

# EFFECTS OF SPRING PRESCRIBED FIRE ON SHORT-TERM, LEAF-LEVEL PHOTOSYNTHESIS AND WATER USE EFFICIENCY IN LONGLEAF PINE

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**Abstract**--Fire is a natural and important environmental disturbance influencing the structure, function, and composition of longleaf pine (*Pinus palustris* Mill.) ecosystems. However, recovery of young pines to leaf scorch may involve changes in leaf physiology, which could influence leaf water-use efficiency (WUE). This work is part of a larger seasonal burning study containing three treatments: spring burn, fall burn, and no burn. The study site is a 21.4-ha (53-acre) longleaf pine plantation planted in 2005 and located on the Winn Ranger District of the Kisatchie National Forest in central Louisiana. This work assessed changes in leaf gas exchange and their resultant WUE in 7-year-old longleaf pine among spring burned and no burn (control) treatments during the 2011 and 2012 growing seasons. Treatment effects on intrinsic WUE [carbon assimilation/ stomatal conductance ( $g_s$ ); iWUE] were assessed using an infrared gas analyzer. We hypothesized that leaf area loss resulting from scorch will: (1) increase photosynthesis, and (2) increase leaf-level iWUE as a result of increased photosynthesis. In the 3 months after the prescribed burn, we observed increases in photosynthesis ( $A_{sat}$ ) in the new foliage of scorched trees that decreased below control levels during the following growing season. During the 2012 growing season, 1 year after the burn, there were larger diurnal increases in iWUE in scorched trees than in controls that increased as temperature increased and water availability decreased. This response was due to greater diurnal reductions in  $g_s$  in scorched trees.

## INTRODUCTION

The longleaf pine (*Pinus palustris* Mill.) ecosystem, once the dominant ecosystem of the southeastern United States, is fire-dependent and currently occupies < 3 percent of its original range (Frost 1993). Prescribed fire is an important management prescription used in longleaf pine stands (Brockway and Lewis 1997). These fires consume the grassy fuel layer and litter layer but do not burn the crowns of large overstory trees. However, the foliage of younger trees and seedlings are often scorched or desiccated resulting in the full or partial defoliation of the tree (Andrews 1917).

Defoliation by fire reduces the photosynthetic area per tree and causes a variety of physiological responses in trees. Some of these responses have been interpreted as recovery and compensatory growth mechanisms, largely because they enhance the rate of photosynthesis and could lead to higher rates of growth relative to a non-defoliated tree (Sword Sayer and Haywood 2009, Vanderklein and Reich 1999). Most studies show that partial or the entire removal of leaf area results in an increase in photosynthetic rates of remaining or new tissue (Detling and others 1979, Heichel and Turner 1983, Painter and Detling 1979,

Reich and others 1993, Vanderklein and Reich 1999, Wallace and others 1984). Defoliation studies done with red pine (*Pinus resinosa* Ait.) have shown that partial defoliation stimulated gas exchange rates that diminished with time (Reich and others 1993). Net photosynthesis was 25 to 50 percent higher in defoliated trees than in non-defoliated control trees 6 weeks after defoliation, and this effect continued at a declining rate until there was no longer any difference between defoliated and non-defoliated control trees (Reich and others 1993). A defoliation study done with red pine and Japanese larch (*Larix leptolepis* Sieb. and Zucc.) seedlings showed increases in photosynthesis during the year following a defoliation (Vanderklein and Reich 1999). Red pine also showed photosynthetic increases in the second year after being defoliated (Vanderklein and Reich 1999).

Research has been conducted on changes in water-use efficiency in plant communities that experience fire or defoliation. Cowan and Farquhar (1977) proposed that plants control stomata to optimally satisfy the trade-off between the amount of carbon (C) assimilated and the amount of water transpired (Cowan and Farquhar 1977). Stomatal conductance ( $g_s$ )

