9	16.1 (1.3) 4.4	8	0.021	March 15, 2013
CB Control (2013)	<i>P. rigida</i> 100	16.4 (1.2)	10	0.025	NA
SL Burned (2012)	<i>P. rigida</i> 37.4 <i>Q. alba</i> 21.7 <i>Q. prinus</i> 20.5 <i>Q. velutina</i> 20.5	11.0 (1.5) 10.7 (0.8) 9.1 (1.2) 15.2 (0.9)	3	0.055	March 6, 2012
SL Control (2011)	<i>P. rigida</i> 0.7 <i>P. echinata</i> 8.4 <i>Q. alba</i> 6.9 <i>Q. stellata</i> 3.7 <i>Q. prinus</i> 58.1 <i>Q. velutina</i> 14.8 <i>Q. coccinea</i> 6.9 Unknown 0.5	5.5 (1.2) 9.3 (1.8) 7.8 (1.2) 6.1 (1.0) 10.0 (0.5) 13.4 (1.5) 12.6 (1.8) 10.9	3	0.302	NA
BTB Burned (2011)	<i>P. rigida</i> 100	18.2 (1.5)	10	0.030	March 20, 2011
BTB Control (2011)	<i>P. rigida</i> 64.5% <i>Q. alba</i> 22.6% <i>Q. velutina</i> 12.9%	19.6 (1.8) 10.7 (1.4) 10.4 (1.1)	9	0.030	NA

Parenthesis denotes standard errors.

Table 2. Definitions of some photosynthetic parameters

Photosynthetic Parameter	Definition	Measurement derived from
Maximum assimilation	Maximum net photosynthetic rate at saturating light and ambient CO ₂	Maximum value of the light response net assimilation curves
Dark Respiration Rate	Respiration rate measured when light levels = 0, with ambient CO ₂ concentrations	X intercept of the light response net assimilation curves
Quantum Yield	Initial change in net photosynthesis for given increase in light levels	Slope of the linear portion of the light response net assimilation curves
Light compensation Point	amount of light needed for photosynthesis=respiration (ie. net photosynthesis = 0)	Y intercept of the light response net assimilation curves
Rubisco-limited carboxylation rates (V_{Cmax})	carboxylation rates approximated as the initial slope of the relationship between photosynthetic rates and internal leaf	Non-linear regression fit to the Rubisco-limited portion of the assimilation to leaf internal CO ₂ concentration ($A-C_i$) curves
Electron-transport limited carboxylation rates (J_{max})	Estimated carboxylation rates at the non-linear	Non-linear regression fit to the electron transport-

	portion of the $A-C_i$ curve	limited portion of the assimilation to leaf internal CO_2 concentration ($A-C_i$) curves
Trio-phosphate utilization (TPU)	Estimated carboxylation rates at the max (end) portion of the $A-C_i$ curve.	Non-linear regression fit to the triose phosphate utilization-limited portion of the assimilation to leaf internal CO_2 concentration ($A-C_i$) curves
Maximum assimilation	Maximum photosynthetic assimilation rate at saturating CO_2 and light levels	Maximum value of the assimilation to leaf internal CO_2 concentration ($A-C_i$) curves
Carboxylation Efficiency	Initial change in net photosynthesis for a given increase in intercellular CO_2 concentration (C_i). Also an indication of rubisco efficiency to carboxylate CO_2	Slope of the linear portion of the assimilation to leaf internal CO_2 concentration ($A-C_i$) curves
CO_2 compensation point	internal leaf CO_2 concentration needed for	Y intercept of the assimilation to leaf internal

photosynthesis = respiration CO_2 concentration ($A-C_i$)

(ie net photosynthesis = 0) curves

at saturating light

conditions

Table 3. Biometric equations for deriving sap wood areas (m^2) necessary for scaling up sap-flux measurements to total canopy conductance.

