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Contingent resistance in longleaf pine (*Pinus palustris*) growth and defense 10 years following smoldering fires

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ABSTRACT

In many fire-prone woodlands and forests, fire exclusion has resulted in substantial litter and duff accumulations capable of long-duration smoldering once fire is reintroduced. While previous research has shown that the soil heating from smoldering fires resulted in short-term reductions in coarse root non-structural carbohydrates and latewood growth, information on the long-term effects of smoldering fire is lacking. Our study compared the effects of three smoldering fire treatments (root only, stem only, root and stem) and two control treatments (no fire and surface fire only) on longleaf pine (*Pinus palustris*) growth and defense ten years after treatments. We cored 17–29 similar sized trees per treatment and measured growth as basal area increment and defense as resin duct properties (e.g., resin duct size, % resin duct area). We used generalized linear mixed models to determine the influence of smoldering treatments and climate on basal area increment and resin duct properties. Variation in basal area increment and resin duct size during the previous ten years were positively correlated with the subsequent ten years, $r^2 = 0.71$ and $r^2 = 0.65$, respectively. Additionally, temporal variation in growth and defense were related to climatic factors. Growth had the strongest correlation with current August temperatures ($r = -0.50$), and defense had the strongest correlation with current December temperatures ($r = -0.64$). Basal area increment was best predicted by summer and fall Palmer Drought Severity Index, while resin duct size was best predicted by the interaction of treatment and precipitation during the previous November. During the three driest years following treatment smoldering duration had a negative relationship with basal area increment ($p < 0.0085$; $r^2 = 0.08$) and resin duct size ($p < 0.0003$; $r^2 = 0.16$). While longleaf pine growth was generally resistant to long-duration soil heating following years of fire exclusion, the proceeding growth response was contingent on the post-fire climate. Longleaf pine resin duct size was sensitive to the effects of smoldering fire, and potential negative impacts may be exacerbated by lower precipitation. Restoring fire to long-unburned sites proceeded by warmer and drier climate conditions may result in reduced longleaf pine growth and defense that may contribute to increased probability of mortality during subsequent disturbances.

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1. Introduction

Declines in fire frequency in many forest and woodland ecosystems have led to numerous structural changes, including increased tree density and altered species composition, favoring more shade-tolerant species and less shade-intolerant, fire-dependent species (Agee, 1996; Gilliam and Platt, 1999; Keane et al., 2002). In many ecosystems, fire exclusion also results in deep ground fuel accumulations, including fermentation and humus layers collectively termed "duff", that are prone to long-duration smoldering when ignited (Varner et al., 2005). These changes in forest and fuel structure have been attributed to altered fire behavior and elevated tree mortality in many forests and woodlands, prompting the need for fuels treatments to mitigate the impacts of fire exclusion (Agee and Skinner, 2005; Ryan et al., 2013).

Prescribed fire is used as a restoration tool in many fire-dependent ecosystems across the United States to reestablish historical fire regimes (Brown et al., 2004; Ryan et al., 2013), but after prolonged exclusion the reintroduction of fire can injure trees, leading to unintended mortality (Swezy and Agee, 1991; Stephens and Finney, 2002; Varner et al., 2007). Increased tree mortality following the reintroduction of fire has been attributed to fine root consumption and thermal girdling as a result of the prolonged heating associated with smoldering fires, and is exacerbated by

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the substantial basal accumulation of duff around trees (Ryan and Frandsen, 1991; Varner et al., 2009; O'Brien et al., 2010). Prolonged heating and loss of roots may also contribute to delayed tree mortality by reducing tree vigor and predisposing trees to drought or biological agents, such as insects and pathogens (Swezy and Agee, 1991). Previous studies have shown that increased allocation to growth and defense are associated with decreased probability of tree mortality from factors such as competitive stress and bark beetles (Das et al., 2007; Kane and Kolb, 2010; Ferrenberg et al., 2014). However, the longer-term influence of smoldering fire on tree vigor and health is not well understood.

Although tree vigor may be influenced by smoldering duff fires, other factors may contribute to the variation in growth and defense within and among trees. For instance, tree vigor may be related to previous growth and defense, where trees that had faster growth and greater defense in the past are suspected to have faster growth and greater defense in subsequent years. Climate is also an important factor known to influence tree growth (Meldahl et al., 1999; Henderson and Grissino-Mayer, 2009) and defense (Rigling et al., 2003; Hood et al., 2015). Research that considers these multiple factors and their relationship with growth and defense will broaden our understanding of tree vigor dynamics under alternative land management practices and a shifting climate.

