



Influence of repeated canopy scorching on soil CO₂ efflux

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ABSTRACT

Forest ecosystems experience various disturbances that can affect belowground carbon cycling to different degrees. Here, we investigate if successive annual foliar scorching events will result in a large and rapid decline in soil CO₂ efflux, similar to that observed in girdling studies. Using the fire-adapted longleaf pine (*Pinus palustris* Mill.) tree species, we experimentally manipulated foliar leaf area and thus, canopy photosynthesis, via foliar scorching over two consecutive growing seasons. We monitored the effect of scorching on soil CO₂ efflux and fine root production, mortality, standing crop, and nitrogen (N) and non-structural carbohydrate (i.e. sugar and starch) concentrations. Despite an immediate 80% reduction in foliar leaf area and sap flow rates from the scorch treatment, there was no effect on soil CO₂ efflux in either year. Likewise, the cumulative soil CO₂ flux after two scorch treatments remained comparable to that of the control treatment, even after assuming a 100% decline in the autotrophic component for the month following the two scorching events. Fine root standing crop was not diminished by scorching because both fine root production and mortality increased commensurately in the scorch treatment. Fine root N and sugar concentrations were not diminished by scorching, but starch concentrations of 5th order roots decreased after the second scorching treatment, presumably because starch was mobilized from larger roots to maintain more metabolically active 1st order roots. The lack of response observed in soil CO₂ efflux following successive canopy scorches differs from the response often observed after girdling and suggests that the carbohydrate reserves of longleaf pine trees are sufficient to maintain root metabolism for extended periods even after an extreme canopy perturbation. We propose that tree species in ecosystems that experience frequent disturbance may allocate more carbon to storage than those in less disturbed ecosystems, and as a result are more resilient to disturbances that affect photosynthate supply. Such species should be capable of maintaining belowground autotrophic respiration during periods of minimal or nonexistent carbon assimilation.

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1. Introduction

Forest ecosystems experience various disturbances that can affect carbon cycling to different degrees. Acute catastrophic disturbances such as hurricanes, bark beetle outbreaks, or severe fires can drastically alter forest carbon cycling via large-scale mortality which transfers carbon from one pool to another. Chronic disturbances such as insect defoliation and moderate fire alter carbon cycling more subtly by influencing canopy leaf area and thus, carbon assimilation. Since carbon assimilation supplies the carbohydrate

substrates required to fuel respiratory processes within non-photosynthetic organs, disturbances that affect assimilation may also affect respiratory processes throughout the plant, including root respiration.

Experiments using stem girdling – a technique that removes bark and phloem and thus terminates substrate transport below the point of phloem interruption – have indicated a strong link between root respiration and recently assimilated carbon (i.e. photosynthate). For example, Höglberg et al. (2001) observed a 27% decline in soil CO₂ efflux within five days of girdling Scots pine (*Pinus sylvestris* L.) in the early summer and a 37% decline within five days of girdling in the late summer. Soil CO₂ efflux rates were approximately 50% lower in the girdled treatments than the corresponding

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control treatment by the end of the growing season. Similar reductions in soil CO₂ efflux and response times have been found when girdling European chestnut (*Castanea sativa* Mill.; Frey et al., 2006), Norway spruce (*Picea abies* (L.) Karst.; Olsson et al., 2005), and European beech (*Fagus sylvatica* L.; Andersen et al., 2005). The rapid and dramatic decreases in soil CO₂ efflux following girdling suggests that root respiration for these species depends on the current availability of photosynthate for a substantial portion of its metabolism.

Catastrophic and chronic disturbances should influence root respiration to different degrees. For example, wood-boring insects can permanently disrupt photosynthate transport to tree roots by removing phloem from the stem in much the same way as physical stem girdling (Kurz et al., 2008). However, reductions in leaf area from insect herbivory and fire are more common landscape-scale disturbances capable of influencing the availability and transport of photosynthate belowground. Relative to the severe and permanent damage that girdling has on phloem transport, foliar scorching and insect defoliation are less severe and reversible perturbations because phloem remains intact, re-foliation occurs, and trees retain the capacity to assimilate carbon and supply non-photosynthetic organs with respiratory substrate. Thus, root respiration and therefore, soil CO₂ efflux, as well as other belowground processes may respond differently to temporary interruptions in photosynthate availability compared to permanent interruptions.

