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Transient changes in transpiration, and stem and soil CO_2 efflux in longleaf pine (*Pinus palustris* Mill.) following fire-induced leaf area reduction

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Abstract In 20-year-old longleaf pine, we examined short-term effects of reduced live leaf area (A_L) via canopy scorching on sap flow (Q; kg H_2O h^{-1}), transpiration per unit leaf area (E_L; mm day^{-1}), stem CO_2 efflux (R_{stem}; μmol m^{-2} s^{-1}) and soil CO_2 efflux (R_{soil}; μmol m^{-2} s^{-1}) over a 2-week period during early summer. R_{stem} and Q were measured at two positions (1.3-m or BH, and base of live crown—BLC), and R_{soil} was measured using 15 open-system chambers on each plot. E_L before and after treatment was estimated using Q measured at BLC with estimates of A_L before and after scorching. We expected Q to decrease in scorched trees compared with controls resulting from reduced A_L. We expected R_{stem} at BLC and BH and R_{soil} to decrease following scorching due to reduced leaf area, which would decrease carbon supply to the stem and roots. Scorching reduced A_L by 77%. Prior to scorching, Q at BH was similar between scorch and control trees. Following scorching, Q was not different between control and scorch trees; however, E_L increased immediately following scorching by 3.5-fold compared to control trees. Changes in E_L in scorched trees corresponded well with changes in VPD (D), whereas control trees appeared more decoupled over the 5-day period following treatment. By the end of the study, R_{stem} decreased to 15–25% in scorched trees at both stem positions compared to control trees. Last, we found that scorching resulted in a delayed and temporary increase in R_{soil} rather than a decrease. No change in Q and increased E_L following scorching indicates a substantial adjustment in stomatal conductance in scorched trees. Divergence in R_{stem} between scorch and control trees suggests a gradual decline in stem carbohydrates following scorching. The absence of a strong R_{soil} response is likely due to non-limiting supplies of root starch during early summer.

Keywords Fire · Longleaf pine · Sap flow · Stem respiration · Soil respiration · Ichauway

Introduction

Longleaf pine savannas provide good model systems in which to investigate short-term changes in water and carbon cycling mediated by fire disturbance. Longleaf pine (*Pinus palustris* Mill.) is the key tree species in a complex of fire-dependent forest ecosystems native to the southeastern United States, and fire is an important environmental disturbance influencing the structure and function of these ecosystems (Chapman 1932; Christensen 1977). Long leaf pine ecosystems have been reduced in extent to ca. 3% of the pre-European settlement extent of 40 million ha (USDA Forest Service, Forest Inventory and Analysis, unpubl. data). Management and restoration of longleaf pine savanna systems have been accomplished primarily through the use of controlled burning which has been shown in many ecosystems to have varying effects on fluxes of carbon and water (Ford et al. 2008). Although fire is an important part of these ecosystems, when properly applied results in

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enhanced function, in young longleaf pine stands fire may result in altered physiological function. These changes may manifest as reduced growth due to either canopy scorching or damage to fine roots in upper soil horizons, increased risk of tree mortality, and/or a potentially ineffective restoration effort. Understanding the effects of prescribed fire and other management options on this ecosystem is critical to the success of management decisions.

Transpiration can change on short- and long-time scales as stomatal conductance, leaf area, climate, and hydraulic conductance change (Andrade et al. 1998; Ewers et al. 2001; Schäfer et al. 2000; Bowman et al. 2005; Addington et al. 2006). With fire as a disturbance, partial canopy scorching can result in the removal of a considerable amount of leaf area. Following reductions in leaf area, increases in transpiration per unit of the remaining foliage (E_L) can result when sap flow (J_s) and sapwood area (A_{SW}) remain unchanged, when stomatal conductance (g_s) and leaf–to–air vapor pressure deficit (D) around the leaf change, or when the gradient between soil and leaf water potential weakens (Ψ_{soil} and Ψ_{leaf}, $\Delta\Psi$). In general, g_s and E_L have been found to increase with leaf area removal (Meinzer and Granz 1991; Reich et al. 1993), but not always (Whitehead et al. 1996; Pataki et al. 1998; Hubbard et al. 1999; Maier and Clinton 2006). Adjustments in g_s and E_L to compensate for changes in functional A_L may translate into consequent changes in carbon available for growth and maintenance of respiring tissues.

Carbon dioxide efflux from woody tissues (i.e., stem, branch, and roots) and soil contributes a large portion of pine ecosystem respiration (Hamilton et al. 2002; Maier et al. 2004). Carbon availability via canopy photosynthesis is tightly linked to stem and soil CO_2 efflux (Tang et al. 2005). Stem CO_2 efflux declined when substrate availability was experimentally manipulated by altering the supply of photosynthates (Edwards et al. 2002) through stem girdling (Edwards and McLaughlin 1978; Martin et al. 1994; Lavigne et al. 2004; Wang et al. 2006; Maier et al. 2010), pruning (Maier and Clinton 2006), or canopy scorching (Cernusak et al. 2006). Cernusak et al. (2006) attributed lower rates of stem CO_2 efflux following burning to reductions in canopy photosynthesis. Stem girdling studies have also shown that much of the temporal and spatial variability in belowground C allocation and respiration is related to the availability of non-structural carbohydrates (Högberg et al. 2001; Johnsen et al. 2007) supplied by current photosynthesis. Johnsen et al. (2007) reported reductions in soil CO_2 efflux up to 30% within 3 days following stem girdling in mid-rotation *P. taeda*. Reductions in leaf area following canopy scorching will likely compromise the availability of photosynthates with immediate effects on ecosystem respiration through reduced stem and soil CO_2 efflux.

Our overall study goal was to determine how tree level carbon and water fluxes were influenced by canopy scorching. Specifically, our objectives were to examine the short-term effects of fire-induced leaf area reduction on transpiration estimated from sap flow, and stem and soil CO_2 efflux in mid-rotation longleaf pine (*P. palustris*) plantations. We hypothesized that following scorching: (1) whole tree water use would be lower in scorch trees compared to control trees, (2) whereas transpiration per unit leaf area would show the opposite response, and (3) lower functional leaf area would cause a reduction in stem CO_2 and soil CO_2 presumably due to a decrease in the production and allocation of photosynthate.