Information on how restoration treatments affect tree vigor in reference to subsequent disturbances (e.g., drought, wildfire) is of increasing interest to scientists and natural resource managers (Millar et al., 2007; D'Amato et al., 2013; Thomas and Waring, 2015). There are concerns that restoration efforts may predispose trees to future mortality, especially when considering the complex interactions of tree vigor, climate, and disturbance regimes. For instance, recent research by Nesmith et al. (2015) found that pre-fire vigor, defined by radial growth rate, had a considerable influence on post-fire mortality for sugar pine (*Pinus lambertiana*) in Sequoia National Park, California. Additionally, van Mantgem et al. (2013) found that a pervasively warming climate can exacerbate tree stress and may contribute to increased mortality following fire and other disturbance events. One way to assess tree vigor following disturbance is through the concepts of ecological resilience. While resilience has been defined in multiple ways (Holling, 1973; Gunderson, 2000), methods describing tree resistance and resilience can reveal how a particular disturbance and the interaction with intrinsic (e.g., genetics and physiological characteristics) and extrinsic (e.g., competition and climate) factors influences tree vigor over time. Resilience in tree vigor can be defined as the ability of a tree to return to pre-disturbance performance levels, while resistance in tree vigor refers to the ability of a tree to withstand negative impacts of a disturbance (Webster et al., 1975; Lloret et al., 2011). Understanding these concepts, and the broader intrinsic and extrinsic variables that influence resistance and resilience, will help inform appropriate management decisions. This is particularly important in a warming climate, which will likely lead to increased tree stress and a reduced capacity for trees to resist and/or recover from disturbance.

Longleaf pine (*Pinus palustris*) is an ecologically important tree species in the southeastern United States and a model species for studying the effects of smoldering fire behavior on growth and defense after years of fire exclusion (Varner et al., 2005). Longleaf pine ecosystems have been reduced to less than 2 million ha (Frost, 2006), and managers across the region are implementing considerable restoration efforts. Fire is a vital component of longleaf pine ecosystems with numerous species adapted to persist in frequent, low severity fire regimes that were historically more common (Platt, 1999). However, fire exclusion in the southeastern U.S. has dramatically reduced fire, leading to reductions in biodiversity and alterations to fundamental ecosystem processes (Noss et al., 1995; Van Lear et al., 2005; Varner et al., 2005). There is increased interest by managers to reintroduce fire to longleaf pine ecosystems, however, there is substantial concern that the reintroduction of prescribed fire after years of fire exclusion could lead to unintended tree mortality (Varner et al., 2005, 2007; O'Brien et al., 2010). Previous work on longleaf pine has attributed basal duff accumulations associated with fire exclusion with increased duration of lethal soil heating (>60 °C). Prolonged smoldering and heating of the mineral soil was linked to reductions in coarse root carbohydrate concentrations that may lead to longer term declines in longleaf pine vigor (Varner et al., 2009).

The primary objective of this study was to assess the longer term impacts of smoldering and other factors affecting longleaf pine vigor following the reintroduction of fire. To better inform which factors were important covariates we examined: (1) the within-tree relationships between previous and subsequent growth and defense; and (2) the influence of climate variables on measures of longleaf pine growth and defense. We then analyzed: (3) the relative importance of treatment and climate on longleaf pine growth and defense; and (4) the relationship between smoldering duration and growth and defense in the years following treatment. It is important to note that this study was concerned with smoldering fire specifically and did not account for the full range of fire effects that contribute to tree damage and may additionally influence tree growth and defense. However, our results provide important insights into the potential impacts of prescribed fire restoration treatments on the long-term growth and defense of longleaf pine following decades of fire exclusion.

2. Methods

2.1. Study site

This study was conducted at the Ordway–Swisher Biological Station near Melrose, Florida (Fig. 1, Putnam County, N29840/W81874) in a stand dominated by longleaf pine with a dense midstory consisting of oak species (*Quercus laevis*, *Quercus geminata*, and *Quercus hemisphaerica*). The area had not burned in 37 years prior to the implementation of experimental treatments, resulting in a dense overstory and deep litter and duff layers (up to 15 cm) on the forest floor (Varner et al., 2009). For reference, observational and fire-scar data suggest that many longleaf pine ecosystems historically burned as frequently as every two to three years (Frost, 2006; Stambaugh et al., 2011), thus this site has missed between 12 and 18 fire events. Soils of the site are deep, well-drained Candler series Lamellic Quartzipsamments (Readle, 1990). The site has gentle (<5%), north-facing slopes averaging 36 m above mean sea level. The climate of the area is characterized by long, warm and humid summers and short, mild winters. Climate for the study site was slightly warmer and drier during the ten years following treatment (2004–2013) than the ten years preceding treatment (1995–2003) with a mean annual temperature of 20.7 °C and a mean annual precipitation of 1192 mm (NCDC, 2014).