Our objective was to determine if levels of canopy disturbance typical of frequent natural disturbance would influence belowground processes. Since longleaf pine (*P. palustris* Mill.) ecosystems have an evolutionary history of chronic disturbance via burning with fires returning as frequently as every 1–3 years (Mitchell et al., 2006) and individual trees commonly withstand crown scorch consuming up to 100% of the foliage (Guo et al., 2008), it was an ideal species for this study. Specifically, we aimed to determine if severe defoliation caused by successive annual foliar scorching events would result in a decline in soil CO₂ efflux, a reduction in fine root production, an increase in fine root mortality, or a decrease in fine root nitrogen (N) or non-structural carbohydrate (i.e. sugar and starch) concentrations. We hypothesized that (1) soil CO₂ efflux would not be reduced by foliar scorching because belowground carbohydrate reserves of longleaf pine would be sufficient to satiate carbohydrate requirements of root respiration under periods of reduced photosynthate availability, and (2) carbohydrate concentrations of the smallest, most metabolically active fine roots would be maintained via the mobilization of carbohydrate reserves from larger roots.

2. Materials and methods

2.1. Study site and experimental treatments

This study was conducted in a 50 ha longleaf pine plantation located at the Joseph W. Jones Ecological Research Center in Newton, GA, USA (31°15' N latitude and 84°30' W longitude). The plantation was established in 1980 using an approximate 1.5 × 2 m planting grid, and longleaf pine was the exclusive overstory species (mean dbh = 16.9 cm and mean height = 14.3 m at the beginning of the experiment). The soil in the plantation is a Typic Quartzipsamment characterized by coarse sand that exceeds 2.5 m in depth, weak development of horizons due to mixing by fauna, low organic matter content, and lack of silt and clay (Goebel et al., 2001). The climate for this region has been characterized as humid subtropical with an average annual precipitation of 1310 mm distributed evenly throughout the year.

Foliar scorching was conducted in four 20 × 20 m plots. There were also four equivalent control plots. To reduce potential edge

effects, sample collections were confined to the central 15 × 15 m subplot within each treatment plot, and plots were separated by at least a 20 m buffer zone. Lateral roots of longleaf pine trees within a similar diameter class (15.4–24.0 cm dbh) as those in our study can extend 5.0–5.3 m from the tap root (Hodgkins and Nichols, 1977); therefore, roots from trees outside of our treatment plots should not have influenced measurements within our central measurement plots. An 18 m hydraulic lift was used to access the canopy, and a hand-held torch connected to a propane tank was used to scorch the foliage. The scorching process took approximately 10 s per needle flush. In the summers of 2006 and 2007, following the development of current year needle production, approximately 80% of the foliage (i.e. all needles except those on the main stem) was killed on each tree in the scorch treatment plots. Following the scorch treatment, needles rapidly desiccated and died, but most needles remained connected to the branches. Although we did not measure leaf elongation, we observed that needles of the post-scorch flush had nearly fully elongated within one month of applying the scorch treatment.

2.2. Xylem sap flow

Whole-tree canopy assimilation is a function of water use which can be estimated via xylem sap flow (Smith and Allen, 1996). We measured xylem sap flow with 30 mm thermal dissipation probes (Granier, 1985, 1987) prior to and following the first scorch treatment in 2006, but not the second scorch treatment in 2007. One thermal dissipation probe was installed at a height of 1.4 m on both the north and east side of two trees in three replicate plots of each treatment. Campbell CR10X and CR23X dataloggers measured the sensors every 30 s and stored 15 min averages (Campbell Scientific Inc., Logan, Utah, USA). Output from the two thermal dissipation probes was averaged per tree. Sapwood area was assumed to be the outer 30 mm band of xylem. This assumption likely underestimated the conducting sapwood area somewhat, although the outer 20 mm has been shown to contain the area of maximum sap conductance (Cohen et al., 1985) which diminishes rapidly with depth in pine (Ford et al., 2004). However, any errors that may have resulted from our assumptions of sapwood area should be of minor consequence as we were primarily interested in relative differences of sap flow between the control and scorch treatments. To determine scorching effects, sap flow rates of scorched trees were standardized by sap flow rates of control trees at the treatment level.

2.3. Soil CO₂ efflux

Soil CO₂ efflux rates were measured monthly in 2006 and 2007 using a Li-6400–09 soil chamber and Li-6400XT portable photosynthesis system (Li-Cor Inc., Lincoln NE, USA). Measurements were collected at five PVC soil collars (10.16 cm wide × 4.4 cm high inserted to a soil depth of 2.2 cm) randomly located in the center of each plot. Soil CO₂ efflux was measured between 11:00 and 14:00 h to standardize maximum daily rates. Soil temperature was measured concurrently at each sample location to a 5 cm depth using a Li-6000–09TC soil probe thermocouple (Li-Cor Inc., Lincoln, NE, USA). Soil moisture at 30 cm depth was measured monthly throughout the observation period at two locations within each plot using a 1502B time-domain reflectometer (Tektronix, Inc., Beaverton, OR, USA).