Materials and methods

Study site description

The study was conducted over a 2-week period in early summer 2002 [day of year (DOY) 150–163] in a 22-year-old *P. palustris* Mill. (longleaf pine) monoculture plantation located at the Joseph W. Jones Ecological Research Center near Newton, GA, USA (34°N, 84°W) (see Atkinson et al. 1996). The dense tree spacing (1.5 m × 2 m) had resulted in an understory essentially devoid of vegetation. The soils are classified as Typic Quartzipsamment characterized by coarse sand that exceeds 2.5 m in depth. These soils have low water holding capacities (18 cm H_2O m^{-1} soil in the upper 3 m), weak horizon development due to mixing by soil fauna, low organic matter content, and lack of significant silt and clay fractions.

An open-field weather station onsite measured (CR10X, Campbell Scientific, Inc., Logan, UT, USA) ambient air temperature (T), relative humidity (RH), solar radiation and precipitation (P) ([1]Models HMP35C, LI200SA, and TE525, respectively; Campbell Scientific, Inc., Logan, UT, USA) and recorded on 15 min intervals. Two plots within 30 m of one other were established for study. In the study plots, soil moisture content in the upper 30-cm soil layer (%) was measured continuously using time domain reflectometry (TDR Model CS615; Campbell Scientific, Inc., Logan, UT, USA). Due to failure of TDR probe in one study plot, soil moisture data presented are from the control plot only, making analysis of treatment effects on soil moisture was not possible. However, extant soil moisture data for a related study from the same site indicated no significant difference in volumetric soil water content across treatments (R. Mitchell unpublished data). From

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[1] The use of trade or firm names in this publication is for reader information and does not imply endorsement by the U.S. Department of Agriculture of any product or service.

ambient T, saturation vapor pressure (e_s) was calculated according to Lowe (1977). Actual vapor pressure (e_a) was calculated from fractional RH and e_s. Mean daytime air vapor pressure deficit (D) was calculated as the difference between e_s and e_a. Long-term average daily air temperature at the site ranges from 21 to 34°C during the summer and 5–17°C during the winter, and mean annual P is 1,310 mm (Goebel et al. 2001).

Canopy scorching treatment

At the time of scorching, two age classes of foliage were present; the previous year's cohort and early production of, but not yet fully expanded, current year foliage (Sheffield et al. 2003). On DOY 150, canopy scorching began and was completed on the next morning (see Guo et al. 2004). All trees in the scorched plot received the scorching treatment. Needle scorch was accomplished using a portable propane torch and access to the canopy was achieved with a hydraulic lift. Although longleaf pine can survive 100% crown scorching, care was taken to ensure that (1) the scorching only desiccated the needles instead of incinerating them, and (2) the scorching did not damage terminal buds and branches (Carter et al. 2004). The goal of the treatment was to reduce photosynthesis and transpiration without impairing foliar recovery.

Sap flux measurements

On each of two plots, eight experimental trees were selected and spanned the range of diameters on each plot (Table 1). We estimated canopy transpiration rates from the measurements of xylem sap flux density ($J_{s;}$ g H_2O m^{-2} sapwood s^{-1}) using 30-mm long, constant heat, thermal dissipation probes (TDP) (Granier 1985, 1987). For each of the eight trees on each treatment plot, two sets of sap flux probes were installed on opposite sides (north and south, N–S) of the stem at 1.3 m above the ground (BH). We also installed an additional N–S pair of sap flux probes at approximately 5 m above the ground surface on three of the eight sample trees. This height was just below the live crown on all the three trees (BLC). Each probe set consisted of one upper heated probe and one lower reference probe. Each probe contained one thermocouple junction (TC) suspended in the shaft at 15 mm. The probes were installed by drilling two holes separated vertically by 5 cm, but not separated horizontally. We used a guide template to ensure that the holes were parallel. The probes were coated with thermally conductive silicone grease before placement in the trees. The areas around the probe insertion points were protected with Styrofoam blocks, and the stem of the tree was wrapped 360° with reflective insulation (Reflectix; Reflectix Inc., Markleville, IN, USA) to shield probes from solar radiation, thermal gradients, and rainfall. All lead wires were soldered to copper, double shielded cable wires (Model 9927; Belden Inc., Richmond, IN, USA). TC wires were differentially connected to a data logger with a multiplexer peripheral (Models CR10X and AM416, Campbell Scientific, Inc.). Sensors were queried every minute and these readings were compiled into 15 min averages. The temperature difference (ΔT) between the upper and lower probes was converted to sap flux density J_s using the equation of Granier (1985) with the maximum ΔT determined every 24 h. All probes were monitored continuously during DOY 150–163 during 2002. Power to the TDP control panels was achieved through the use of portable generators that maintained a constant voltage in 12 v deep cycle marine batteries. We omitted all data from analyses that resulting from voltages of <12.0 v DC delivered to the TDP control panel.

Sap flow (Q, kg H_2O h^{-1}) was calculated by averaging J_s measurements from replicate N–S sensors, multiplying by cross-sectional sapwood area (A_{SW}), and integrating for time. At each probe location, we measured over-bark stem diameter and bark thickness. In longleaf pine, heartwood begins to form at around the age of 20 and at age 30 is still predominantly sapwood (Wahlenberg 1946). For calculations of sap flow, we assumed that the entire cross-sectional xylem area to be hydro-active sapwood, and thus estimated A_{SW} from these measurements and the area of a circle (i.e., assuming circular symmetry) (Table 1). Increment cores were also taken at the end of the sampling period to estimate A_{SW} by visual inspection. No heartwood was visible on any tree or at any stem position. For the trees that had probes placed at BLC, sap flow was further scaled to transpiration per unit leaf area (E_L, mmol m^{-2} s^{-1}) by dividing Q by estimated projected leaf area (A_L, described below) and integrated over time. We recognize that variation in sap flux density likely exists along the radial profile for this and other species (Ford et al. 2004) which could result in overestimates of Q and consequent, but proportional overestimates of E_L in both control and scorched trees.