2.2. Experimental design

Experimental treatments were established in the fall of 2003 as part of a previous study examining the short-term (one year) impacts of duff smoldering on longleaf pine radial growth and root non-structural carbohydrates (Varner et al., 2009). The experiment included five treatments across 116 randomly selected trees, ranging from 30 to 40 cm in diameter at breast height (DBH; breast height = 1.37 m), with 20 replicates per treatment, except for the no fire control which had 36 replicates. The burn treatments were designed to expose specific areas of the pines to heating injury, including the root system (root burn), stem of the tree (stem burn),

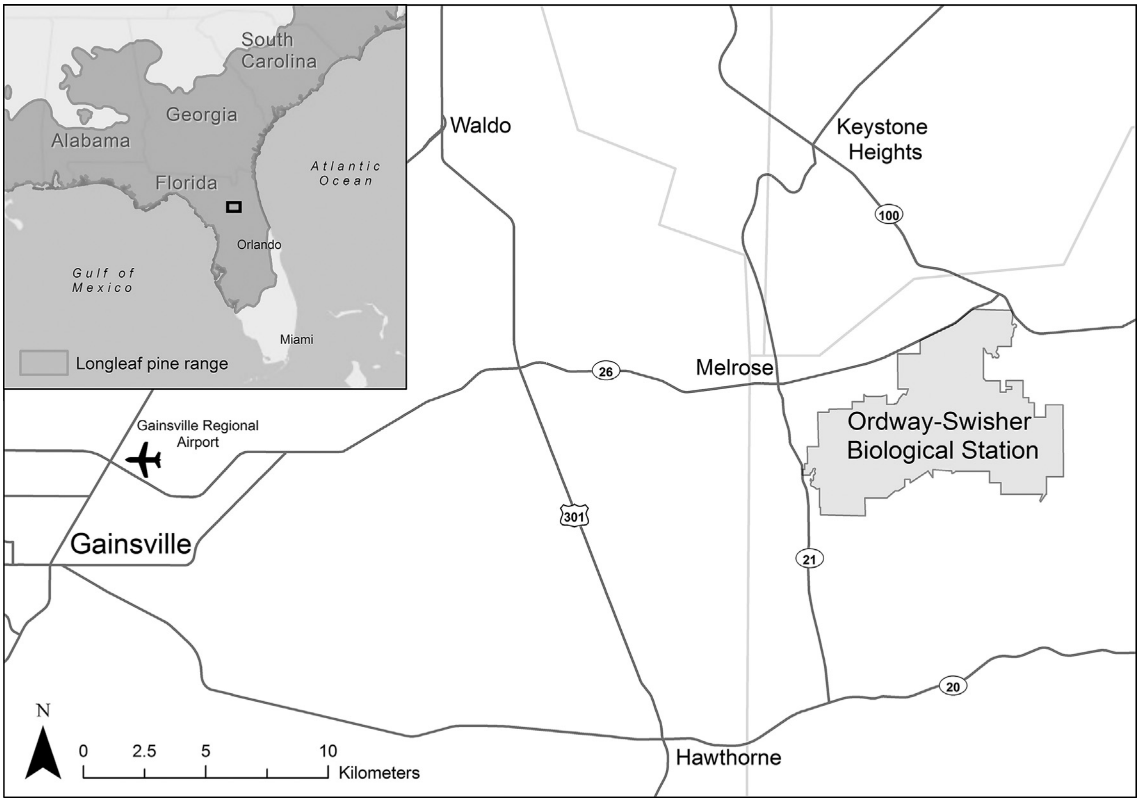

Fig. 1. Map of study area, located at the Ordway–Swisher Biological Station near Melrose, Florida in Putnam County (N 29840/W 81874). The inset map displays the natural range of longleaf pine ecosystems in the southeastern United States and the airplane symbol shows the location of the weather station at the Gainesville Regional Airport.

a combined root and stem burn (root and stem burn), surface fire only, and a no fire control. In the root treatments, litter and debris accumulations were gently removed 5–10 cm away from the base of the tree stem to create an effective buffer against basal heating on the stem while simultaneously minimizing disruption of accumulated materials on the forest floor (Varner et al., 2009). In the stem treatments, fire was isolated to a 20 cm radius directly around each tree base by shielding the adjacent forest floor and underlying root system with a 10 cm tall aluminum barrier encased in fire shelter material (Cleveland Laminating Corp., Cleveland, OH, USA). The bases of these barriers were buried to a depth of around 2 cm in the surface mineral soil. The root and stem treatment was facilitated by burning the entire 1 m radius without any protection, thus heating the stem base and root system simultaneously. Trees in the surface fire treatment were burned but immediately extinguished with a flapper at the conclusion of flaming combustion, effectively prohibiting duff smoldering. To ensure combustion had fully ended, water was used as needed on the surface fire trees if smoldering persisted. The final treatment included unburned trees that were randomly assigned to the no fire control treatment. Fire temperatures were recorded using Type J thermocouples (range 0–1200 °C; Omega Laboratories, Stamford, CT, USA) on a subset of trees from all treatments. Residual smoldering time was also recorded in seconds using a stopwatch on a subset of 71 trees. Details of the treatments and corresponding fire behavior (including stem, duff, and soil heating profiles) and post-fire tree measures are reported elsewhere (Varner et al., 2009).