To determine long-term effects of canopy scorching on soil CO₂ efflux, we estimated cumulative soil CO₂ efflux from individual soil CO₂ efflux rates measured across our observation period. Each measurement date was considered the midpoint of a sampling period, so the mean soil CO₂ efflux rate of consecutive measurement dates were used to estimate the soil CO₂ efflux rate for the time

period between measurement dates. Cumulative soil CO₂ efflux was calculated as the sum of daily soil CO₂ efflux throughout the observation period with the first measurement date set to zero. These calculations were performed at the plot level. To account for short-term declines in soil CO₂ efflux that could potentially have occurred immediately after scorching events and gone undetected due to our sampling frequency, we also decreased soil CO₂ efflux rates in the scorch treatment plots by one-half for the measurement dates prior to and immediately following the scorching event. The rationale to decrease soil CO₂ efflux rates by one-half is because root respiration comprises, on average, 50% of bulk soil CO₂ efflux in forest ecosystems (Hanson et al., 2000; Bond-Lamberty et al., 2004; Subke et al., 2006) and previous work has shown that longleaf pine root respiration at this site is quite high (Cheng et al., 2005).

2.4. Fine root indices

Fine root (<2 mm diameter) production and mortality estimates were measured using the minirhizotron approach described by Guo et al. (2008). Acrylic tubes were installed at a 45° angle to a depth of 50 cm at three randomly located positions near the center of each plot. Each month, root images in numbered cells along each tube were recorded with digital photographs and analyzed with the software package RooTracker (Ver. 2.0, David C. Tremmel, Duke University Phytotron, Durham, NC, USA). The longleaf plantation canopy had closed and the understory consisted of pine needles, so only pine roots were captured in root images.

Fine root standing crop and N concentration were assessed post-scorch (one month after treatment) in 2006 and 2007 using an intact soil monolith approach (Guo et al., 2004). Three soil monoliths were collected in each plot by manually inserting a 30 cm l × 20 cm w × 30 cm d metal core. Extracted monoliths were placed on a two-layer sieve box to separate roots from soil. The top sieve had a 12.7 mm metal mesh and the bottom sieve had a 6.35 mm metal mesh. Once the soil had passed through the two-layer sieve, it was then passed through a 2 mm metal mesh sieve to remove fine roots that were not collected by the two-layer sieve box. The collected roots were placed in plastic bags in a cooler for transport to the laboratory where they were sorted by branch order (Guo et al., 2004) and oven-dried at 70 °C to a constant mass. Root samples were then weighed, ground, and homogenized using a SPEX 8000-D mixer mill (SPEX, Edison, NJ, USA). To determine N concentration, sub-samples were analyzed on a FlashEA 1112 Series NC Soil Analyzer (Thermo Electron Corp., Waltham, MA, USA).

Root samples for non-structural carbohydrate concentration assessments were collected and processed following the approach described by Guo et al. (2004). Root tissues were analyzed for non-structural carbohydrates in a two-step process to determine both sugar and starch concentrations. Dried root samples were weighed then extracted overnight in 10 ml of 80% ethanol (v/v) followed by centrifuging at 2200 rpm for 15 min. The resulting supernatant was transferred to a 50 ml volumetric flask. The residual pellet was extracted again with 5 ml of 80% ethanol and centrifuged at 2200 rpm for 5 min. The supernatant was composited with that from the first extraction, diluted to 50 ml with 80% ethanol, and analyzed for sugars. The residue from the ethanol extractions was transferred to a glass tube, dried, and then boiled for three hours in 5 ml 3% HCl (w/w). The filtrate was then diluted to 50 ml with 3% HCl and analyzed for starch. A modified phenol-sulfuric acid method was used for both sugar and starch analyses (Buisse and Merckx, 1993). In a glass tube, 1 ml of solution was combined with 1 ml of 28% phenol in 400 ml of 80% ethanol and 5 ml of concentrated sulfuric acid. The tube was shaken for 1 min and allowed to stand for 15 min. Finally, absorption was measured

at 490 nm on a Shimadzu UV-2101PC spectrophotometer (Shimadzu Scientific Instruments, Columbia, MD, USA) and concentrations determined by standard curves.