We estimated live A_L on each tree following the treatment using allometric equations developed from nine trees of each treatment harvested after the experiment in June–July 2002. For trees harvested from the control treatment, an equation was developed to predict total foliage mass of the tree from DBH as follows: ($y = \log(\mathrm{DBH}) \times 3.1397 - 0.0601) \times$ CF, where CF is a correction factor = 1.046 (Sprugel et al. 1983) ($R^2 = 0.85$). Predicted dry leaf mass and average specific leaf area (31.56 cm^2 g^{-1}, R. Mitchell, unpubl. data) were used to convert to A_L (Table 1). From the scorched harvested trees, the foliage remaining on the tree was sorted into live and scorched categories. The above equation was used to predict what total live foliage area would have been before the scorching treatment and then calculated the percent live foliage area reduction.

Table 1 Experimental tree characteristics: diameter at 1.3 m (BH) and 5 m (BLC) above the ground surface, estimated sapwood area (A_{SW}), projected leaf area (A_L) and the ratio of A_{SW} to A_L for control and scorched trees

Treatment	Tree	Diameter (cm)		A_{SW} (cm^2)		A_L (m^2) pre-scorch[a]	A_L (m^2) post-scorch[a]	A_{SW}:A_L (cm^2 m^{-2}) post-scorch	
		BH	BLC	BH	BLC			BH	BLC
Control	1	9.6		58.1		3.68	3.68	15.79	
	2	13.0		113.1		9.53	9.53	11.87	
	3	15.0		144.0		14.93	14.93	9.65	
	4	16.8		183.9		21.32	21.32	8.63	
	5	16.8	11.4	180.0	95.0	21.32	21.32	8.44	4.46
	6	18.2	14.9	218.0	162.0	27.41	27.41	7.95	5.91
	7	22.9		343.1		56.38	56.38	6.09	
	8	25.0	18.7	417.6	244.4	74.26	74.26	5.62	3.29
Scorched	1	9.8		60.8		3.92	0.85	71.53	
	2	12.5		109.4		8.43	1.82	60.11	
	3	16.0		174.4		18.29	3.96	44.04	
	4	18.3	13.9	243.3	143.1	27.88	6.03	40.35	23.73
	5	19.4	15.0	271.7	151.7	33.49	7.25	37.48	20.92
	6	21.1	17.2	309.2	213.8	43.60	9.43	32.79	22.67
	7	22.5		356.3		53.34	11.54	30.88	
	8	28.3		498.8		109.60	23.72	21.03	

[a] Estimates of A_L use DBH

CO_2 efflux measurements

Mean daily stem and soil CO_2 efflux (R_{stem} and R_{soil}, respectively, μmol CO_2 m^{-2} s^{-1}) measurements were made using an automated, multi-chamber sampling system (ACES, Butnor et al. 2005) that consisted of stem and soil chambers, an infrared gas analyzer (EGM-2, PP Systems) and a series of solenoids that allowed the sequential measurement of each chamber. The system had an open flow-through design where CO_2 efflux was estimated as the difference between the CO_2 concentration entering and exiting the chamber.

We measured R_{stem} at 1 m above ground height on the eight experimental trees per treatment that were being monitored for sap flux. We also randomly selected three of the eight trees to measure R_{stem} at BLC, co-located with BLC sap flow sensors. Stem chambers were constructed of Teflon film fastened to the bark using closed-cell foam and double-sided tape and completely surrounded the stem (Maier and Clinton 2006). Simultaneous measurements of chamber air- and stem cambium-temperature (at 3 mm depth, T_{stem}) were made using type-T thermocouples. Stem diameter was measured at the mid-point of each stem chamber location. Mean daily R_{stem} for each chamber was calculated from the average of 15–16 diel measurements.

We measured R_{soil} using 15 chambers per treatment placed systematically throughout the study plots: five chambers each were randomly placed at 0–1.0, 1.0–1.5, and >1.5 m distances from the nearest tree stem. This design was used to minimize any bias from root density distribution. Soil chambers were constructed from 25-cm diameter PVC pipe (491 cm^{-2}, 10 cm height) covered with a clear Lexan^{TM} (Dupont Corp., Wilmington, DE) (Butnor et al. 2005). Chambers were equipped with a pressure equilibration port to maintain ambient air pressure. Chamber air temperature and soil temperature (T_{soil}) at 10 cm were measured with type-T thermocouples. Mean daily R_{soil} was calculated from the average of nine diel measurements.

Statistical analyses

To test the hypothesis that Q was reduced in scorched trees compared with control trees, we tested for the differences in daily total Q ($n = 8$) during DOY 151–161 using PROC MIXED (SAS v9.1, Cary, NC, USA, SAS 2004). Treatment was modeled as a fixed effect, and consecutive measurements of Q within each tree were modeled as a random effect and given AR (1) covariance structure. Post-hoc comparisons of least-squares means were interpreted as significantly different at the one-tailed $\alpha = 0.05$ level.

To test the hypothesis that E_L was greater in scorched trees compared with control trees, we tested for differences in mean daily E_L measured at BLC ($n = 3$) during DOY 151–161 using PROC MIXED (SAS 2004). Treatment was modeled as a fixed effect and consecutive measurements of E_L within each tree were modeled as random effects and given AR (1) covariance structure. Post-hoc comparisons of least-squares means were interpreted as significantly different at the one-tailed $\alpha = 0.05$ level. We tested for differences in the E_L versus D relationship between treatments during DOY 151–161 using a repeated-measure, mixed effects, zero-intercept linear model (PROC NLMIXED, SAS 2004). Our model took the form:

$$E_L = f\left(D_{ij}, \beta, u_i\right) + e_{ij}, \tag{1}$$

where f is a function of known vector covariates (D_{ij}); a vector of unknown fixed parameters (β); and a vector of unknown random effect parameters (u_i); and e_{ij} is unknown random errors (Peek et al. 2002). The β parameter represents the rate of increase in E_L with each unit D. We contrasted β parameters between treatments and interpreted differences as significant at $\alpha = 0.05$ level.