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determines both diffusion of CO<sub>2</sub> into the leaf and diffusion of water out of the leaf with the diffusion coefficient being higher for the lighter H<sub>2</sub>O molecules. Decreased stomatal apertures restrict diffusion of H<sub>2</sub>O about 1.6 times more than CO<sub>2</sub> (Whelan and others 2013). Because this process acts on the leaf water use efficiency (WUE), the ratio between photosynthesis and g<sub>s</sub> called intrinsic WUE (iWUE) is more appropriate than WUE for describing the biochemical functions of vascular plants (Beer and others 2009). Whelan and others (2013) showed increased iWUE in longleaf pine in the 30 days after being burned due to reductions in evapotranspiration and g<sub>s</sub>. Busch and Smith (1993) examined changes in iWUE in the dominant woody taxa from low-elevation riparian plant communities of the southwestern U.S that were recently burned. These plants experienced higher iWUE when burned compared to unburned control plants. However, Reich and others (1993) reported a tendency for defoliated plants to have lower iWUE than control plants due to large increases in g<sub>s</sub>. Sword Sayer and Haywood (2009) have identified increased photosynthesis as a possible recovery mechanism to crown scorch in young longleaf pine and increased iWUE as a function of increased photosynthesis.

When resulting in crown scorch, prescribed fire may increase rates of C capture in new foliage and increase iWUE in longleaf pine during the hot and dry summer months in Louisiana. The overall objective of this study was to determine how spring prescribed fire affects photosynthesis under saturating light (A<sub>sat</sub>) and intrinsic water-use efficiency (iWUE) in a young longleaf pine stand. We monitored the changes in photosynthesis and iWUE for 15 months in longleaf pine following a spring prescribed fire. Our first objective was to analyze the immediate changes in photosynthesis and iWUE in new foliage during the same growing season that the burn was prescribed. Our second objective was to analyze the diurnal changes in photosynthesis and iWUE during the growing season 1 year following the spring burn. Understanding the effects of crown scorch on water-use as well as photosynthetic capacity of longleaf pine is needed to develop sustainable management practices to restore these threatened ecosystems and to minimize growth loss in plantation grown longleaf pine.

## **MATERIALS AND METHODS**

### **Study Site**

The study site is located in a 7-year-old longleaf pine stand on the Winn Ranger District of Kisatchie National Forest in central Louisiana (compartment 24, stand 20, T12N, R5W, sec 2, latitude: 32° 3, 10.345°N, longitude: 92° 51' 20.279" W). This region has an average annual temperature of 18.44 °C and receives an average of 116.84 cm of precipitation annually (NOAA 2012). Prior to longleaf pine planting, this site was used as a loblolly pine plantation that was clearcut in 2001. The site is a 21.4-ha (53-acre) longleaf pine plantation that was planted in 2005 and previously burned in 2008. The soil at the site consists of a fine sandy loam (0 to 20 percent slopes) and is classified as the Sacul series (fine, mixed, active, thermic Aquic Hapludults)(NRCS 2012). The Sacul series consists of very deep, moderately well-drained, slowly permeable soils that formed in acid, loamy, and clayey marine sediments. These soils are located on the uplands of the western and southern coastal plains (NRCS 2012).

The study was set up as a randomized complete block (RCB) design replicated three times. Each plot was subjected to either a spring burn or no burn (control) treatment designed to result in significant crown scorch. In September 2010 firebreaks were laid out using GPS equipment (Trimble Juno SD Handheld; Sunnyvale, CA) to prevent the spread of fire to undesired areas. Firebreaks were also installed and maintained around the entire perimeter of the study area.

The spring plots were burned on May 16, 2011, just prior to a significant drought event in Louisiana that lasted until the summer of 2012. The three spring plots that were burned consisted of 9.3 ha (22.98 acres). Fuel samples were collected from three randomly located 0.22-m<sup>2</sup> vegetation subplots per plot (nine total subplots) that were scheduled to be burned. Vegetation was sampled as described by Haywood (2009). Pre-burn fuel loading for the spring burn plots was done on May 12, 2011, and the post-burn sampling was done on May 26, 2011 (table 1). All vegetation was oven dried at 70 °C and weighed to determine the fuel consumption per plot on a dry-weight basis.