2.3. Growth and defense measures

In November 2013, ten years following the burning treatments, all subject trees were cored once along the bole (*ca.* 30 cm above the base) of the tree using a large diameter (12 mm) increment borer. Some of the sampled trees had rot within the wood and we were not able to extract a viable core. This reduced the final sample size within each treatment: no fire control ($n = 36$), surface fire control ($n = 20$), root burn ($n = 18$), root and stem burn ($n = 17$), stem burn ($n = 17$).

Extracted tree cores were processed and measured using standard dendrochronology methods. Cores were mounted and progressively sanded with 80- to 600-grit sandpaper on a belt sander then scanned to produce a high-resolution image (1200 dpi) for each core. These images were processed in WinDendro (Regent Instruments, 2014), annual ring boundaries for each core were visually identified and total ring width (mm y^{-1}) was measured. Tree ring measurements for all subject trees were subsequently analyzed in COFECHA to determine correlations between ring patterns to help assess crossdating accuracy (Grissino-Mayer, 2001). All samples were successfully crossdated against the master chronology with an overall mean sensitivity of 0.303 and a series intercorrelation of 0.473. The master chronology was constructed by averaging the individual tree chronologies together for all 108 cores, since a site- or region-specific master chronology was not available.

Growth was measured as basal area increment (BAI, cm^2 y^{-1}), and was calculated for each tree using DBH, bark thickness, and annual ring widths. Bark thickness was estimated using an equation specific to longleaf pine based on DBH (Lutes, 2013). The computation of BAI assumed that ring width was constant within each annual ring and that ring circumference was geometrically circular. BAI was used as a standardization method to account for age- or size-related growth trends, but maintained suppression and release events that may have resulted from fire injury or climate (Biondi and Qeadan, 2008; Speer, 2010).

Vertical resin ducts in the xylem (Fig. 2) were visually identified and measured using ImageJ software (Rasband, 2014). Three

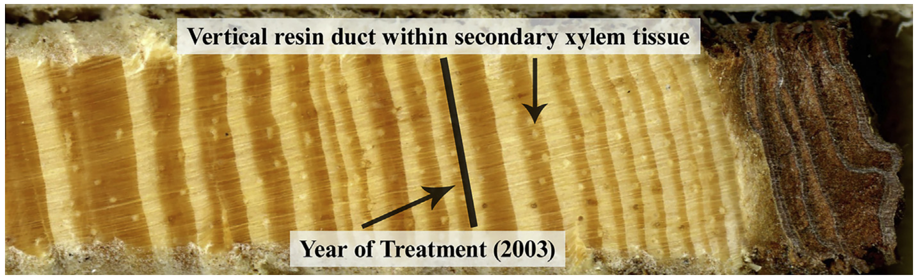

Fig. 2. A photograph of a magnified tree core with vertical resin ducts and year of treatment (2003) distinguished with arrows.

measurements were made in ImageJ for each annual ring: a count of vertical resin ducts; the area (mm^2) of each resin duct; and the area (mm^2) of each ring. From these measurements, we calculated resin duct production (# ducts y^{-1}), mean resin duct size ($mm^2\,y^{-1}$), and total resin duct area ($mm^2\,y^{-1}$).

Since we measured multiple resin duct characteristics, preliminary correlation analysis was conducted to reduce the number of defense response variables. Results indicated that resin duct area had a strong positive relation to resin duct production ($r^2 = 0.62$, $p < 0.01$) and thus resin duct production was excluded from further analysis and model considerations.

2.4. Statistical analyses

Linear regression was used to examine the relationship of growth and defense before and after treatment. The coefficient of determination (r^2) was calculated to assess how well the data for each variable fit the linear model. Results from the relationships between growth and defense before and after treatment determined the need for us to include tree as a random effect when developing and conducting the generalized linear mixed modeling (explained in more detail below).