To test the hypothesis that R_{stem} was reduced by the scorching treatment, we tested for the differences in mean daily R_{stem} as a function of treatment, and as a function of treatment and stem position (BH and BLC) with diameter as a covariate. Two analyses were done: one used pre-scorching data (DOY 149–150), and the other one used post-scorching data (DOY 151–163). In addition, to facilitate comparisons of the relative effects of scorching treatment over time, mean daily R_{stem} at each stem position was normalized to the mean R_{stem} measured on DOY 150 before the scorching treatments began. Treatment and stem position were treated as fixed effects, and consecutive daily mean measurements (i.e., DOY 151–163) within each stem were modeled as random effects using mixed model repeated measures analysis of variance utilizing an AR (1) covariance structure (PROC MIXED; SAS 2004).

To test the hypothesis that R_{soil} was reduced by the scorching treatment, we tested for the differences in mean daily R_{soil} as a function of treatment and chamber distance from the tree. We anticipated that root biomass would be greater proximal to trees. Two analyses were done: one used pre-scorching data (DOY 149–150), and the other one used post-scorching data (DOY 151–163). Treatment and chamber distance were treated as fixed effects, and consecutive daily mean measurements (i.e., DOY 151–163) within each soil chamber were modeled as random effects using mixed model repeated measures analysis of variance utilizing an AR (1) covariance structure (PROC MIXED; SAS 2004). Post-hoc comparisons of adjusted least-squares means of R_{stem} and R_{soil} were made using Tukey's paired comparison procedure and considered significant at $\alpha \leq 0.05$.

Results

Climate

The study period was characterized by relatively hot and humid conditions (Fig. 1a). Air temperatures ranged from 17.5 to 37.6°C over the study period and averaged at 26.2°C. During the day, D ranged from 0 to 3 kPa, and mean daytime D was moderate at 1.2 kPa. Three precipitation events occurred during the 2-week period that ranged from 0.3 mm on DOY 159 to 13.0 mm on DOY 150. Rain events occurred during the early evening except on DOY 159. Only the 13.0 mm rain event substantially and consistently altered the soil moisture in the treatment plots. Soil moisture ranged from 5 to 28% by volume and averaged 10% over the study period. Mean daily soil temperature at 5 cm (T_{soil}) ranged from 21.1 to 28.6°C and was slightly higher in the control treatment than the scorched (25.1 ± 0.1°C vs. 24.2 ± 0.1°C, respectively; $F_{1, 24} = 20.03$, $P < 0.001$).

Sap flow and transpiration

Prior to scorching, sap flow in control and scorched trees was similar (17.9 ± 4.8 kg day^{-1} vs. 20.0 ± 5.7 kg day^{-1}, respectively, Fig. 1b). As the foliage was being scorched

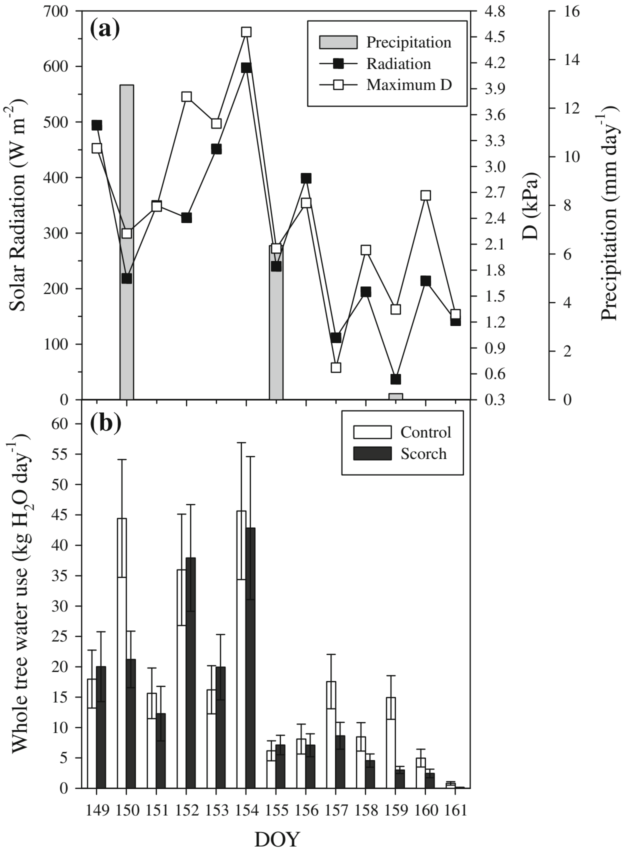


Fig. 1 Mean daytime air vapor pressure deficit (D), total precipitation (P), and mean daytime solar radiation (**a**), and whole tree water use in scorch and control trees (**b**) during the study period. Canopy scorching treatment was applied on day 150, and removed ca. 77% of the leaf area. *Vertical bars* in *lower panel* represent the mean of replicate trees ($n = 8$); one standard error also shown

(DOY 150), sap flow substantially decreased (52% lower) in those trees compared to the control trees indicating that our experimental treatment was effective in reducing transpiration. Following scorching on DOY 151, both scorch and controls trees exhibited similar rates of water use, a pattern that was repeated for several days after the treatment. However, scorching reduced live leaf area on average by 77%, most of which was the loss of previous year's foliage (Table 1). As a result, disproportionately more current-year foliage remained on the scorched trees, although this foliage was not yet fully expanded. Due to loss of live leaf area, the ratio of sapwood area (A_{SW}) to projected leaf area (A_L) increased markedly after scorching (Table 1). Following scorching, sap flow did not differ significantly between treatments ($F_{1,\ 14} = 0.45, P = 0.51$) (Fig. 1b), resulting in a rejection of our first hypothesis that sap flow would be reduced by reduction in live leaf area in scorched trees. Sap flow differed significantly among days ($F_{10,\ 140} = 28.28$, $P < 0.001$), driven primarily by changes in atmospheric conditions; however, trees from both treatment groups responded similarly (no interaction, $F_{10,\ 140} = 0.75$, $P = 0.67$) over the study period.

