

RESEARCH ARTICLE

ACUTE PHYSIOLOGICAL STRESS AND MORTALITY FOLLOWING FIRE IN A LONG-UNBURNED LONGLEAF PINE ECOSYSTEM

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ABSTRACT

One important legacy of fire exclusion in ecosystems dependent upon frequent fire is the development of organic soil horizons (forest floor) that can be colonized by fine roots. When fire is re-introduced, the forest floor is often consumed by fire and heavy overstory mortality, often delayed by months, results. We hypothesized that the delayed post-fire tree mortality is a manifestation of a cascade of physiological stresses initiated by root damage that can also magnify the impact of other kinds of damage. We investigated the physiological impact of forest floor consumption on longleaf pines (*Pinus palustris* Mill.) subjected to a wildfire in 2005 in a long-unburned (>50 years) forest by measuring forest floor consumption, whole tree water use, and leaf chlorophyll content. Ten of the 23 study trees died within three years post fire. Post-fire sap flux was unrelated to crown scorch, but was negatively correlated with forest floor consumption. A segmented linear regression revealed declines in sap flux until a threshold of 31% forest floor consumption, after which further consumption had no additional effect on tree water use. Trees with >30% forest floor consumption beneath their crowns were more than 20 times as likely to die as those with less consumption. Chlorophyll content in needles that flushed post fire was negatively correlated with crown scorch ($R^2 = 0.60$, $P = 0.009$) though all trees with scorch also experienced varying degrees of forest floor consumption. Our results suggest that the consumption of the forest floor with the likely concomitant loss of roots initiated a decline spiral, driven by an inability to supply sufficient water to the crown. Though we did not measure loss of stored carbohydrates in consumed roots directly, we infer that this likely effect, coupled with decreased crown photosynthetic capacity, eventually resulted in substantial overstory tree mortality.

Keywords: chlorophyll, crown scorch, duff, forest floor consumption, *Pinus palustris*, transpiration

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INTRODUCTION

The natural history of forests is a history of fire (Spurr and Barnes 1980); however, fire management has often ignored this history with catastrophic consequences (Dombeck *et al.* 2004). Nowhere are these consequences more evident than in coniferous ecosystems that are sustained by frequent fire, such as those dominated by ponderosa pine (*Pinus ponderosa* C. Laws.) (Covington and Moore 1994), Caribbean pine (*Pinus caribaea* Morelet) (O'Brien *et al.* 2009), slash pine (*Pinus elliottii* Engelm.) (Abrahamson and Hartnett 1990), and longleaf pine (*Pinus palustris* Mill.) ecosystems (Hendricks *et al.* 2002, Varner *et al.* 2005). Conifers adapted to frequent fire regimes possess many traits that confer resilience to low intensity surface fires, including self pruning limbs, thick bark, insulated buds, and reserves of stored carbohydrates that facilitate repair of damaged crowns. When repeatedly burned, these ecosystems are characterized by low fuel loads, little to no forest floor accumulation, and short fire residence time (Varner *et al.* 2005). The lack of forest floor accumulation restricts roots to mineral soil because roots do not colonize undecomposed leaf litter. Given sufficient time, a forest floor develops that includes fermentation (F) and humic (H) layers in frequently burned coniferous forests. These strata are prone to colonization by tree roots (Figure 1) and form an atypical fuel in these ecosystems (Covington and Moore 1994, Hendricks *et al.* 2002, Varner *et al.* 2005).

Forest fragmentation, urbanization, management decisions, changes in land uses, and land ownership have all contributed to a reduction in fire frequency in many longleaf stands across the southeast, with fire often excluded



Figure 1. Abundant fine roots in the forest floor in a longleaf stand at Fort Gordon, Georgia, USA.

for decades (Croker 1987, Frost 1993, Van Lear *et al.* 2005). When fires are reintroduced after long periods of exclusion, they typically burn with greater severity, resulting in reduced tree growth and increased mortality (Swezy and Agee 1991, Stephens and Finney 2002, McHugh and Kolb 2003). While mature longleaf pine mortality rates are low in surface fires (Boyer 1979), the smoldering ground fires that can occur in stands with a well developed forest floor have resulted in up to 80% overstory pine mortality (Varner *et al.* 2005). Loss of these trees can be catastrophic for ecosystem structure, composition, and function in these biologically diverse ecosystems (Kirkman *et al.* 2004, Mitchell *et al.* 2006, O'Brien *et al.* 2009). Although this problem has been observed in numerous frequently burned coniferous ecosystems, it is particularly acute in the southeastern United States in longleaf pines (Varner *et al.* 2005, 2007, 2009). Longleaf pine communities were historically one of the most frequently burned ecosystems in the world, with fires recurring annually in some stands (Mitchell *et al.* 2006). Longleaf pine ecosys-

tems are dependent on these frequent fires to regenerate overstory pines, suppress competing hardwoods, and maintain the high species richness characteristic (Kirkman *et al.* 2004, Pecot *et al.* 2006, Hiers *et al.* 2007).