To examine the influence of climate on growth and defense, we used the *treeclim* package (Zang and Biondi, 2015) in the statistical program *R* (R Development Core Team, 2015) to determine which climate variables best explained variability in growth and defense. The package performed correlation analysis by estimating Pearson's correlation coefficient (r) and confidence intervals based on bootstrapping methods with 1000 iterations. Median correlation coefficients were considered significant ($\alpha = 0.05$) if the absolute value surpassed half the difference between the 97.5th and 2.5th quantile of the 1000 estimates (percentile range method). Climate variables included in our analysis were monthly temperature (minimum, maximum, and mean), total monthly precipitation, and seasonal (spring, summer, winter, and fall) Palmer Drought Severity Index (PDSI; Palmer, 1965) for the current and previous year from 1994 to 2013 (ten years prior to and ten years after burning treatments). Climate data were recorded from the weather station at the Gainesville Regional Airport in Florida, located 16 km west of our field site (NCDC, 2014). We opted to use data from this single weather station due to its close proximity to the study site and its full coverage over the 20 year study period.

The influence of the smoldering fire treatments and climate on longleaf pine growth and defense measures were tested using generalized linear mixed modeling with the lme4 package (Bates et al., 2015) in the program R (R Development Core Team, 2015). This statistical approach was most appropriate given the nature of the data, which included a nested structure of annual measurements within tree. All growth and defense models included a log link function in the gamma distribution family to account for the non-normal distribution of the growth and defense data. Covariates included previous year's growth (BAI) to control for temporal autocorrelation and the specific climate parameters that had the best correlation with growth and defense. The no fire treatment was selected as the reference category when assessing the effect of each treatment on growth and defense. Akaike's information criterion (AIC) was used for model evaluation and to assess the relative importance of treatment and climate on longleaf pine growth and defense. All models were compared to a null model that included previous growth and random effect of tree to determine if treatment, climate, or a combination of these factors best explained the observed differences in growth and defense. Substantial differences in model fit were indicated by a change in AIC values greater than 2 (Anderson and Burnham, 2002).

Linear regression was used to examine the relationship of smoldering duration with longleaf pine growth and defense. To meet statistical assumptions of linear regression, measurements for lethal heating and smoldering duration were log-transformed. A box–cox test determined that a square root transformation was most appropriate for BAI. To identify possible variation in longleaf pine response during dry years, growth and defense measures were also averaged for the three driest years during the ten years following treatment. The driest years were selected separately for growth and defense based on the strongest correlations with seasonal PDSI. Following treatment, the three driest years relative to growth were based off the lowest values for average summer and fall PDSI and included 2006, 2007, and 2011 (−3.39, −3.87, and −2.91, respectively). The three driest years relative to defense and based on average winter PDSI were 2007, 2008, and 2011 (−3.72, −2.90, and −3.40, respectively).

3. Results

3.1. Within-tree and climate relationships

In general, growth and defense measures were highly variable among trees, but pre-treatment measures were positively correlated to post-treatment measures (Fig. 3). Among all sampled trees, average BAI over a ten year period varied from 1 to 30 $cm^2\,y^{-1}$, while resin duct total area ranged from 0.01 to 1.32 $mm^2\,y^{-1}$. Longleaf pines with greater BAI and more resin duct total area during the ten years prior to treatment consistently had greater values in the ten years following treatment ($r^2 = 0.71$, $p < 0.01$ and $r^2 = 0.72$, $p < 0.01$, respectively). Based on these findings, we chose to include tree as a nested random factor in our generalized linear model analysis to account for tree-based differences in growth and defense.

Longleaf pine BAI and resin duct area were related to several measures of climate, throughout the 20 years analyzed (Table 1). BAI had a significant negative relationship with current August temperature ($r = -0.49$) and a positive relationship with current April precipitation ($r = 0.42$). Resin duct area exhibited a positive relationship with precipitation during November of the previous year ($r = 0.46$) and no identifiable relationship with temperature.