	DBH<0.054 (m)	DBH>0.054 (m)	R^2
D_{HW}	0	$0.5*DBH - D_{BK} D_{SW}$	NA
D_{BK}	0.0035	$0.0909*DBH - 0.000484$	0.87
A_{HW}	0	$D_{HW}^2 * \pi$	NA
D_{SW}	$DBH/2 - D_{BK}$	$DBH*0.2234 + 0.000484$	0.84
A_{SW}	$D_{SW}^2 * \pi$	$TA - A_{HW}$	NA
TA	A_{SW}	$(DBH/2 - D_{BK})^2 * \pi$	NA

The biometric parameters used were heart wood depth (D_{HW}), bark depth (D_{BK}), heart wood area (A_{HW}), sapwood depth (D_{SW}), sapwood area (A_{SW}), and total area (TA).

Table 4. Leaf nutrient analysis results of recent dead leaves. Values are concentrations by percent for Nitrogen (N), Phosphorous (P), Potassium (K), Calcium (Ca), Magnesium (Mg), and Sodium (Na), and in ppm for Zinc (Zn), Copper (Cu), Manganese (Mn), Iron (Fe), and Boron (B).

Leaf Type	N*	P*	K*	Ca*	Mg*	Na	Zn*	Cu*	Mn*	Fe*	B*
Oak	1.1	0.05	0.12	0.68	0.12	0.008	26	7.6	1398	46	26
	<i>0.07</i>	<i>0.006</i>	<i>0.084</i>	<i>0.045</i>	<i>0.008</i>	<i>0.0008</i>	<i>2.2</i>	<i>0.29</i>	<i>97.9</i>	<i>3.2</i>	<i>1.8</i>
Pine	0.6	0.02	0.08	0.35	0.06	0.010	49	5.2	610	33	13
	<i>0.05</i>	<i>0.006</i>	<i>0.011</i>	<i>0.028</i>	<i>0.006</i>	<i>0.002</i>	<i>1.7</i>	<i>0.22</i>	<i>139.8</i>	<i>3.3</i>	<i>1.3</i>

Titles with a ‘*’ indicate a significant difference between oak and pine leaves ($\alpha=0.05$). Standard errors are shown below values in italics.

Table 5. Results of photosynthetic parameters derived from light curves. Table displays average values and standard errors (in parenthesis) grouped for all control and burned plots pre-fire and all post-fire values.

	Pre-fire			Post-fire		
Light Curve Parameter	Control	Burned	<i>P</i> -values	Control	Burned	<i>P</i> -values
Maximum Assimilation ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	8.7 (1.72)	11.2 (1.72)	0.30	15.4 (1.09)	13.6 (0.96)	0.29
Quantum Yield ($\mu\text{mol CO}_2 \mu\text{mol}^{-1}$ photon)	0.025 (0.0018)	0.029 (0.0037)	0.45	0.040 (0.0030)	0.039 (0.0021)	0.44
Light Compensation Point ($\mu\text{mol photon m}^{-2} \text{ s}^{-1}$)	67.0 (14.02)	12.64 (2.58)	<0.01	38.8 (5.34)	26.8 (3.81)	0.03
Dark Respiration Rate ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	2.11 (0.66)	0.43 (0.127)	0.06	1.59 (0.237)	1.11 (0.203)	0.26

Burned and control plots that were different are marked by bold lettering for the *P*-values ($\alpha=0.05$)

Table 6. Results of photosynthetic parameters derived from $A-C_i$ curves. Table displays average values and standard errors (in parenthesis) grouped for all control and burned plots pre-fire and all post-fire values.