The mechanisms regulating pine mortality following forest floor consumption are poorly understood, yet may have important implications for restoring fire regimes. Exactly what kind of injury drives delayed mortality remains unclear (Varner *et al.* 2009). Multiple studies have investigated different kinds of damage, though most focus on bole damage and crown scorch. For example, Ryan and Frandsen (1991) and Ryan (2000) proposed fire damage to stem vascular tissue as a cause of ponderosa pine stress and death. Crown scorch was inferred as the driver of post-fire mortality in slash pine by several authors (Dixon *et al.* 1984, Wade and Johansen 1987, Menges and Deyrup 2001). Although cambial damage and scorch represent injuries that could cause mortality, none of these studies measured the magnitude of physiological responses to observed damage or posited a specific mechanism for the delayed mortality. Studies attributing mortality to root consumption are fewer, though these were similarly unable to relate immediate effects of forest floor consumption on tree physiological function (Wyant *et al.* 1986, Ryan *et al.* 1988, Ryan and Reinhardt 1988, Saveland and Neuenschwander 1990, Swezy and Agee 1991, Haase and Sackett 1998, Ryan 2000, Stephens and Finney 2002, Varner *et al.* 2009). In long-unburned longleaf pine forests, Varner and others (2009) found that root nonstructural carbohydrates declined precipitously following smoldering forest floor fires, but they failed to quantify the acute cause for the carbohydrate drain.

We propose that the consumption of forest floor with the concomitant loss of bound roots results in a loss of below ground stored resources and reduced resource acquisition (water and minerals), thereby reducing canopy conductance and C fixation as well as a tree's ability to repair fire injury. These impairments

act as inciting stressors and initiate a decline spiral (*sensu* Manion 1981) with positive feedbacks driven by a decline in C fixation rates that result in the collapse of defenses (Wallin *et al.* 2003), ultimately resulting in tree death from secondary causes. In order to test the hypothesis that forest floor consumption results in acute water stress, we measured whole tree water use and leaf chlorophyll content in trees with varying degrees of forest floor consumption and crown scorch, both prior to and after fire, and tracked mortality for three years post fire.

METHODS

Study Site and Tree Selection

The measurements were collected in a long-unburned longleaf pine stand at Fort Gordon, near Augusta, Georgia, USA. Fort Gordon is located within the fall line region of eastern Georgia. Soils of the study area are typified by deep, excessively drained thermic, coated typical Quartzipsamments of the Lakeland series. The climate of the study area consists of warm summers (average July temperature of 27°C) and cool winters (average January temperature of 7°C), with annual precipitation averaging 1135 mm per year. The 100 ha study site had slopes ranging from 2% to 5%. The site had not burned in over 50 years and had a well-developed forest floor (Figure 1) with an average depth of 16.1 cm \pm 3.1 cm. While we did not quantify other components of the fuel bed, the understory and woody fuels were sparse and the fuel bed was dominated by the forest floor (Figure 2).

Within the study site, 20 trees in dominant and co-dominant crown positions with similar diameters at breast height (~35 cm dbh) were selected. The study trees had a mean dbh of 37.1 cm (\pm 2.7 cm) and a mean height of 19.6 m (\pm 2.4 m). The original plan had been to experimentally manipulate fire injury in a completely replicated manner with control, scorch, and for-