2.5. Statistical analyses

We analyzed the impact of the scorch treatment on sap flow using a linear regression with time since scorching as the independent variable and scorch treatment sap flow rates expressed as a percent of control treatment sap flow rates as the dependent variable. We analyzed soil CO₂ efflux, fine root standing crop, production, mortality, and N and non-structural carbohydrate concentrations using a completely randomized multi-factorial repeated measures design. The experimental unit (plot) was treated as the random subject factor in all repeated measures analyses. Scorch treatment ($n = 2$) was treated as a fixed factor and year ($n = 2$) was treated as the fixed repeated factor when analyzing fine root standing crop, production, and mortality. A similar model was used for soil CO₂ efflux, but monthly sampling period ($n = 19$) was treated as the fixed repeated factor. Treatment effects on cumulative soil CO₂ efflux at the end of our observation period (i.e. December 2007) were analyzed using a one-way ANOVA with plot as a random factor. Root order ($n = 3$) was included as an additional fixed factor in the N and non-structural carbohydrate concentration analyses. Fine root production, mortality, and N and non-structural carbohydrate concentrations were proportional values and presented as such throughout the report; however, data were arcsine square root transformed to satisfy ANOVA assumptions (Zar, 1996). Denominator degrees of freedom were estimated according to the Kenward–Roger method (Kenward and Roger, 1997). Treatment means were compared using Fisher's Least Significant Difference (LSD) test. When interactions occurred, we performed tests of simple main effects (Schabenberger et al., 2000; Littell et al., 2006). All repeated measures analyses and the one-way ANOVA were performed using a mixed model procedure (PROC MIXED; Version 9.1.3, SAS Inc., Cary, NC, USA) with a type-I error rate of 0.05. Data presented in text are means ± standard error.

3. Results

3.1. Sap flow

Sap flow was reduced to 20% of that in the control treatment immediately after the scorch treatment was applied; however, recovery occurred surprisingly rapidly reaching 90% of that in the control treatment within one month (Fig. 1).

3.2. Soil CO₂ efflux

Despite large and immediate reductions to sap flow rates, soil CO₂ efflux was not influenced by the scorch treatment ($P = 0.2254$) and seasonal dynamics ($P < 0.0001$) were independent of treatment (i.e. no treatment × time interaction Fig. 2a). In 2006, soil CO₂ efflux rates increased from 2.0 μmol CO₂ m⁻² s⁻¹ in May, to a peak of slightly more than 3.0 μmol CO₂ m⁻² s⁻¹ in July, followed by a steady decline to less than 1.0 μmol CO₂ m⁻² s⁻¹ in December. A similar pattern was observed in 2007 with maximum annual soil CO₂ efflux rates occurring in August followed by a steady decline through the remainder of the year. The scorch treatment was applied just after peak annual soil CO₂ efflux rates in 2006 and the subsequent flux rates in control and scorch treatments declined in a comparable manner. In 2007, the application of the scorch treatment preceded the maximum annual soil CO₂ efflux rates, and the post-scorch efflux in both the control and scorch

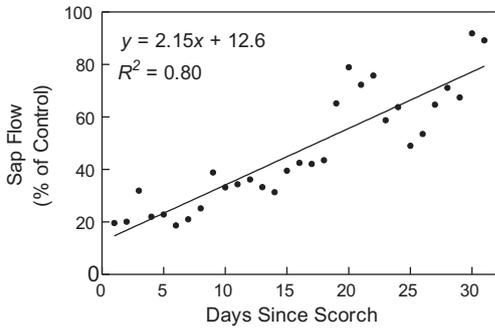


Fig. 1. Recovery of sap flow for the scorch treatment expressed as a percent of the control treatment sap flow rate. Sap flow rates in the scorch treatment were approximately 20% of those in the control treatment immediately after treatment application, but recovered to approximately 90% of that in the control treatment within one month. Each point on the figure represents the mean of the scorch treatment plots expressed as a percent of the mean of the control treatment plots. Data are from the 2006 growing season.