Pre-treatment estimates of E_L were similar in control and scorched trees (0.63 ± 0.03 vs. 0.47 mmol m^{-2} s^{-1} ± 0.11 SE, respectively, Fig. 2). For the 5 days following the scorching treatment, E_L in scorched trees was significantly greater than in controls and averaged 3.4 times greater over that period ($F_{1,\ 4} = 14.79$, $P = 0.02$). No response in sap flow after removing 77% of A_L suggests an adjustment in E_L of the remaining foliage sufficiently enough to account for the observed no change in whole tree water use, confirming our second hypothesis. Like sap flow, E_L differed significantly among days ($F_{10,\ 40} = 31.89$, $P < 0.0001$) as climate varied; however, the magnitude of the increase in E_L in the scorched trees was greater on days with high D (interaction $F_{10,\ 140} = 0.75$, $P = 0.67$, Fig. 3). Scorched trees had a significantly greater increase in E_L with increasing D compared to the control trees ($\beta = 1.19$ vs. $\beta = 0.42$, $F_{1,\ 5} = 6.86$, $P = 0.047$).

Stem CO_2 efflux

Prior to scorching, R_{stem} in the control trees was significantly greater than that in the scorched trees (2.60 ± 0.17 vs. 1.71 ± 0.17 μmol m^{-2} s^{-1}, respectively; $F_{1,\ 18} = 13.93$, $P = 0.002$). R_{stem} increased linearly with stem diameter and was greater at BLC than at BH (2.94 ± 0.20 vs. 1.37 ± 0.14 μmol m^{-2} s^{-1}, respectively; $F_{1,\ 18} = 37.39$, $P < 0.001$). The differences between R_{stem} at BLC and BH were consistent between treatments (no significant interaction, $F_{1,\ 18} = 1.04$, $P = 0.32$). Thus, normalizing the data with respect to pretreatment R_{stem} rates corrected the data for these size- and location-dependent effects.

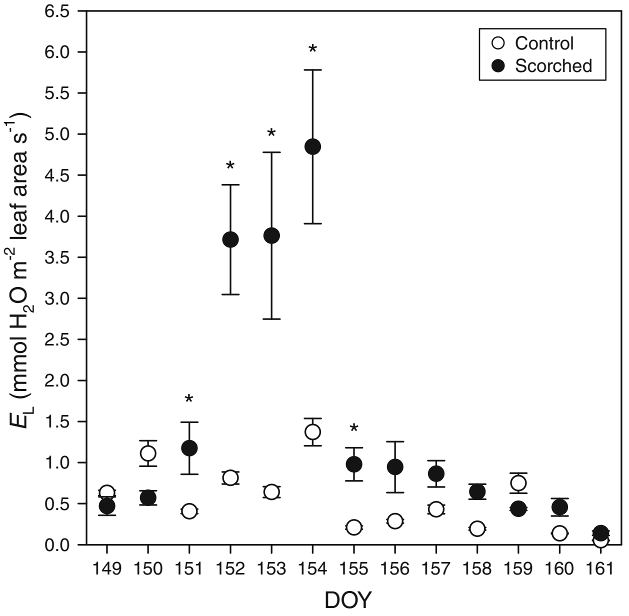


Fig. 2 Transpiration per unit leaf area (E_L) in scorch and control trees during the study period. Canopy scorching treatment was applied on day 150, and removed ca. 77% of the leaf area. *Symbols* represent the mean ($n = 3$); *error bars* are one standard error. *Asterisks* indicate significant differences between scorch and control on those days at $\alpha = 0.05$ (one-tailed)

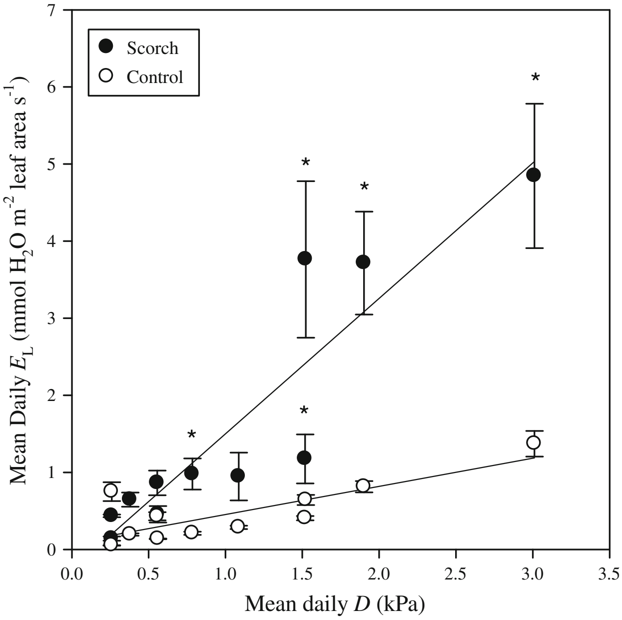


Fig. 3 Mean daytime transpiration per unit leaf area (E_L) in scorch ($R^2 = 0.83$) and control ($R^2 = 0.64$) trees during the treatment period (DOY 151–161) versus mean daytime air vapor pressure deficit (D). Lines differ significantly ($P = 0.047$): control $E_L = 0.42\ D$, scorched $E_L = 1.19\ D$. Canopy scorching treatment was applied on day 150, and removed ca. 77% of the leaf area. *Symbols* represent the mean ($n = 3$); *error bars* are one standard error. *Asterisks* indicate significant differences between scorch and control on those days at $\alpha = 0.05$ (one-tailed)