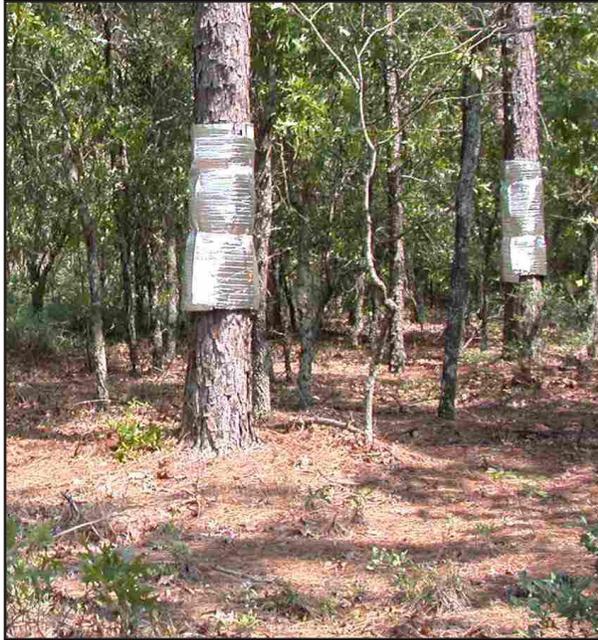


Figure 2. Pre-fire photograph of two study trees showing typical conditions in a long unburned forest: little herbaceous understory vegetation (Hiers *et al.* 2007), scattered woody fuels, and a deep forest floor.

est floor consumption as treatments. The forest floor consumption treatments were conducted on 23 June 2005, but on 25 June 2005, a wildfire, likely resulting from the initial experimental treatment, burned through most of the study area. Only two initially selected study trees remained unburned and 18 experienced various degrees of crown scorch and forest floor consumption. After the wildfire, three randomly selected undamaged trees were added as controls, bringing the total sample size to 23, of which 18 burned. These additional unburned trees were within 3 cm of the average diameter of the pre-selected trees and were within 100 m of the original study area. Although no direct observations were made of the wildfire behavior, post-fire measurements indicated that forest floor consumption and crown scorch were extensive among burned study trees (Figure 3).



Figure 3. Post-fire photograph of a study tree showing extensive though heterogeneous consumption of the forest floor.

Forest Floor Consumption

Following the fire, we estimated the amount of forest floor consumed in a 4 m diameter circle centered on each tree. Consumption was estimated using both wire pins that were installed prior to the fire and by visual estimates to the nearest 10%. We included visual estimates because several of the trees designated for other treatments had forest floor consumption due to the wildfire but did not have pins installed. We installed 24 pins in the potential pine rooting area around each tree, with six pins placed in transects at 10 cm, 40 cm, 80 cm, 120 cm, 160 cm, and 200 cm from the bole in the four cardinal directions within the drip-line of the tree canopies. With forest floor accumulation, substantial fine pine root ingrowth occurs, located in underlying duff and concentrated within the crown drip-line (Gordon and Varner 2002). Each pin was inserted into the soil until its preformed right angle bend contacted the surface of the fermentation layer of the forest floor. The visual estimates were based on the percentage of the area in a 2 m radius around the bole where mineral soil was exposed. There was no exposed mineral soil around the study trees prior to the fire, so the percent mineral soil exposed post fire was assumed to be caused by

forest floor consumption. After the fire, the distance between the bend and the consumed surface was measured to the nearest millimeter. We adjusted the visual estimates for use in subsequent analyses with the following equation derived from a correlation analysis:

$$\text{Consumption} = 0.8(\text{Visual Estimate}) + 24 \quad (1)$$

$\beta = 0.80$, adjusted $R^2 = 0.95$, $P < 0.001$.

Crown Scorch

Crown scorch was estimated in 10% increments as a proportion of the total crown volume (Peterson 1985). Downed woody, shrub, and herbaceous fuels were not measured prior to the wildfire, but the relative contribution of these loads is minor in many long-unburned stands (Varner *et al.* 2007). To account for delayed tree mortality, we censused tree mortality for three years (2005 to 2008).

We collected 27 root cores (4.8 cm in diameter) within the canopy drip-line of three of the unburned trees to estimate the proportion of fine roots found in the forest floor and upper 30 cm of the mineral soil. These cores were collected in three transects spaced at 120° intervals around the bole with samples taken at three distances: 30 cm from the bole, at the midpoint between the drip line of the crown (~2 m), and at the drip line (~2 m). Root cores were separated into forest floor and mineral fraction and passed through a 2 mm sieve, and then live and dead longleaf pine roots (≥ 2 mm) were separated, dried at 70°C for 72 hours, then weighed to the nearest 0.001 g.