	Pre-fire			Post-fire		
$A-C_i$ Curve Parameter	Control	Burned	P -values	Control	Burned	P -values
Maximum Assimilation	11.6	12.2	0.85	21.1	19.6	0.97
($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	(1.34)	(2.53)		(1.69)	(1.83)	
Carboxylation Efficiency	0.077	0.042	0.03*	0.10	0.13	0.08
($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} \text{ ppm}^{-1}$)	(0.0130)	(0.0048)		(0.007)	(0.032)	
CO ₂ Compensation Point	68.9	34.2	0.21	59.6	57.6	0.93
(ppm)	(21.39)	(5.77)		(7.05)	(6.58)	
V_{Cmax}	41.9	49.9	0.38	60.2	70.3	0.01
($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	(8.36)	(7.85)		(4.83)	(7.26)	
J_{max}	81.1	72.4	0.94	120.4	105.7	0.80
($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	(25.95)	(10.62)		(13.95)	(14.55)	
Trio-Phosphate Utilization	3.7	3.3	0.75	7.6	7.1	0.82
($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	(1.08)	(0.36)		(0.75)	(0.88)	
Rubisco-Limited	10.9	11.5	0.92	14.4	18.0	<0.01
Assimilation ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	(2.49)	(2.82)		(0.74)	(1.60)	
Ribulose-1,5-bisphosphate	8.9	8.0	0.630	13.2	13.0	0.982
Limited Assimilation	(1.32)	(1.36)		(0.75)	(0.90)	

($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)

Burned and control plots that were different are marked by bold lettering for the P -values ($\alpha=0.05$)

Table 7. Results of instantaneous photosynthetic parameters derived from saturated light (PAR 1500 and greater) and ambient CO₂ (400 parts per million). Table displays average values and standard errors (in parenthesis) grouped for all control and burned plots pre-fire and all post-fire values.

	Pre-fire			Post-fire		
Leaf- Level	Control	Burned	<i>P</i> -values	Control	Burned	<i>P</i> -values
Parameters						
C_i/C_a instantaneous	0.64	0.63	0.90	0.65	0.57	<0.01
	(0.051)	(0.062)		(0.014)	(0.021)	
G_{si}	0.13	0.13	0.80	0.20	0.15	0.10
(mol H ₂ O m ⁻¹ s ⁻¹)	(0.02)	(0.03)		(0.016)	(0.013)	
Water Use	3.9	4.1	0.60	3.2	3.6	0.08
Efficiency (μmol	(0.54)	(0.68)		(0.19)	(0.35)	
CO ₂ mol ⁻¹ H ₂ O)						
Intrinsic Water Use	80.1	83.5	0.91	76.5	95.9	<0.01
Efficiency (μmol	(12.45)	(14.07)		(3.44)	(5.15)	
CO ₂ mol ⁻¹ H ₂ O)						

Burned and control plots that were different are marked by bold lettering for the *P*-values ($\alpha=0.05$)

Table 8. Results of isotopic analysis. Table displays average values and standard errors (in parenthesis) grouped for all control and burned plots pre-fire and all post-fire values.

Isotopic Parameter	Pre-fire			Post-fire		
	Control	Burned	<i>P</i> -values	Control	Burned	<i>P</i> -values
$\delta^{13}\text{C}$ (‰)	-30.6 (0.39)	-30.1 (0.39)	0.54	-30.5 (0.16)	-30.4 (0.17)	0.30
$\delta^{15}\text{N}$ (‰)	-4.3 (0.35)	-3.9 (0.17)	0.57	-3.8 (0.17)	-4.1 (0.16)	0.10
Carbon (%)	51.1 (0.87)	48.6 (1.26)	0.20	48.3 (0.76)	50.0 (1.17)	0.37
Nitrogen (%)	1.1 (0.07)	1.1 (0.07)	0.60	1.1 (0.03)	1.1 (0.03)	0.34
C/N	46.7 (2.72)	46.6 (2.72)	0.93	47.0 (1.4)	44.8 (1.04)	0.56
Isotopic Water Use Efficiency ($\mu\text{mol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$)	93.2 (4.3)	99.0 (4.3)	0.52	94.3 (1.79)	95.1 (1.99)	0.31
Δ (‰)	18.5 (0.37)	18.0 (0.37)	0.49	18.4 (0.16)	18.3 (0.18)	0.34
C_i/C_a	0.62 (0.017)	0.61 (0.017)	0.52	0.62 (0.007)	0.62 (0.008)	0.33