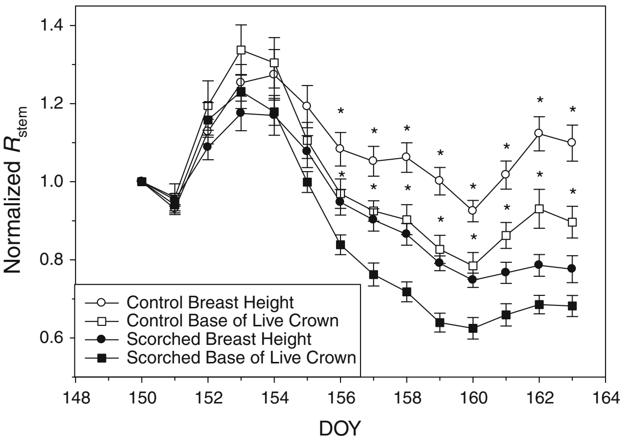


Fig. 4 Mean daily stem CO_2 efflux (R_{stem}; μmol m^{-2} s^{-1}) normalized to day of year (DOY) 150 before scorching for chambers at breast height (BH) and base of live crown (BLC). *Symbols* represent the mean (BH, $n = 8$, BLC, $n = 4$); *error bars* are one standard error. *Asterisks* indicate significant differences between treatments in both stem positions at $\alpha = 0.05$

Following scorching, normalized R_{stem} was lower in scorched trees compared with control trees (treatment effect $F_{1,\ 28} = 22.3$, $P < 0.0001$), and the effect of scorching increased in magnitude over time (treatment by time interaction, $F_{13,\ 259} = 5.33$, $P < 0.0001$, Fig. 4). Normalized R_{stem} in scorched trees was noticeably lower than controls 3 days after treatment and significantly different after 6 days at BH and BLC. From this point until the end of the experiment, normalized R_{stem} in scorched trees was 18–34 and 16–25% lower than in control trees at BH and BLC, respectively. There was no treatment by position ($F_{1,\ 28} = 0.06$, $P = 0.80$) or treatment by position by time ($F_{13,\ 259} = 0.70$, $P = 0.76$) interaction effects on normalized R_{stem}. However, there was a strong position by time interaction ($F_{13,\ 259} = 5.56$, $P < 0.0001$). Within a treatment, R_{stem} at BLC initially increased and then gradually declined relative to the rates at BH.

Soil CO_2 efflux

We found no support for our fourth hypothesis—that R_{soil} would decrease in response to the loss of A_L via scorching. Prior to scorching, there was no significant difference in mean R_{soil} between treatments ($F_{1,\ 24} = 0.22$, $P = 0.64$; Fig. 5a). Following scorching, R_{soil} ranged from 1.5 to 3.7 μmol m^{-2} s^{-1} and was strongly correlated with changes in control plot soil moisture in control ($R^2 = 0.70$, $P < 0.0001$) and scorched ($R^2 = 0.65$, $P = 0.0003$) trees. There was no consistent treatment effect on mean R_{soil} (control 2.53 ± 0.11 μmol m^{-2} s^{-1}, scorch 2.68 ± 0.11 μmol m^{-2} s^{-1}, $F_{1,\ 24} = 0.95$, $P = 0.34$). Five days after scorching began (DOY 155), R_{soil} increased in the scorched plot relative to the control and then converged again near the end of the measurement period (treatment by time interaction, $F_{13,\ 312} = 9.42$, $P < 0.001$).

There was no treatment by chamber distance interaction ($F_{2,\ 24} = 0.90$, $P = 0.42$) or treatment by chamber distance by time interaction ($F_{26,\ 311} = 1.20$, $P = 0.23$); however, R_{soil} was dependent on chamber distance within the plot. R_{soil} was greater in chambers within 1.0 m of the tree stem than at distances greater than 1.0 m ($F_{2,\ 26} = 6.03$, $P < 0.01$) (Fig. 5b). In addition, there was a strong chamber distance by time interaction ($F_{26,\ 311} = 1.85$, $P = 0.01$). Following the maximum R_{soil} measured on DOY 151, R_{soil} at distances <1.0 m declined at a slower rate than at distances greater than 1.0 m.