Sap Flux Measurements

Transpiration rates were measured on each sampled longleaf pine using two xylem sap velocity sensors (Granier 1987). These sensors were inserted into the tree trunk at 1.3 m with one sensor placed on the south side and another on the east side of the bole. Transpiration rates were measured every 30 s, and 30 min aver-

ages were stored by a CR10X™ or CR23X™ datalogger (Campbell Scientific, Logan, Utah, USA). One month before the fire, transpiration rates were measured on the initial 20 sample trees. The wildfire destroyed most sensors and replacements were deployed approximately one month post fire. The first post-fire sap flux measurements were taken in August 2005 immediately after damaged crowns had produced new foliage. Transpiration rates were averaged and transformed into sap flux estimates after Granier (1987).

The effects of scorch and forest floor consumption on sap flux were analyzed using a general linear mixed model. We chose the linear mixed model in order to include the three additional undamaged trees sampled post fire in the analysis (Krueger and Tian 2004). We performed a *post-hoc* segmented (piecewise) regression on the sap flux data (Toms and Lesperance 2003) to test for threshold functions in sap flux and duff consumption. We chose a segmented regression because we were interested in testing if a forest floor consumption mortality threshold reported by Varner *et al.* (2007) would be expressed in the sap flux data. We used post-fire percentage of pre-fire sap flux as the dependent variable to minimize within tree variation in sap flux.

Chlorophyll Concentration

Because the lower portions of the crown are more prone to scorch, allowing for comparisons of chlorophyll content after repair, foliage samples were collected from the bottom third of the crown three weeks before and three months after the fire. Three fascicles of fully expanded needles from the same cohort were collected from each tree; one needle from each fascicle was macerated and immersed in a 10 mL N, N-Dimethylformamide (DMF) aliquot in a glass vial (Moran and Porath 1980, Yoder and Daley 1990). These samples were immediately covered and kept on ice and stored in a cooler throughout the extraction period (~48 h).

Absorbance measurements were taken using a UV-Vis™ spectrophotometer (Varian Inc., Palo Alto, California, USA) at wavelengths of 647 nm and 664.5 nm. Extracted foliage tissue was then oven dried at 50 °C for 48 h and weighed. We chose to dry the tissue at 50 °C rather than 70 °C because we had intended to do further analyses on the tissue and wanted to minimize volatilization of residual organic compounds. Chlorophyll content was calculated after the methods of Inskeep and Bloom (1985). Post-fire chlorophyll (Chl_{post}) content was standardized by pre-fire content (Chl_{pre}) and presented as an index (Chl_{std}):

$$Chl_{std} = \frac{(Chl_{pre} - Chl_{post})}{Chl_{pre}} \quad (2)$$

The combined impacts of scorch and forest floor consumption on chlorophyll concentration were analyzed by ordinary least-squares linear regression.

RESULTS

Live fine root biomass was approximately evenly distributed between the forest floor and the top 30 cm of the mineral soil (Figure 4). These results are similar to results from other

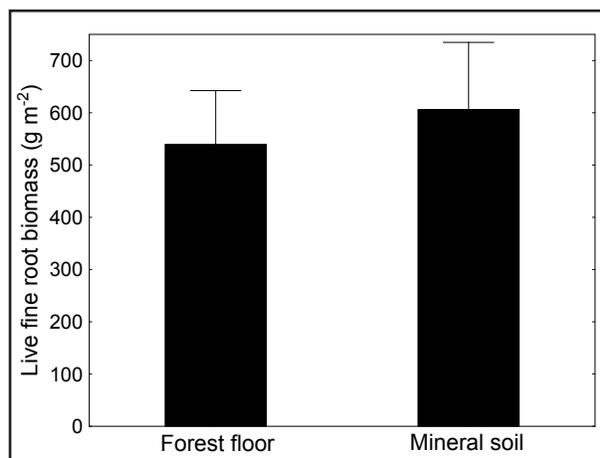


Figure 4. Mean live root dry weight in the forest floor and top 30 cm of the mineral soil in long-unburned longleaf pine forest in Georgia, USA (whiskers indicate standard error).

long-unburned Coastal Plain longleaf stands (Varner 2005). Fire damaged study trees had a minimum of 20% forest floor consumption (mean = 50.2%, ±35.6%) and an average scorch of 10% (±19.2%). No crown scorch occurred on 11 of the 18 trees with forest floor consumption (Figure 5). By August 2008, 10 study trees had died, all of which experienced >30% forest floor consumption and varying degrees of crown scorch (Figure 6). Mean sap flux rates (1.324 kg dm⁻² hr⁻¹ (±0.33 kg dm⁻² hr⁻¹) did not differ among the 20 original study trees during