Figure 1. Results from Light Response and $A-C_i$ curves for carboxylation efficiency, isotopic water use efficiency, and light compensation point when separating oak/pine (red) and pine (green) stands. Dark colors represent the burned plot values and light colors represent the control plots. Pre-fire encompasses pre fire conditions of all three years pooled together for each stand type, while post-fire includes all times post fire, including the growing season and second growing season values when available.

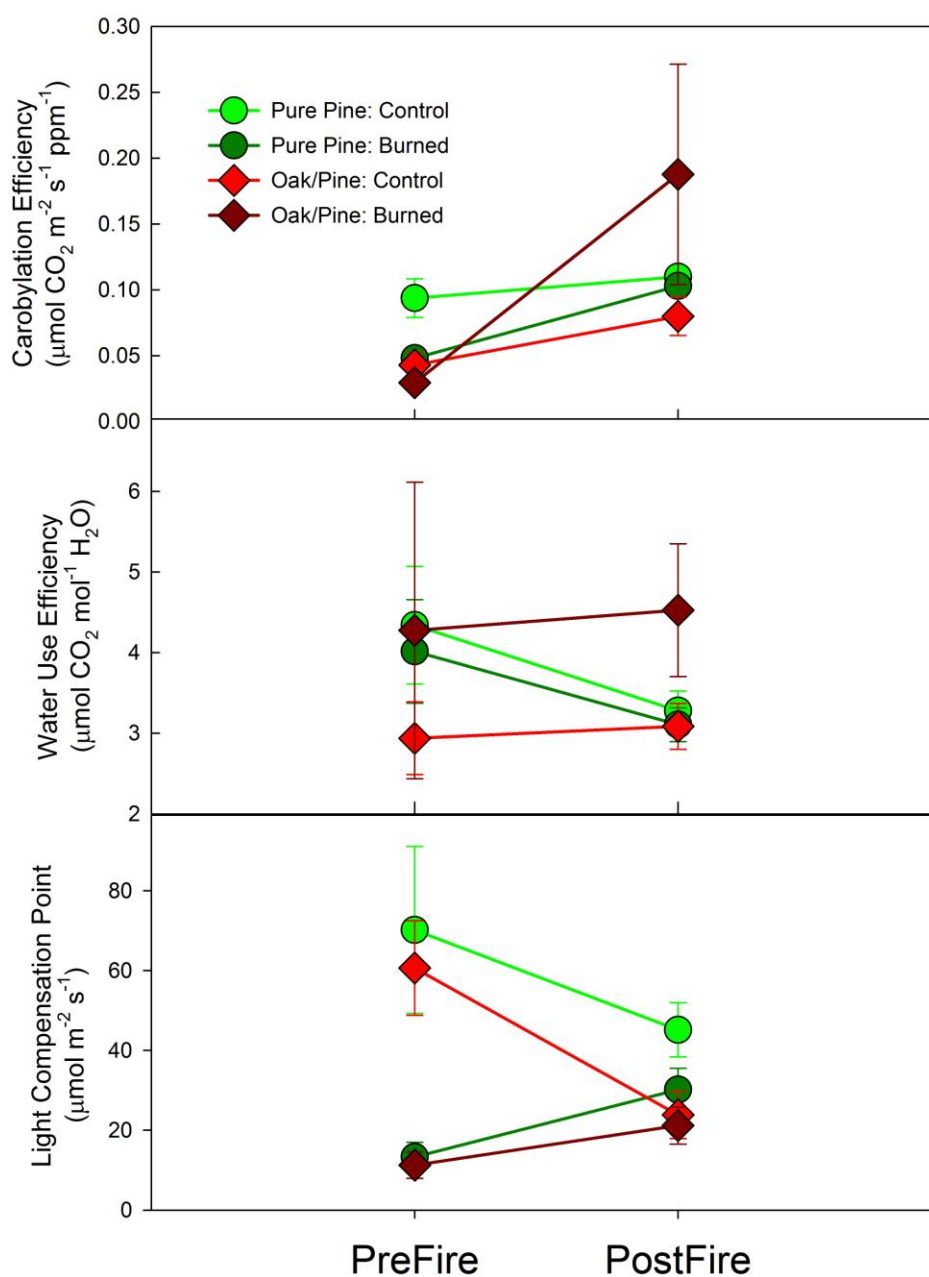


Figure 2. Results from isotopic data for $\delta^{13}\text{C}$, isotopic water use efficiency, and C_i/C_a when separating oak/pine (red) and pine (green) stands. Dark colors represent the burned plot values and light colors represent the control plots. Pre-fire encompasses pre fire conditions of all three years pooled together for each stand type, while post-fire includes all times post fire, including the growing season and second growing season values when available.