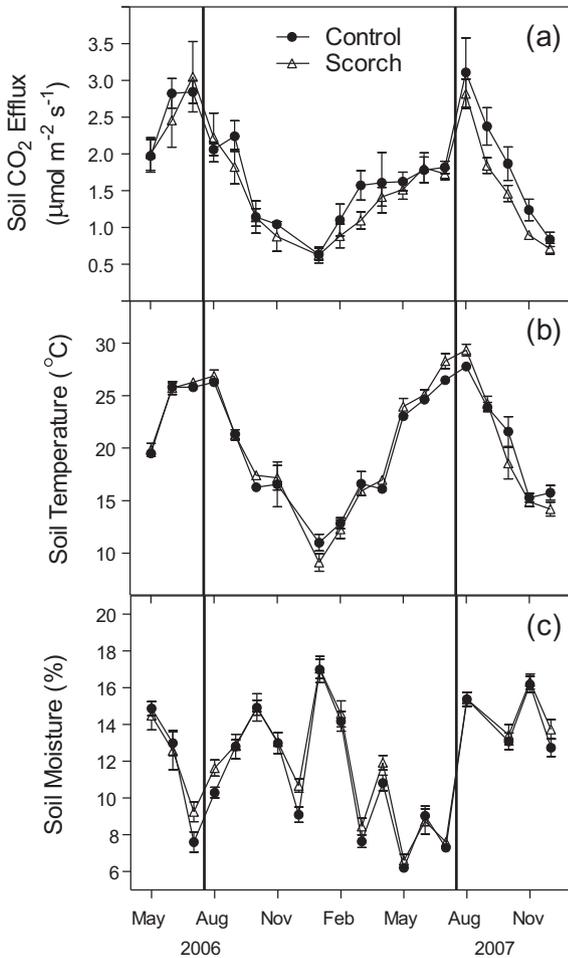


Fig. 2. Soil CO₂ efflux (mean ± SE) for control and scorch treatments showed no treatment differences over two consecutive years and scorching applications. Vertical lines indicate when scorching occurred.

treatments increased to a peak in August (3.12 and 2.82 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for the control and scorch treatments, respectively) before falling consistently to the annual lows in December (0.84 and 0.72 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for control and scorch treatments, respectively). Soil temperature varied with time ($P < 0.0001$), but was not influenced by the scorch treatment ($P = 0.9709$; Fig. 2b). Soil

moisture also varied with time ($P < 0.0001$) and was higher in the scorch treatment, but this treatment effect only occurred in July and December of 2006 (i.e. treatment × time interaction; $P = 0.0248$; Fig. 2c).

At the end of our observation period, the cumulative soil CO₂ efflux in the scorch treatment ($951.92 \pm 68.57 \text{ g C m}^{-2}$) was 10% lower, but statistically similar, to that in the control treatment ($1062.99 \pm 97.38 \text{ g C m}^{-2}$; $P = 0.5279$). Likewise, there was no statistical difference between cumulative soil CO₂ efflux of control and scorch treatments after accounting for potential declines in root respiration immediately following each scorch application ($878.85 \pm 62.34 \text{ g C m}^{-2}$; $P = 0.2502$).

3.3. Fine root indices

Both fine root production and mortality were higher in the scorch than the control treatment ($P = 0.0056$ and $P = 0.0414$, respectively) and followed seasonal dynamics (both $P < 0.0001$) that were independent of treatment (i.e. no treatment × time interaction Fig. 3a and b). The higher rates of fine root production and mortality observed in the scorch treatment apparently offset each other as fine root standing crop was not influenced by the scorch treatment ($P = 0.3878$) and remained relatively stable between 2006 and 2007 ($P = 0.2019$; data not presented). Averaged across all plots and both years, fine root standing crop was $1.66 \pm 0.12 \text{ Mg ha}^{-1}$.

Fine root N concentration varied significantly by root order in 2006, but not in 2007 (i.e. root order × year interaction, $P = 0.0043$), and were not influenced by the scorch treatment ($P = 0.7772$, data not presented). Fine root sugar concentrations varied significantly by root order ($P < 0.0001$) and were larger in 2007 than in 2006 ($P = 0.0004$), but were not influenced by the scorch treatment ($P = 0.9568$, data not presented). Regardless of treatment or year, fine root starch concentrations varied significantly among