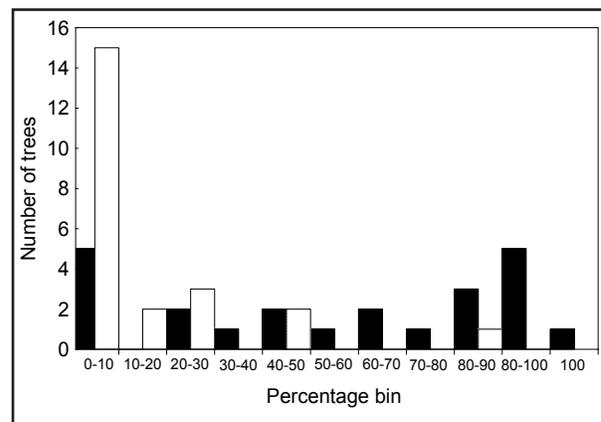


Figure 5. The degree of crown scorch (hatched bars) and forest floor consumption (filled bars) in longleaf pines following a 2005 wildfire.

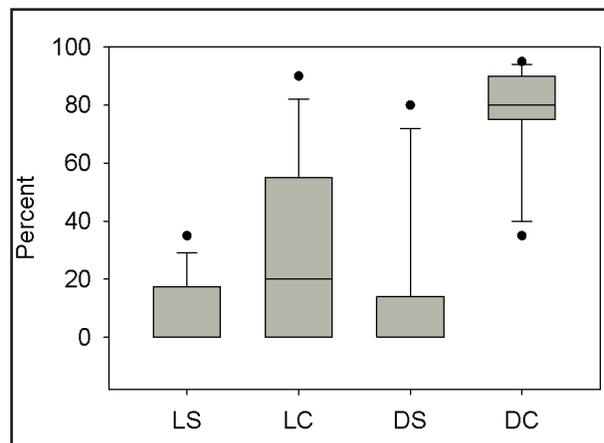


Figure 6. Box plot (median, 10th, 25th, 75th and 90th percentiles, observations >90th percentile are represented by points) of percent crown scorch in living (LS) and dead trees (DS) as well as percent forest floor consumption in living (LC) and dead (DC) trees.

the 11 consecutive measurement days prior to the fire ($F_{1,19} = 0.653$, $P = 0.861$). The estimated sap flux rate for all 23 trees for a nine-consecutive-day period following the wildfire was $0.488 \text{ kg dm}^{-2} \text{ h}^{-1}$ ($\pm 0.35 \text{ kg dm}^{-2} \text{ h}^{-1}$). The general linear mixed model showed that only forest floor consumption significantly influenced mean post-fire sap flux rates, and no interaction with scorch treatments was observed (Table 1). The significant interaction between time and consumption was due to the lower sap flux by trees post-fire. Sap flux was negatively correlated with consumption as indicated by the beta coefficient of -0.80 ($t = 3.98$, $P = 0.001$).

A two-regression segment model explained a combined 67.7% of the variance, and the breakpoint parameter was estimated to be 31.3% forest floor consumption (Figure 7); mortality occurred exclusively in trees that exceeded threshold forest floor consumption. A logistic regression on mortality versus root consumption revealed that trees with greater than 30% consumption were 20.3 times more likely to die as trees with less than 30% consumption, ($P = 0.013$). Ten of the 18 (56%) burned trees died over the three years since fire, although death occurred more than four months after the fire.

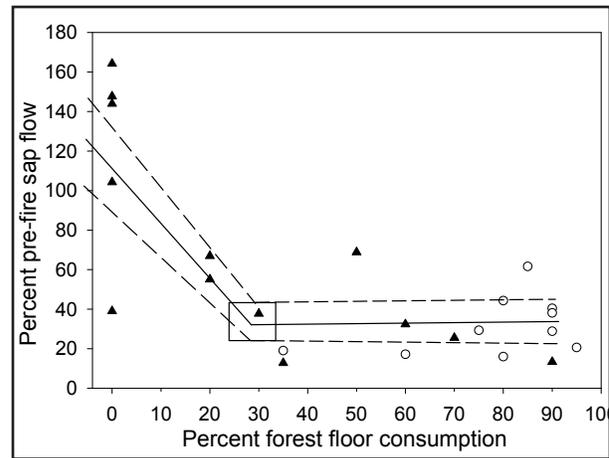


Figure 7. Post-hoc segmented regression of forest floor consumption effects on longleaf pine sap flux. The post-fire sap flux data are presented as a percentage of mean pre-fire sap flux. Living trees are indicated by filled triangles (▲), trees suffered delayed mortality by open circles (○). The estimated breakpoint was 31.3% forest floor consumption. The left segment had a slope of -2.8 and the right 0.0 with the R^2 of the entire analysis being 0.677 . Also shown are the 90% confidence block for the breakpoint (rectangle) and the 90% confidence belt for the regression (dashed lines).