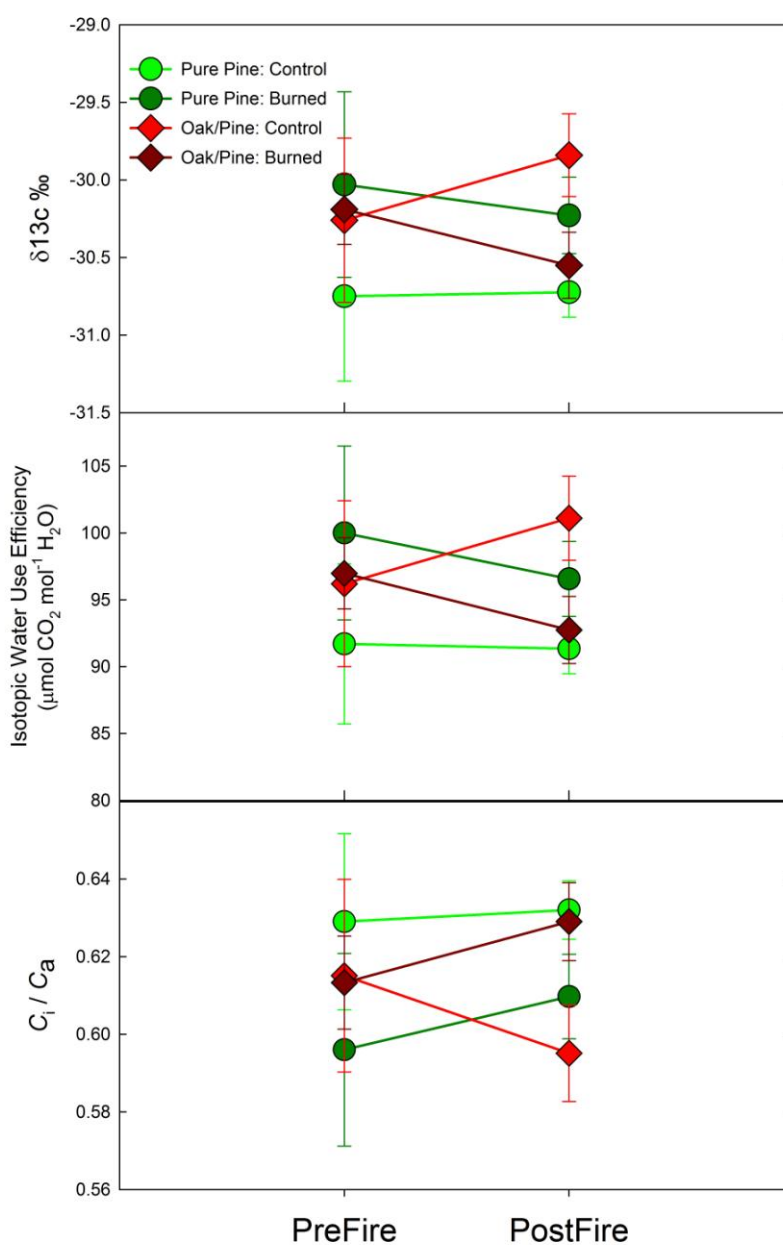


Figure 3. Daily sap-flux m^{-2} sapwood area averaged by month for all plots, year of the fire. BTB(a), burned in 2011 is at the top, with SL (b) , burnt in 2012 in the middle, and CB (c) burnt in 2013 at the bottom. Only days where both burned and control plots had sufficient data were analyzed. Alongside each graph is the corresponding meteorological data for that year with air temperature in $^{\circ}\text{C}$ at the top, VPD in kPa in the middle, and volumetric water content in % soil moisture at the bottom for each year, recorded at the control plot for each corresponding main site.