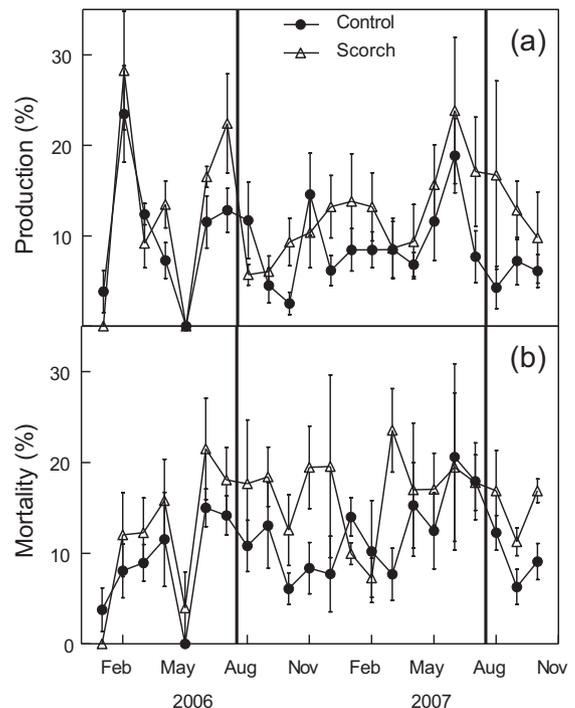


Fig. 3. Mean ± SE (a) percent fine root (<2 mm) production and (b) percent fine root mortality differed between treatments prior to treatment application and differences remained independent of treatment through time. Vertical lines indicate when scorching occurred.

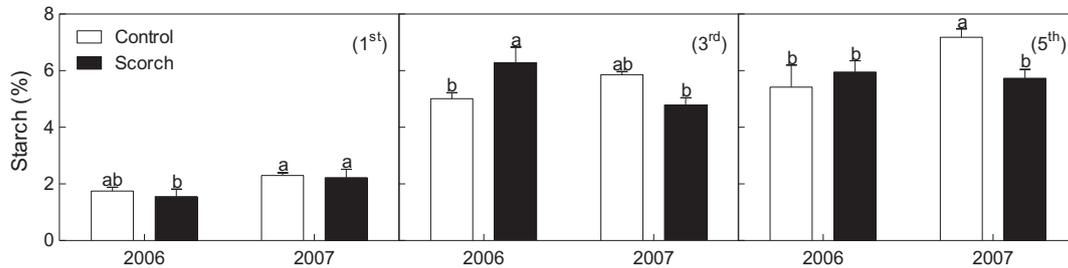


Fig. 4. Mean \pm SE fine root starch concentrations expressed on a percent basis in 1st, 3rd, and 5th order fine roots (<2 mm) for control and scorch treatments. Fine root starch concentrations were significantly impacted by the scorch treatment, but the effect was dependent upon root order and year. Means sharing a letter within each root order are not significantly different (Fisher's LSD, $\alpha = 0.05$).

1st, 3rd, and 5th order fine roots ($P < 0.0001$) as starch concentrations were generally highest in 5th order roots and lowest in 1st order roots (Fig. 4). Fine root starch concentrations were significantly influenced by the scorch treatment, but the effect was dependent upon root order and year (i.e. root order \times scorch treatment \times year interaction, $P = 0.0225$). For example, starch concentrations in the larger 5th order roots were lower in the scorch treatment than the control treatment in 2007, but not in 2006. Starch concentrations of smaller and more metabolically active 1st order roots were not influenced by the scorch treatment in either year. In 2006, starch concentrations of 3rd order roots were higher in the scorch treatment than the control treatment; however, after the 2007 scorch treatment, starch concentrations of 3rd order roots were not statistically different from the control treatment. Starch concentrations of all root orders tended to increase from 2006 to 2007 in the control treatment and in the 1st order roots in the scorch treatment, but decreased in 3rd order roots in the scorch treatment and remained relatively static in 5th order roots in the scorch treatment.

3.4. Estimates of stored carbon

We explored the question of how long stored carbon in roots could maintain respiration of the existing root standing crop if the supply of current photosynthate was interrupted (i.e. it assumes that new root growth and mortality is not occurring – only maintenance of the existing root system is considered). First, we calculated the total nonstructural carbohydrate content of coarse roots in this longleaf pine plantation. We assumed coarse root biomass was 50% of the stem biomass (Albaugh et al., 2006). Stem biomass was estimated using site-specific allometric equations (unpublished data) that predicted stem biomass as a function of dbh. In addition, supplemental sampling showed that higher order lateral roots (8th order) were similar in non-structural carbohydrate concentration to that of 5th order roots (i.e. 6% of dry weight Fig. 4). Based on these assumptions, we estimated a coarse root carbohydrate reserve of 111 g C m^{-2} at this plantation. Second, if autotrophic respiration is assumed to account for 50% of total soil CO_2 efflux (Hanson et al., 2000), it would be a flux of approximately $500 \text{ g C m}^{-2} \text{ year}^{-1}$ in this plantation. Under this scenario, coarse root carbohydrate reserves represent roughly one-half of the annual belowground autotrophic respiration demand in this ecosystem. This estimate likely represents a minimum value since it does not include carbohydrate reserves stored in stumps, tap roots, or fine roots.