We also found significant reductions in standardized leaf chlorophyll linked to increasing crown scorch ($\beta = -0.81$, $R^2 = 0.60$, $P = 0.009$; Figure 8). The regression of chlorophyll

Table 1. Results of general linear mixed model. The time effect refers to the repeated measures within subject variation. The time by consumption effect was significant because all trees with consumption had lower sap flux values post fire. The adjusted R^2 for the post fire model was 0.42 ($P = 0.008$).

Effect	SS	df	MS	F	P
Intercept	0.006219	1	0.006219	48.74	0.000
Scorch	0.000095	1	0.000095	0.74	0.402
Consumption	0.000741	1	0.000741	5.80	0.028
Scorch*consumption	0.000244	1	0.000244	1.91	0.185
Error	0.002041	16	0.000128		
Time	0.000017	1	0.000017	0.23	0.637
Time*scorch	0.000049	1	0.000049	0.68	0.419
Time*consumption	0.000824	1	0.000824	11.54	0.004
Time*scorch*consumption	0.000040	1	0.000040	0.55	0.466
Error	0.001143	16	0.000071		

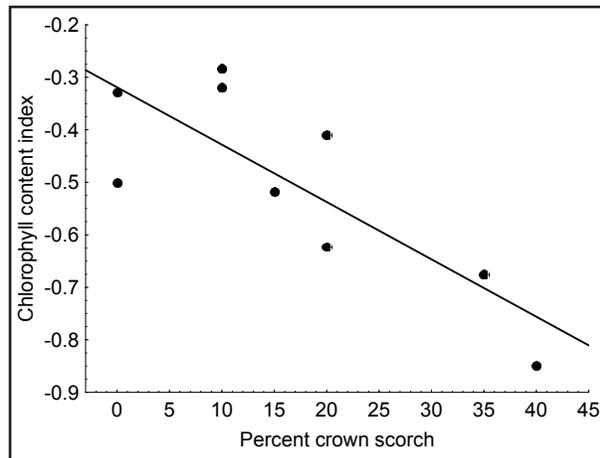


Figure 8. Linear regression of leaf chlorophyll content index and crown scorch in longleaf pines burned in a 2005 wildfire. Leaves were collected after the crowns flushed (3 months) following the fire. All pines had at least 20% forest floor consumption.

concentration had a significant negative correlation with crown scorch. We did not detect any relationship between forest floor consumption and chlorophyll content; however, all trees with significant crown scorch (>10%) exceeded the threshold of forest floor consumption (31.3%), which was associated with loss of transpiration and mortality described above.

DISCUSSION

Combustion of the forest floor and the resulting root damage in longleaf pines is consistent with a cascade of chronic stressors resulting in tree mortality months to a few years after fire. We observed, however, that the inferred loss of fine roots after forest floor consumption created an acute stress due to the immediate reduction in transpiration rates (Figure 7). Beyond a threshold of 31.3% consumption, no further reduction in transpiration was observed. Furthermore, the 31.3% threshold in this study corresponds closely to the 40% consumption threshold correlated to longleaf pine mortality observed in large-scale prescribed fires by Varner *et al.* (2007). This threshold of forest floor consumption (30% to 40%) is related both to

reduced transpiration rates and to subsequent observed mortality, suggesting that the acute stressor of fine root loss was inferred as the proximal cause of mortality in longleaf pine subjected to smoldering fire.