### **Gas Exchange Measurements**

Gas exchange data was collected after the spring burn during the growing season. Rates were monitored using a Li-Cor 6400 infrared gas

analyzer/portable photosynthesis system (Li-Cor Biosciences, Lincoln, NE). The cuvette of the analyzer was operated under ambient CO<sub>2</sub> concentrations, and saturating light (photosynthetically active radiation of 1800 μmol m<sup>-2</sup> s<sup>-1</sup>) was applied so that photosynthesis was maximized throughout the measurement period. All rates were measured at ambient air temperature and ambient relative humidity. Measurements were made on the spring burn and control plots in August and October of 2011, 3 and 5 months after the spring plots were burned, respectively. Morning and afternoon gas exchange measurements were collected three times during the summer of 2012 (June, July, and August). Rates were measured on six individuals per experimental unit during each campaign along with tree height, scorch height, and diameter. Gas exchange rates were monitored on the current year's most recently elongated flush. All needles were excised from the eastern, upper one third of each tree. Two needle fascicles per tree were measured, and the rates were averaged and adjusted for needle area. Needle surface area was calculated by measuring fascicle diameters for all needles measured. Needle area was computed using the following formula from Ginn and others (1991):

$$SA = 3.14159(d)(l) + (n)(d)(l) \quad (1)$$

where d = fascicle diameter, l = needle length in cuvette, and n = number of needles in the fascicle. The Li-Cor 6400 calculated A<sub>Sat</sub> and g<sub>s</sub>, and iWUE was calculated following each gas exchange campaign by dividing A<sub>Sat</sub> by g<sub>s</sub>.

### Statistical Analysis

Statistics were conducted on the absolute values for objective 1, and the results are displayed in a relative differences graph showing the percentage change from the control absolute values. The results for objective 2 are displayed showing the diurnal ratio of change from morning to afternoon measurements for each treatment. All statistics for objective 2 were conducted on the ratio of change from a.m. to p.m. for each variable in each treatment. All

analyses were performed using the GLM and REG procedures. The treatment effects were analyzed by ANOVA at α = 0.05 significance level. All data were analyzed using the SAS statistical package Version 9.1 (SAS Institute Inc., Cary, NC).

### RESULTS AND DISCUSSION

The range of A<sub>Sat</sub> values we observed were similar to the photosynthetic rates reported for loblolly pine (*Pinus taeda* L.) and white pine (*Pinus strobus* L.) grown in the southeastern United States (Maier and Teskey 1992, Teskey and others 1987). After the initial renewal of leaf area following the prescribed fire we observed short-term (3 to 4 month) increases in A<sub>Sat</sub> (p < 0.001) and g<sub>s</sub> (p < 0.001) in scorched trees (fig. 1). These increases returned to control levels by October 2011 (5 months post-burn). This short-term increase in A<sub>Sat</sub> is consistent with most defoliation studies (Detling and others 1979, Ericsson and others 1980, Eyles and others 2013, Heichel and Turner 1983, Quentin and others 2010, Painter and Detling 1979, Reich and others 1993, Vanderklein and Reich 1999, Wallace and others 1984). Reich and others (1993) showed that photosynthesis is possibly enhanced via reduced stomatal limitation, showing a tendency for defoliated plants to have greater g<sub>s</sub> and lower iWUE than control plants. Increases in A<sub>Sat</sub> after defoliation may be due to increased leaf nitrogen (N) concentrations, since photosynthetic capacity and leaf N are functionally related (Kozlowski and Keller 1966); however Reich and others (1993) showed that red pine foliar N concentrations were consistently unaffected by defoliation, regardless of intensity of defoliation or the timing of defoliation. The physical structure of a tree canopy can also influence photosynthetic rates. Gold and Caldwell (1990) showed that increases in photosynthesis in defoliated tussock grass were directly related to a higher proportion of younger foliage and a smaller fraction of shaded foliage. Crown scorch on young longleaf pine inherently removes the lower canopy foliage and reallocates new foliage to the upper crown

**Table 1--Pre-burn and post-burn fuel loads and levels of consumption for the spring prescribed burning treatment**

Treatment	Pre-burn fuel biomass	Standard error	Post-burn fuel biomass	Standard error	Fuel consumption	p-value
	<i>mg ha<sup>-1</sup></i>		<i>mg ha<sup>-1</sup></i>		<i>percent</i>	
Spring	16.24	±1.97	1.76	±0.51	89.17	<0.001