4. Discussion

Our results indicate that severe canopy scorches in successive years had negligible and statistically non-significant effects on soil

CO_2 efflux in this longleaf pine plantation. There was a statistically non-significant decrease in soil CO_2 efflux in the scorch treatment during the second month after the first scorch event, and for four months after the second scorch event. However, we also found that the cumulative soil CO_2 flux after two scorch treatments remained comparable to that of the control treatment – even after assuming a 100% decline in the autotrophic component. It was clear that soil CO_2 efflux was not affected by the scorch treatment to any large extent, in contrast to the large reductions observed in girdling studies that permanently disrupt the transport of carbohydrates to the root system (Högberg et al., 2001). Scorching also did not result in reduced fine root production. In fact, trees in the scorch treatment showed higher fine root production and mortality, which may have been an indication that nutrients were a greater limitation than carbon for rebuilding canopy leaf area. Fine root N concentration, a surrogate for enzyme concentration and respiration rates (Ryan et al., 1996; Vose and Ryan, 2002), was not influenced by scorch treatments. In the same study plots Sims et al. (2007) reported that production of mycorrhizal fungi, which are functional extensions of fine roots, were not impacted by scorch treatments.

There are a few possible explanations as to why soil CO_2 efflux was not affected by the scorch treatment. One possibility is that heterotrophic respiration might have been much greater than autotrophic respiration, which would have obscured changes in the autotrophic component of soil CO_2 efflux. To our knowledge, there are no published reports describing the relative contributions of belowground autotrophic and heterotrophic respiration in longleaf pine systems; however, we know that longleaf pine root respiration at this site is quite high (Cheng et al., 2005) and we assume that decomposition plays a relatively minor role in these sandy soils that lack a substantial aboveground detrital input because of the short fire intervals. Therefore, treatment-induced impacts on the autotrophic component should have been detectable via changes in soil CO_2 efflux. Another possible explanation is that the decrease in sap flow after the scorch events could have influenced the relative importance of the internal (xylem) and external (soil) pathways for root-respired CO_2 movement. The quantity of root-respired CO_2 that can be transported internally via xylem has been shown to rival that diffusing from the soil surface and the magnitude of internally transported CO_2 is largely dependent on the quantity of water transpired (Aubrey and Teskey, 2009). When sap flow decreased immediately after the scorching events, a portion of the root-respired CO_2 that would normally move via the internal pathway might instead have diffused into the soil atmosphere. Thus, even if root respiration decreased after the scorching events, there may have been an increase in diffusion of root-respired CO_2 into the soil that might have obscured differences in soil CO_2 efflux between the two treatments. However, the internal transport of root-derived CO_2 has only been demonstrated in a single species (Aubrey and Teskey, 2009), so this

explanation is highly speculative but remains a possibility. Consistent with our hypothesis, the most likely explanation for lack of substantial effects on soil CO₂ efflux from crown scorching is that carbohydrate reserves maintained root respiration in the absence of current photosynthate. This was due to the combination of storage carbohydrates in the roots, and perhaps elsewhere, and a rapid recovery of leaf area after the scorch event. Starch concentrations of 5th order roots decreased after the second canopy scorching treatment indicating that stored carbohydrates were being used for the maintenance of root respiration. However, sap flow rates recovered quickly after the scorch event indicating a rapid recovery of leaf area, alleviating the demand on stored carbohydrates.

The utilization of carbohydrate reserves to support belowground autotrophic growth and respiration after disturbance is supported in other field studies. A ¹³C tracer study conducted in a regenerating scrub oak ecosystem prone to frequent fires indicated that 33% of carbon in newly established roots originated from a source other than recent photosynthate (Langley et al., 2002). Following complete removal of leaf biomass by hurricane force winds in a tropical forest, new roots were produced using carbohydrate reserves that had been stored 2–10 years prior to the disturbance (Vargas et al., 2009). Stored carbohydrates may be used for root functions even in the absence of disturbance. Studies in a black spruce (*Picea mariana* (Mill.) Britton, Sterns, & Poggenb.) forest using ¹⁴C suggested the predominant fraction of carbohydrates supporting root respiration was approximately 3–5 years old (Czimczik et al., 2006; Schuur and Trumbore, 2006; Carbone et al., 2007).