The observed critical threshold of forest floor consumption could have physical and physiological explanations. First, the presence of long-duration smoldering fire leads to direct damage to roots in the portion of the duff consumed. Varner *et al.* (2009) demonstrated that lethal temperatures penetrated up to 20 cm into mineral soil under smoldering duff in a long-unburned longleaf stand. Second, temperatures of smoldering fires could cause significant thermal damage to roots in the adjacent patches of forest floor not directly consumed by smoldering fire. Because roots are a connected network of segments, when structural roots near the tree are killed, all roots downstream are also lost (Guo *et al.* 2008). This indirect fire-caused root mortality may include the death of downstream roots deep into the mineral soil as well. Physiologically, root systems have been shown to have some degree of functional redundancy (Froelich *et al.* 1977), and 30% to 40% consumption may represent sufficient root loss to compromise root function. Under these circumstances, the remaining roots simply cannot supply sufficient water to the crown, resulting in either stomatal closure or vascular embolism and declines in transpiration.

Crown scorch is a common phenomenon in these frequently burned ecosystems, and roots and associated mycorrhizae are critical for providing the resources to rebuild the photosynthetic capacity of a damaged tree. The linear decrease in chlorophyll content with increasing scorch could indicate mineral nutrient uptake inhibited by loss of roots and associated mycorrhizae (Izaguirre-Mayoral *et al.* 2000). Resources could be allocated to other damage repair, such as rebuilding injured root tissue. Regardless, the reduced photosynthetic capacity of the crown would further inhibit C available for cell maintenance or damage repair. Recent

research also suggests that longleaf pines maintain a constant C allocation ratio between roots and leaves (Hendricks *et al.* 2006). Qualitative observations of study trees post fire suggest that leaf area decreased following forest floor consumption (J.J. O'Brien, Forest Service, personal observation; Figure 9). Ten of the 18 study trees with root consumption died within three years, and three more appeared to have low vigor (sparse canopies) by 2008. The immediate loss in the ability to supply leaves with water could lead to chronic carbon limitations through a compensatory reduction in both leaf area and canopy conductance. Crown scorch is an additional acute stressor that may or may not occur simultaneously with root consumption. Because mineral nutrients are required to replace scorched leaves, root loss has the potential to further limit photosynthetic capacity. Diminished transpiration and resulting lower C



Figure 9. Sparse canopy of a study longleaf four months after fire (18 October 2005) with forest floor consumption.

fixation could lead to a cascade of indirect effects such as inhibited chemical defenses and reduced overall vigor (Waring 2004). It appears that the inhibition of herbivore defenses might be critical as all 10 dead study trees finally succumbed to beetle attack (*Ips* spp. and *Dendroctonus* spp.), a pattern observed following large prescribed fires elsewhere (Varner *et al.* 2007).

Alternative explanations for post-fire tree stress and mortality observed here and elsewhere deserve discussion. Combustion of the forest floor would likely result in some loss of nitrogen through volatilization, though nitrogen and phosphorus remineralization would also occur (Boring *et al.* 2004). Although these effects could offer an alternate hypothesis for the chlorophyll responses, they would not immediately impact transpiration rates. In fact, loss of the forest floor could exacerbate water stress due to the high water storage capacity of the F and H layers, and the loss of roots in the moist forest floor layers following consumption would likely multiply water stress. It also seems likely that there would not be a threshold response but rather a continuous function if nitrogen loss were the driver of post-consumption stress.

We provide evidence supporting our hypothesis that root damage is the inciting stressor in a decline spiral resulting in longleaf mortality following forest floor consumption (Varner *et al.* 2009). Our results link forest floor consumption with short-term physiological impairment and subsequent tree mortality, a missing link in previous research on longleaf pine and other North American conifers that suffer decline and mortality following fires. The acute physiological stress observed in the individual trees of this study showed a threshold relationship between transpiration and forest floor consumption. This threshold of declining transpiration rates of individual trees mirrors the observed threshold in stand-level tree mortality correlated to forest floor consumption (Varner *et al.* 2007). Our results provide further sup-

port for the need to minimize smoldering fire and subsequent root damage when reintroducing fire to long-unburned longleaf pine stands.

Post-fire tree mortality is increasingly important given ongoing efforts to reintroduce fire to areas that have suffered long periods of fire exclusion in many areas of North America (Covington *et al.* 1997, Wade *et al.* 2000, Agee 2003, Varner *et al.* 2005, Kolb *et al.* 2008). Reintroduction of fire to long-unburned stands

in the southeastern US is of particular concern for old-growth forests, half of which occurs in a fire-excluded state (Varner and Kush 2004). Because forest floor consumption appears to bring about acute water stress that then initiates a decline spiral, our results suggest that managers could mitigate the impacts of forest floor consumption on trees by burning when evaporative demand was low to limit water stress and minimize forest floor consumption.

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