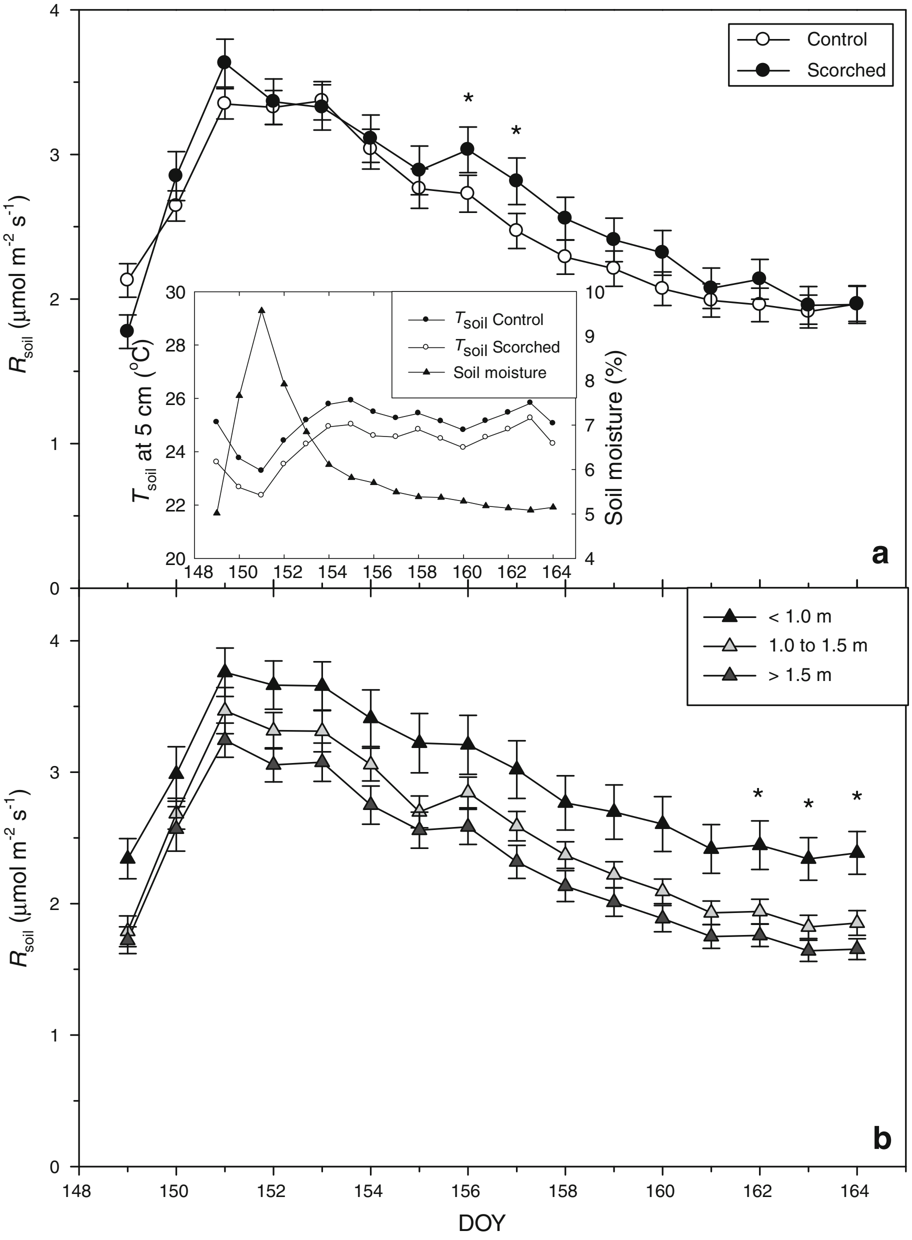
Discussion

On a whole-plant level, trees did not decrease the amount of water transpired (Q) after removal of 77% of their live leaf area by scorching. Several mechanisms could be involved in this outcome: (1) after scorching, the ratio of sapwood area to leaf area markedly increased (Table 1) causing adjustments to g_s and increases in transpiration rate of the remaining live foliage (E_L); however, before scorching, the younger needles may have accounted for more than a proportional share of total transpiration so that the adjustment in g_s in the younger unscorched needles is somewhat overestimated based on sap flow and (2) loss of waxy cuticle during scorching that allowed continued transpiration in the scorched needles albeit at a much reduced rate. Individually or in combination, these mechanisms could have certainly been a factor in our observed increase in E_L.

The immediate increase in water use on the scorched trees illustrates a strong coupling between D and E_L (Fig. 3) immediately following treatment. Although this coupling clearly exist in both treatments, a response of similar magnitude was not observed in the control trees; the average E_L in the scorched stems was 3.4 times that of the control stems over the 5-day period following scorching. On days with rain events, E_L in both control and scorch stems decreased to similar values.

The hydraulic system of leaves accounts for most of the resistance to water flow in trees and leaf hydraulic and stomatal conductance largely control transpiration and photosynthetic rates (Sack and Holbrook 2006; Tsuda and Tyree 2000; Aasamaa et al. 2001). Since damaged foliage was primarily the older of two needle cohorts, scorching effects may have been less than first assumed (e.g., younger foliage likely had higher photosynthetic and transpiration rates per unit leaf area compared to older foliage). In this species, A_L does not reach maximum until September (Sheffield et al. 2003); hence, stomatal adjustment in the not yet fully expanded current-year foliage would not seem

Fig. 5 Mean daily soil CO_2 efflux (R_{soil}; µmol m^{-2} s^{-1}) (**a**) in control and scorched treatments, and (*inset*) mean daily soil temperature (T_{soil}; °C) and control plot moisture (% v/v). *Symbols* represent the mean ($n = 15$); *error bars* are one standard error. Mean daily R_{soil} (**b**) at each chamber distance to the nearest tree stem. There was no distance × treatment interaction so *symbols* represent the mean averaged across treatments ($n = 5$); *error bars* are one standard error. *Asterisks* indicate significant differences among (**a**) treatments, and (**b**) chamber distances at $\alpha = 0.05$



to have reached the capacity needed to fully account for the observed post-treatment water use. However, comparing the observed mean daily rates of E_L from this study with mean daily rates for this species in another study at the same site (Ford 2004; Ford et al. 2008) suggests that adjustments in g_s to the scorching treatment in our trees may fully account for the increased E_L. Ford (2004) observed mean daily E_L of up to 5.4 mmols m^{-2} s^{-1} which is in line with the estimated mean daily E_L of up to 5 mmols m^{-2} s^{-1} in our scorched trees; hence, our estimates of E_L are reasonable and represent an adjustment in g_s that may alone explain estimated post-treatment whole-tree water use.

Stem CO_2 efflux

R_{stem} declined in response to scorching. R_{stem} in scorched trees stabilized at roughly 66 to 86% of control R_{stem} about 8 days after treatment (Fig. 4). This response is most likely due to a direct effect of reduced carbohydrate supply from canopy photosynthesis. A decline in R_{stem} could have been observed if the rate of transport of dissolved CO_2 from respiration in the xylem stream had increased (Teskey et al. 2008; Teskey and McGuire 2002; McGuire et al. 2007; Steppe et al. 2007); however, we did not observe increased J_s or Q in our study, so this indirect mechanism is not likely to explain our results. The majority of R_{stem} in our trees likely originated from the metabolism of cambium and phloem tissue near the stem surface (Maier and Clinton 2006); however, we caution that our measurements of R_{stem} probably underestimated true stem respiration because some portion of respired CO_2 will become dissolved in the xylem stream. Depending on the species, underestimates of total stem respiration can be as high as 45% (Teskey and McGuire 2002). The large reductions in leaf area in scorched trees likely compromised carbohydrate supply and transport, thus reducing substrate supply for stem metabolism. Reductions in carbohydrate supply from canopy pruning (Lavigne et al. 2004), girdling (Ogawa 2006) or phloem chilling (Johnsen et al. 2007) lowered R_{stem} within several days. Maier et al. (2010) found that R_{stem} in young loblolly pine stems was reduced to 10–40% several days after phloem girdling. Cernusak et al. (2006) found that R_{stem} declined in several tropical savanna tree species following fire disturbance that reduce canopy leaf area. Wang et al. (2006) showed that the magnitude of diel R_{stem} in *Pinus koraiensis* Sieb. & Zucc. stems was correlated with radiation intercepted the previous day. The results of these studies indicate a close coupling between R_{stem} and carbon supply from recent photosynthesis.