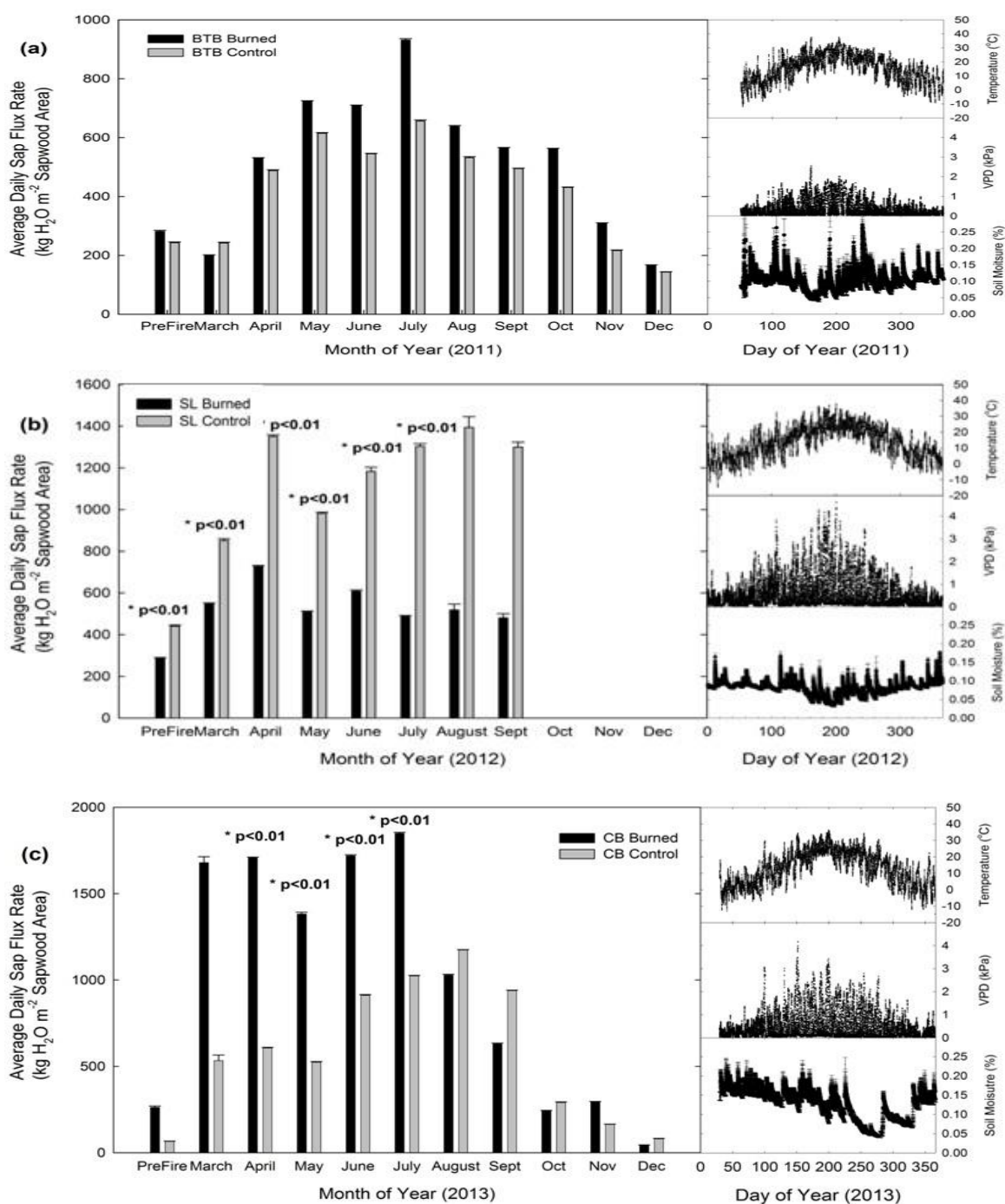


Figure 4. Average ratio of the response of canopy stomatal conductance to VPD: Slope ($\Delta G_{si} / \Delta \ln(\text{VPD})$) vs intercept at the three highest par bins (mean $\sim 1600 \mu\text{mol m}^{-2} \text{s}^{-1}$) for all 3 sites, burned plots and control plots, the year of their respective fires. Cedar Bridge (2013) is denoted by green squares, SL (2012) is denoted by blue diamonds, and BTB (2011), is denoted by red circles, while dark versions are burned plots and light versions are control plots. Bi-directional error bars denote deviations from the mean for the slope and intercept for the 3 highest light bins. The solid line denotes a 0.60 ratio, which is the optimal ratio for stomatal control to prevent uncontrollable embolism.