In the scorch treatment, starch in the higher order roots (i.e. larger diameter, secondary roots that presumably serve a carbon storage function) was transferred to the more distal lower order roots, i.e. to the smaller diameter, primary roots that function in concert with mycorrhizal fungi in resource uptake and assimilation (Guo et al., 2004; Varner et al., 2009; O'Brien et al., 2010). The temporal patterns of carbohydrate accretion and depletion observed in the control and scorch treatment suggest that allocation of photosynthate to carbohydrate reserves occurred between 2006 and 2007 in the control treatment, but not in the scorch treatment. There were reduced starch concentrations in 5th order roots following the 2007 scorch treatment, but apparently root metabolic demands were satisfied because soil CO₂ efflux remained unaffected. The observed patterns of starch depletion in higher order roots while lower order roots maintained relatively static starch concentrations lends support to our mobilization hypothesis.

Stem girdling of trees can result in relatively rapid and dramatic decreases in soil CO₂ efflux, indicating that current photosynthate supplies a large proportion of the carbohydrates used for belowground autotrophic respiration (Högberg et al., 2001; Andersen et al., 2005; Olsson et al., 2005; Frey et al., 2006). However, other girdling studies indicate that there can be less direct coupling between the supply of current photosynthate and belowground processes, presumably due to a larger use of stored carbohydrates. For example, girdling *Eucalyptus* resulted in only modest reductions in soil CO₂ efflux (Binkley et al., 2006) and girdling of tulip poplar (*Liriodendron tulipifera* L.) had no effect on soil CO₂ efflux for at least two years (Edwards and Ross-Todd (1979). Initially, girdling the stems of Norway spruce had no effect on soil CO₂ efflux but efflux rates eventually decreased by 57% two months following girdling (Subke et al., 2004). This suggests that in contrast to the results in yellow poplar (Edwards and Ross-Todd (1979), carbohydrate reserves in Norway spruce were insufficient to maintain root metabolic requirements for an extended period. The season of disturbance may also influence the linkage between canopy photosynthesis and soil CO₂ efflux. Reducing phloem transport by chilling the stems of loblolly pine (*P. taeda* L.) in the autumn resulted in a 30% decline in soil CO₂ efflux, whereas in the spring that treatment

had no effect (Johnsen et al., 2007). The lack of response in the spring coincided with seasonal maximum carbohydrate reserves, whereas the decrease in soil CO₂ efflux following stem chilling in the autumn coincided with seasonal minimum carbohydrate reserves (Sampson et al., 2001).

Guo et al. (2004) hypothesized that species differences in the response of soil CO₂ efflux to girdling may be reconciled, at least in part, by considering the evolutionary life history of a species with respect to disturbance regimes. For example, extensive carbohydrate reserves confer a competitive advantage to species that root sprout after disturbance (Kosola et al., 2001; Langley et al., 2002; Clarke et al., 2010). Longleaf pine has adapted to frequent fire regimes in many ways. The carbohydrate reserves in the root system help buffer longleaf pine trees from disruption of the supply of current photosynthate if the foliage is burned. The capacity to buffer the loss of current photosynthate production begins in the seedling stage of this species, called the grass stage, in which the foliage is repeatedly burned off and replaced by a new cohort of foliage from root carbohydrate reserves.

5. Conclusions

Our results indicate that canopy scorching, typical of severe natural disturbance in longleaf pine ecosystems, did not decrease root respiration or fine root growth. Successive years of canopy scorching did not significantly influence soil CO₂ efflux, suggesting that longleaf pines are well-adapted to buffer a disruption of canopy photosynthesis from disturbance events. We attribute the lack of response in soil CO₂ efflux to the use of stored carbohydrate reserves and a rapid recovery of canopy leaf area. The origin of carbohydrate reserves used for root respiration and re-foliation was not identified in our study, but the rapid recovery of leaf area following the scorch treatment suggests that longleaf pine has extensive carbohydrate reserves and possess a capacity to quickly mobilize these reserves in response to a perturbation that reduces or prevents canopy carbon assimilation, which is likely to allow trees to more effectively buffer the lack of current photosynthate, at least temporarily. Our results, combined with those of other studies, suggest that species that allocate more carbon to storage will be more resilient to disturbance. We therefore expect a continuum of responses to disturbances related to ecological niche and adaptation that influence the availability of photosynthate for belowground processes, as well as a continuum in belowground carbohydrate reserves and root respiratory buffering capacity among species as well as spatially, temporally, and developmentally within individuals of the same species. A poor understanding of carbon storage pools and fluxes at tree and ecosystem scales impedes our ability to fully appreciate the role of carbohydrate reserves in the forest carbon cycle. Future investigations that address the patterns and mechanistic controls of carbohydrate accretion and depletion can provide valuable insight into carbon cycling dynamics, and may be critical to our understanding of the impact of natural and anthropogenic disturbances in forest ecosystems.

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