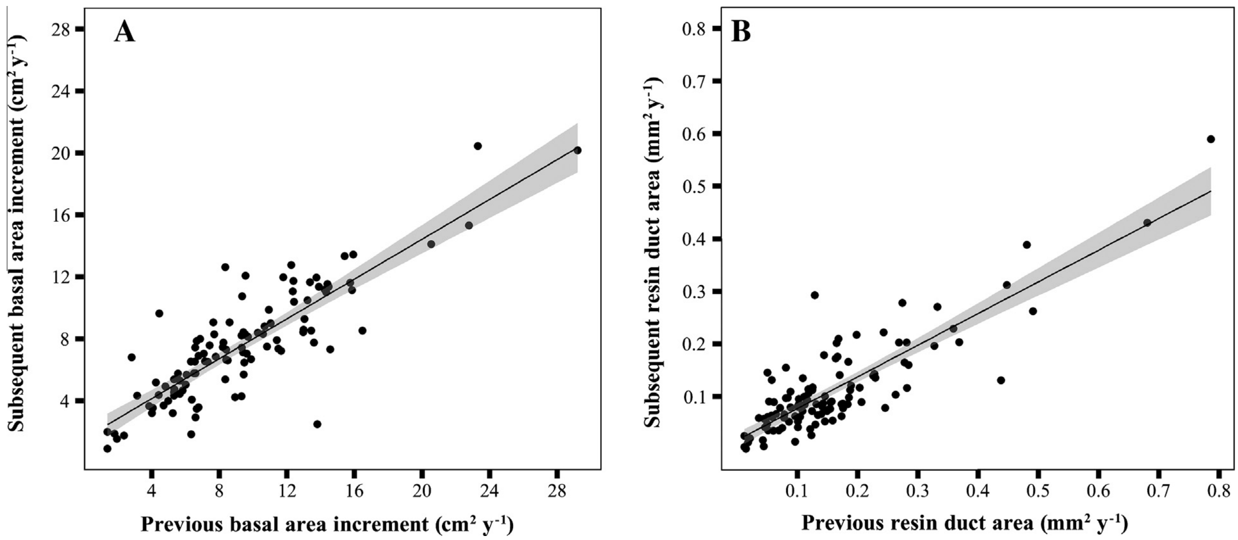

Fig. 3. The relationship of previous longleaf pine growth and defense (1994–2003) on subsequent growth and defense (2004–2013). The coefficient of determination (r^2) for basal area increment was 0.71 (A), and the r^2 for resin duct area was 0.72 (B). The area shaded gray represents the 95% confidence interval for each linear model.

Table 1
Significant correlations between climatic factors (temperature, precipitation, and the Palmer Drought-Severity Index, PDSI) and longleaf pine growth and defense characteristics. For PDSI, the summer and fall average included the months June–November; the winter average included the previous December, and the current January–February.

Variable	Month/season	Correlation coefficient	Confidence interval	
			Lower	Upper
Basal area increment ($cm^2\ y^{-1}$)				
Temperature	August	−0.49	−0.71	−0.13
Precipitation	April	0.42	0.13	0.71
PDSI	Fall and summer average	0.40	0.11	0.65
Resin duct area ($mm^2\ y^{-1}$)				
Precipitation	Previous November	0.48	0.15	0.75
PDSI	Winter average	0.46	0.23	0.68

BAI and resin duct size were correlated with monthly PDSI across seven months and four months, respectively. Average PDSI during the summer months (June, July, August) and fall months (September, October, November) was positively correlated with BAI ($r = 0.40$), while average PDSI during the winter months (previous December–current February) was positively correlated with resin duct area ($r = 0.48$).

3.2. Treatment and climate effects

Longleaf pine growth was reduced following all treatments when compared to the ten years before treatment (Fig. 4). Of all treatments, the root and stem burn showed the largest decrease, where BAI decreased by 24%. Despite this decrease, the model that included treatment alone performed worse than the null model when predicting longleaf pine BAI (Table 2). The climate factor (summer and fall PDSI) was the top performing model followed by the additive and interaction models between treatment and climate.

Resin ducts had less total area and were smaller in size following all treatments. The greatest decrease occurred in the root and stem treatment, where area was reduced by 36% and resin ducts were 27% smaller (Fig. 5). Resin duct total area was best predicted by precipitation from the previous November, and treatment alone did not outperform the null model (Table 2). The second and third best model included the additive and interaction models between treatment and precipitation from the previous November. The best model in predicting average resin duct size included the interaction between treatment and November precipitation from the previous year (Table 2), however, there was no substantial difference between the top model and the second best model. Compared to the no fire control, all three smoldering fire treatments had a negative impact on resin duct size. The interaction between treatment and precipitation had the greatest effect on trees from the root and stem burn, which experienced the greatest reduction in resin duct size when precipitation from the previous November was low.

Smoldering duration and lethal heating in the soil and at the stem base were not significantly related to longleaf pine growth and defense. However, when specifically assessing the three driest years relative to growth and defense post-treatment, smoldering duration had a negative relationship with BAI ($p < 0.0085$; $r^2 = 0.08$; Fig. 6a) and mean resin duct size ($p < 0.0003$; $r^2 = 0.17$; Fig. 6b).

4. Discussion

4.1. Within-tree and climate factors

Despite notable variation among trees, previous and subsequent growth and defense characteristics were strongly related regardless of treatment (Figs. 4 and 5). Longleaf pines that allocate proportionally more resources to growth and/or defense prior to treatment continued to similarly allocate resources after treatment. This result suggests that other factors such as microsite conditions or genotypic differences may influence growth and defense more than exposure to our fire treatments. Microsite differences may be associated with variability in the competitive environment that can influence the availability of light, water, and nutrients (Meldahl et al., 1999; Mitchell et al., 2006). Recent evidence indicates that allocation to growth and resin defense traits in pines are strongly heritable (Strom et al., 2002; Rosner and Hannrup, 2004; Westbrook et al., 2015), suggesting a potential genetic contribution to the observed variation. Neither microsite nor genetic differences were measured as part of this study, but may explain substantial differences in future research.