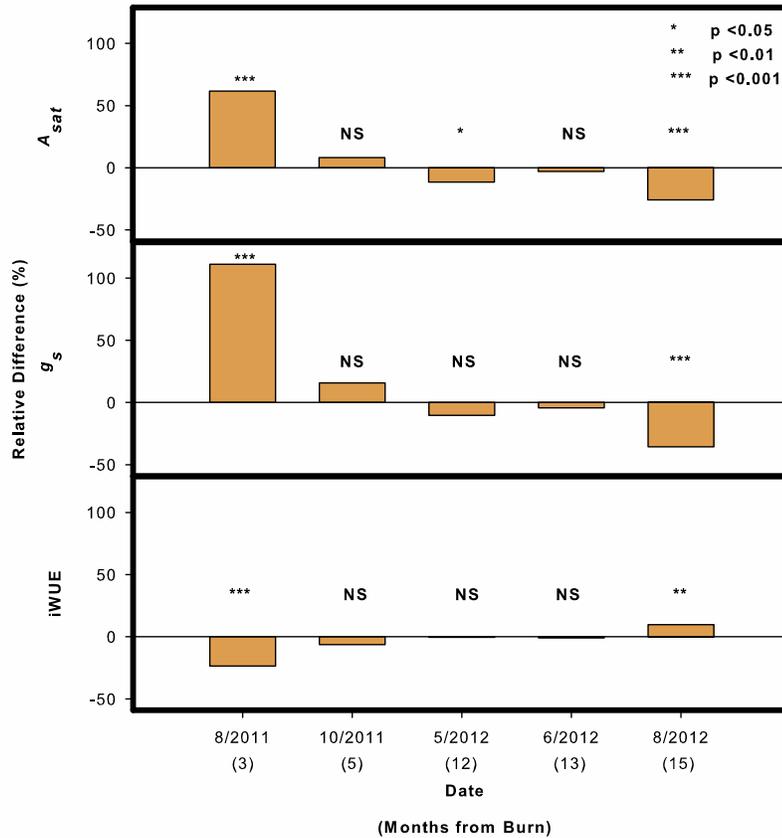


Figure 1-- Comparison of relative changes of  $A_{sat}$ ,  $g_s$ , and iWUE between spring burned and unburned trees. The bars represent the relative difference of the burned value, showing the percentage change from the control absolute values.

where light levels are more favorable. During May 2012 (the following growing season),  $A_{sat}$  in the scorched trees was slightly lower ( $p < 0.05$ ) than control trees while there were no statistical differences in  $g_s$ . As the summer of 2012 progressed,  $A_{sat}$  and  $g_s$  continually declined to well below control levels ( $p < 0.001$ ;  $p < 0.001$ ) as the climate became increasingly hotter and drier at the end the 15-month study (fig. 1). These findings support our hypothesis for greater  $A_{sat}$  in scorched trees; however, the

decrease in  $A_{sat}$  during the 2012 growing season was unexpected. We expected to see increases in  $A_{sat}$  during the second growing season (2012) similar to Prudhomme (1982) and Vanderklein and Reich (1999).

Most studies show increased iWUE and decreased  $g_s$  in the days after defoliation (Ewers and others 2001, Whelan and others 2013); however, some studies have suggested that iWUE may be reduced in defoliated plants as a