For a given diameter, R_{stem} was greater in upper compared to the lower stem positions. R_{stem} is generally greater within or near the crown compared at BH (Damesin et al. 2002; Pruyn et al. 2002; Ceschia et al. 2002). We also found that over the study period, R_{stem} at BLC was more dynamic than at BH. Relative to R_{stem} at BH, R_{stem} at BLC increased more early in the study when soil water supply was high and decreased more as soil water content declined (Fig. 4). This suggests that R_{stem} at BLC is more closely coupled with canopy metabolism than R_{stem} at BH. Pruyn et al. (2002) observed 50% higher rates of both mass- and volume-based respiratory potentials near tree tops in young *Pinus ponderosa* trees. They suggested that higher rates in the crown were due to the fluxes being measured more proximal to the source of current photosynthate.

A decrease in R_{stem} represents primarily loss in stem growth respiration. Maier et al. (2010) found that reductions in R_{stem} corresponded well with changes in stem soluble sugar and starch concentration and concluded that reductions in non-structural carbohydrate supply constrained growth respiration and hence, apparent stem respiration. In addition, severe crown scorch can have significant long-term impacts on stem growth (Johansen and Wade 1987) and ecosystem productivity (Cernusak et al. 2006).

Soil CO_2 efflux

We did not find evidence to support the hypothesis that reduced leaf area from the scorching treatment reduced R_{soil} during our measurement period. Instead, R_{soil} in the scorched plot increased temporarily relative to the control plot. While C supply to the roots may have decreased with reductions in A_{L}, the lack of response in R_{soil} may indicate: (1) root and microorganism respiration relied on a secondary source of carbon (e.g., stored carbohydrates) (Guo et al. 2004); (2) during this time of the year when aboveground growth is normally rapid, proportionally less C is allocated belowground; or (3) a combination of the two. For example, girdling 11-year-old loblolly pine trees during the fall when root starch concentrations were low reduced R_{soil} by 10–30% and responses were observed within 3 days of treatment; however, girdling in the spring did not reduce R_{soil} presumably because root starch was plentiful (Johnsen et al. 2007). Similarly, in longleaf pine, C allocation belowground is the greatest during the spring and early summer (Sword-Sayer and Haywood 2006), and starch concentrations belowground are at maximum in June and July. Similar to the loblolly pine study by Johnsen et al. (2007), R_{soil} did not respond to a reduction in the flow of carbohydrates due to a non-limiting supply of root starch during our early summer study period. Further, repeated sampling in these stands has shown no reduction in root biomass (Guo et al. 2004) or root growth and mortality (Guo et al. 2008) due to the scorching treatment. Hence, the lack of R_{soil} response belowground, but the presence of R_{stem} response aboveground supports the contention (cf. Guo et al. 2004) that in this disturbance-driven system, the relationship between current carbohydrate supply and belowground dynamics is decoupled, particularly during the periods of the greatest belowground C allocation and storage.

Soil chamber distance had a strong effect on R_{soil}, which increased with proximity to tree stems. R_{soil} was strongly related to changes in soil moisture and R_{soil} greater than 1 m from a tree stem declined with decreases in soil water content at a faster rate than R_{soil} close to stems. The significant soil chamber distance by time interaction indicates that small roots and associated soil microbes distal to the stem are more sensitive to changes in soil moisture than roots more proximal to tree stems.

Conclusions

Even though it has been shown that longleaf pine has high water use efficiency (Ford et al. 2008), our study suggests that this may not be the case immediately following fires that result in substantial loss of leaf area. If the dissimilar rates of E_{L} between treatments in this study were partially due to tissue damage in scorched foliage, then during particularly dry periods, this response to fire could result in extreme moisture stress possibly leading to mortality, or at least result in reductions in growth, in addition to responses reported by others (Cary 1932; Boyer 1994; Boyer and Miller 1994). Hence, taken together, these results support findings that using prescribed fire in young longleaf pine stands brings risks via canopy scorching that may translate into reduced long-term growth due to altered physiological function.

Our observed response in whole tree water use (Q) to leaf area reduction was unexpected. Our expectation was a reduction in water use proportional to reductions in leaf area following scorching with some stomatal adjustment, as opposed to no change in Q. The relationship between E_L in the scorched trees and D (Fig. 3) suggests that the direct linkage between atmospheric conditions and water loss may have been enhanced by damaged tissues in the scorched foliage. The combination of water loss due to damaged foliage and stomatal adjustment in remaining live foliage may together better account for the observed increase in E_L. The decline in R_{stem} was likely a function of reduced carbohydrate supply. In these trees, R_{stem} originates primarily from respiration of cambial and phloem tissues near the stem surface. While variation in sap flux density can greatly influence R_{stem}, it had little effect in our study as rates of J_s between treatments were similar. We therefore conclude that reduced R_{stem} in these trees was a result of reduced transport of photosynthate to stems. In contrast to R_{stem} results, R_{soil} did not decrease following canopy scorching. This may be because these stands have large carbohydrate reserves in roots and are able to maintain root metabolism, at least in the short-term. Hence, given the emphasis on restoration of this beleaguered ecosystem, careful planning to avoid canopy scorching would minimize impacts of fire management.

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