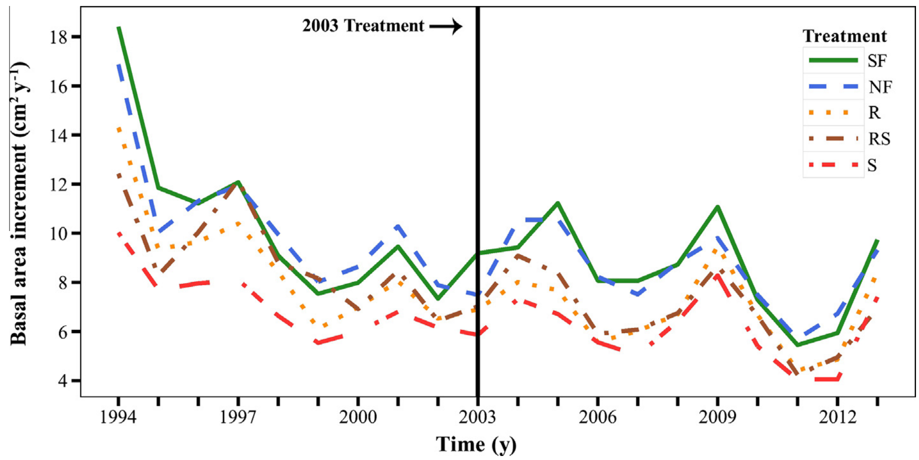

Fig. 4. Mean basal area increment (cm^2 y^{-1}) for each smoldering treatment from 1994 (ten years prior to treatment) to 2013 (ten years after treatment). The vertical solid line represents the 2003 treatments, which included surface fire (SF), no fire (NF), root burn (R), root and stem burn (RS), and stem burn (S). There was no significant difference in growth between any of the treatments in the ten years following the smoldering fire treatments.

Table 2
Longleaf pine growth (BAI, cm^2 y^{-1}) and defense (resin duct total area and mean size, mm^2 y^{-1}) generalized linear mixed model results. Growth was best predicted by summer and fall PDSI (Palmer Drought Severity Index) and defense was best predicted by smoldering fire treatment and precipitation during the previous November. The null model included Tree as a nested random effect and previous year's growth (BAI) as a covariate. *K* represents the relative number of parameters, and Akaike's information criterion (AIC) was used to select the best model.

Models	*K*	AIC	ΔAIC	AIC weights	Log likelihood
Growth: basal area increment					
PDSI	5	4852.50	0.0	0.71	−2421.25
Treatment + PDSI	9	4854.32	1.82	0.28	−2418.16
Treatment ∗ PDSI	13	4861.56	9.06	0.01	−2417.78
Null (previous growth + tree)	4	5043.70	191.20	0.00	−2517.85
Treatment	8	5045.48	192.98	0.00	−2514.74
Defense: resin duct total area					
Precipitation	5	−1898.17	0.00	0.88	954.09
Treatment + precipitation	9	−1893.97	4.20	0.11	955.99
Treatment ∗ precipitation	13	−1888.72	9.45	0.01	957.36
Null (previous growth + tree)	4	−1887.97	10.21	0.01	947.98
Treatment	8	−1883.63	14.55	0.00	949.81
Defense: resin duct size					
Treatment ∗ precipitation	13	−4668.60	0.00	0.48	2347.30
Treatment + precipitation	9	−4668.45	0.14	0.45	2343.23
Precipitation	5	−4664.56	4.04	0.06	2337.28
Treatment	8	−4657.12	11.48	0.00	2336.56
Null (previous growth + tree)	4	−4653.21	15.39	0.00	2330.60

The results from our climate and growth relationship analyses were consistent with previous studies on longleaf pine across multiple sites in the southeastern Coastal Plain (Meldahl et al., 1999; Henderson and Grissino-Mayer, 2009). We found that current August temperature had a negative relationship with longleaf pine growth, consistent with the relationship found for growth in Texas and latewood growth in both Texas and South Carolina (Henderson and Grissino-Mayer, 2009). Similar to our study, Henderson and Grissino-Mayer (2009) also found that longleaf pine growth in Florida was positively correlated with April precipitation and PDSI from July–November of the current year. In contrast to previous studies that found the relationship between temperature and growth to be the weakest among climate variables (Meldahl et al., 1999; Henderson and Grissino-Mayer, 2009), we found temperature to have a higher correlation with growth than precipitation and PDSI. One possible explanation for this difference could be that longleaf pine growth at our site is becoming more limited by temperature due to a stronger influence on potential evapotranspiration than precipitation. However, our study investigated different timespans, years, and geographic regions than the other two studies. Given increased warming over the past few decades in Florida, continued research on growth and climate relationships is warranted.