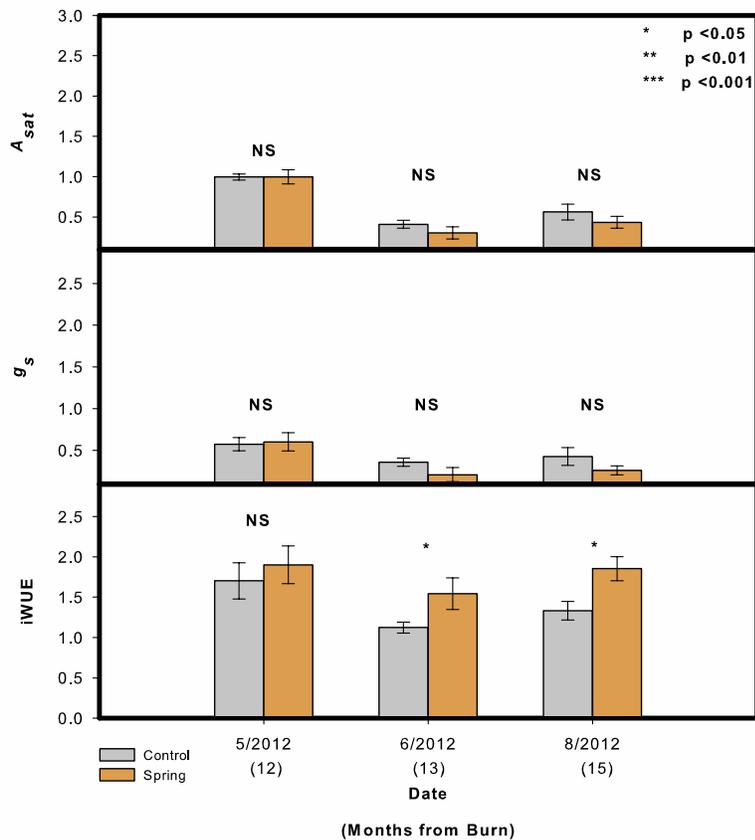


Figure 2-- Comparison between spring burned and unburned diurnal changes in  $A_{sat}$ ,  $g_s$ , and iWUE. The bars represent the ratio of change for each measurement from a.m. to p.m. A value of 1 indicates no change from a.m. to p.m., a value above 1 indicates an increase from a.m. to p.m., and a value below 1 indicates a decrease from a.m. to p.m. The orange bars represent the spring burned values, and the gray bars represent the unburned values.

result of increased  $g_s$  associated with a defoliation-induced shift in plant leaf area per unit root surface (Gold and Caldwell 1990, Reich and others 1993). We observed significant decreases in iWUE ( $p < 0.001$ ) 3 months after the prescribed fire due to large increases in  $g_s$  ( $p < 0.001$ ). Five months following the spring burn, these differences were no longer present. These findings are consistent with other defoliation studies conducted on pines (Reich and others 1993). During the summer after the spring plots were burned, there were no differences in iWUE until late summer. In August 2012 (15 months after the prescribed fire), iWUE increased significantly ( $p < 0.01$ ) above control levels due to large decreases in  $g_s$  ( $p < 0.001$ ) (fig. 1). Our findings partially support our original hypothesis in that we expected to see increases in iWUE in the scorched trees throughout the summer of

2012; however, we hypothesized these increases would be due to greater  $A_{Sat}$ .

During the summer of 2012 we observed no difference in diurnal changes in  $A_{Sat}$  or  $g_s$  between scorched and un-scorched trees. There were larger diurnal increases in iWUE in the scorched trees than in control trees in June and August as the year progressed into the hot and dry summer months ( $p < 0.05$ ) that occur in central Louisiana (fig. 2). This increase was due to greater diurnal changes in  $g_s$ . So as temperature increased and water availability decreased, trees defoliated through crown scorch had significantly greater diurnal increases in iWUE than control trees

## CONCLUSIONS

A prolonged drought after the prescribed fire during the 2011 and 2012 study period may have interfered with recovery from crown scorch and may have affected gas exchange rates. Interactions among environmental stresses such as drought and crown scorch may decrease plant resistance to structural damage (Ellsworth and others 1994). The initial short-term increase in  $A_{\text{Sat}}$  in the new foliage of scorched trees may represent an initial recovery mechanism. However, in the year after the prescribed fire, the new foliage in scorched trees unexpectedly had lower  $A_{\text{Sat}}$  levels than control trees. Even though new foliage in scorched trees assimilated C at a lower rate than control trees,  $i\text{WUE}$  increased. This increase was not a result of increased  $A_{\text{Sat}}$  in new foliage of scorched trees but rather a function of decreased  $g_s$ . Our results demonstrate potential reductions in longleaf pine C fixation a year after foliage removal. Future research will continue to monitor how the crown scorch affects gas exchange during different seasonal prescribed fires in young longleaf pine and how leaf area removal influences above and belowground carbohydrate allocation.

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