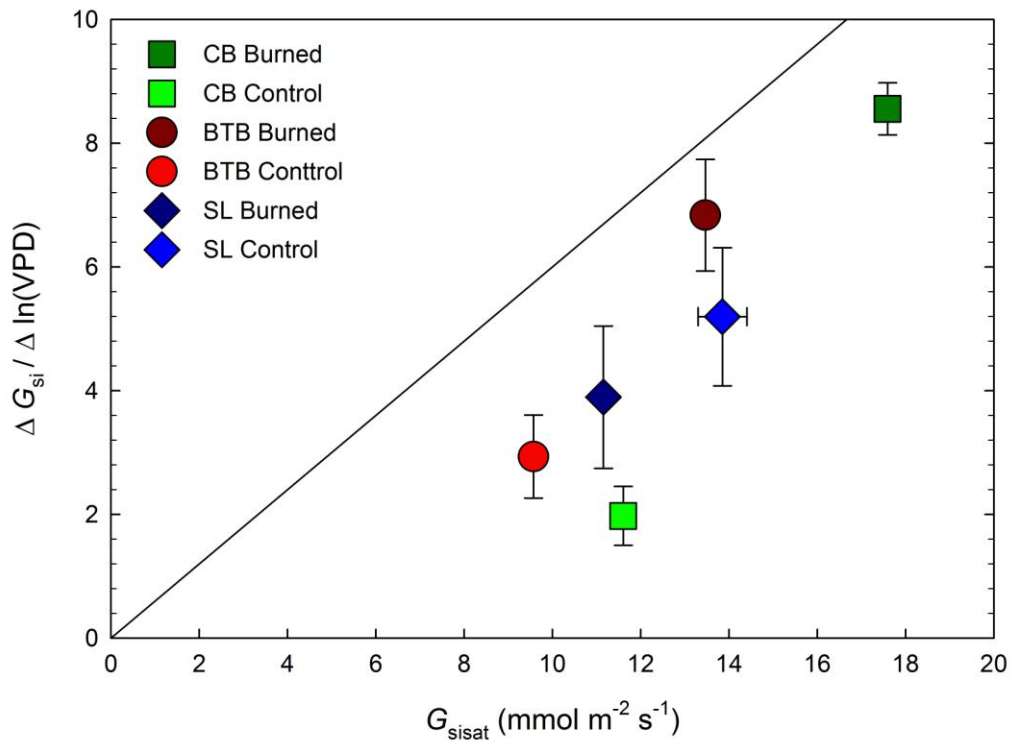
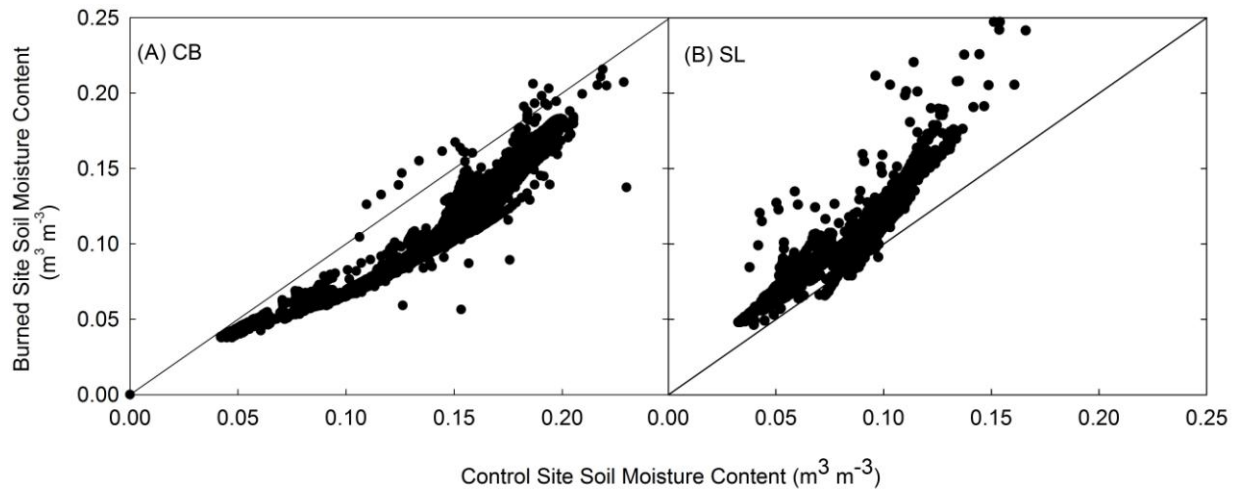


Figure 5. Comparisons of average soil moisture between burned and control plots for both CB (2013, Left) and SL (2012, Right) year of the fires. The solid line represents a 1:1 ratio, which indicates an equality among corresponding burned and control plots.



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1. Renninger HJ, **Carlo N**, Clark KL and KVR Schäfer. 2014. Physiological strategies of co-occurring oaks in a water- and nutrient-limited ecosystem. *Tree Physiology* 34: 159-173.
2. Renninger HJ, **Carlo N**, Clark KL and KVR Schäfer. 2014. Modeling respiration from snags and coarse woody debris before and after an invasive gypsy moth disturbance. *Journal of Geophysical Research - Biogeosciences* 119: 630-644.
3. Schäfer KVR, Renninger HJ, **Carlo N**, and D Vanderklein. 2014. Forest response and recovery following disturbance in upland forests of the Atlantic Coastal Plain. *Frontiers in Plant Science*. doi: 10.3389/fpls.2014.00294.

Submitted:

1. Renninger HJ, **Carlo N**, Clark KL, and KVR Schäfer. Functional convergence in resource use efficiency of oak and pine in an Atlantic Coastal Plain ecosystem. *Oecologia*
2. **Carlo N**, Renninger HJ, Clark KL, and KVR Schäfer. Impacts of prescribed fire on water use efficiency and photosynthetic capacity in an upland oak-pine and pine forest. *Tree Physiology*