We are aware of only a few studies that directly compared vertical resin duct properties to climate variables. In eastern Germany, Wimmer and Grabner (1997) found Norway spruce (*Picea abies*) resin duct density had a positive relationship with above average summer temperature and a negative relationship to spring precipitation, both during the current year. Furthermore, in the northern Rocky Mountains of the United States, Hood et al. (2015) found ponderosa pine (*Pinus ponderosa*) total resin duct area to have a positive relationship with a warmer and wetter July. Our study found that resin duct size in longleaf pines was positively correlated with precipitation during the previous November. Comparisons of our results with these studies are difficult for many reasons including non-standardized measurements for resin duct properties, different tree species, and varying ecological characteristics. For instance, the aforementioned studies were from areas with more continental climates when compared to our study site in north-central Florida. Continental climates have higher fluctuations in temperature and precipitation, with over a third of the precipitation falling as snow, which considerably differs from the climate found in our study site. More research exploring the relationship between climate and tree defense is needed because tree defense has been shown to be an important factor in reducing pine mortality (Kane and Kolb, 2010; Ferrenberg et al., 2014; Gaylord et al., 2015; Hood et al., 2015), and defense–climate relationships may shift with increased temperatures and altered climatic patterns associated with climate change.

We observed decreases in mean longleaf pine growth and defense over the 20 years examined independent of treatment effects. These trends may reflect broader climate changes in the region, as temperature increased by 0.06 °C and precipitation decreased by 0.46 cm over study period. However, changes in temperature and precipitation were not statistically significant ($p > 0.6$). Alternatively, the continued growth of adjacent trees may have increased the competitive load, influencing growth in subject trees over the course of the twenty years examined (Das, 2012).

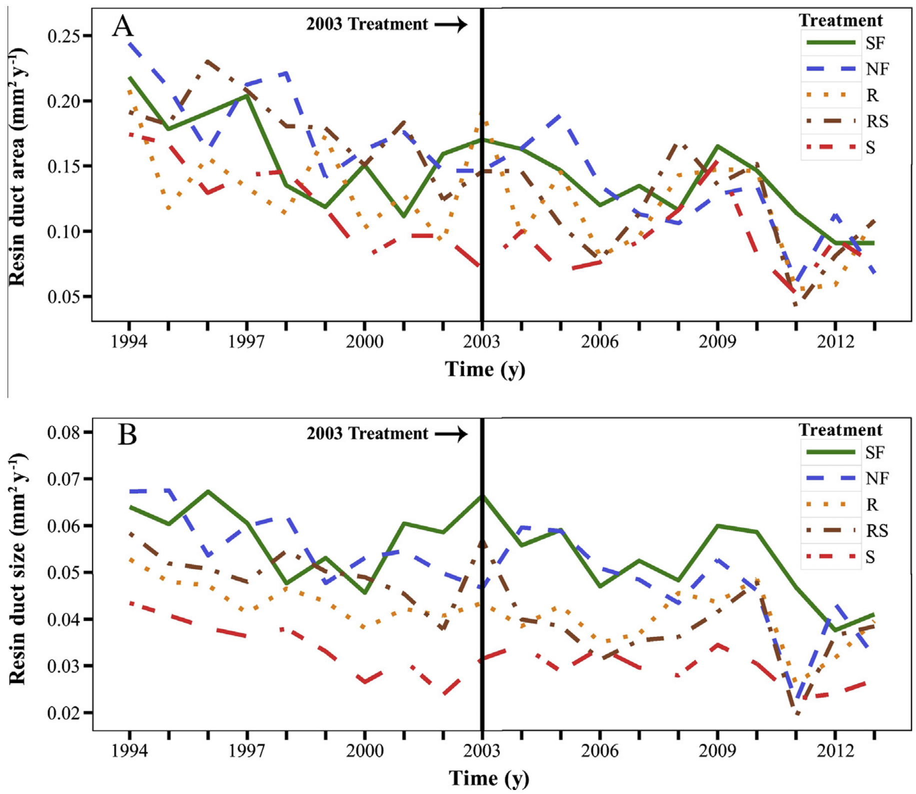

Fig. 5. (A) Resin duct total area and (B) mean resin duct size (mm^2 y^{-1}) for each treatment from 1994 (ten years prior to treatments) to 2013 (ten years after treatments). The vertical solid line represents the 2003 treatments, which included surface fire (SF), no fire (NF), root burn (R), root and stem burn (RS), and stem burn (S). Resin duct size from trees in the stem burn were significantly smaller than the no fire control in the years following treatment.

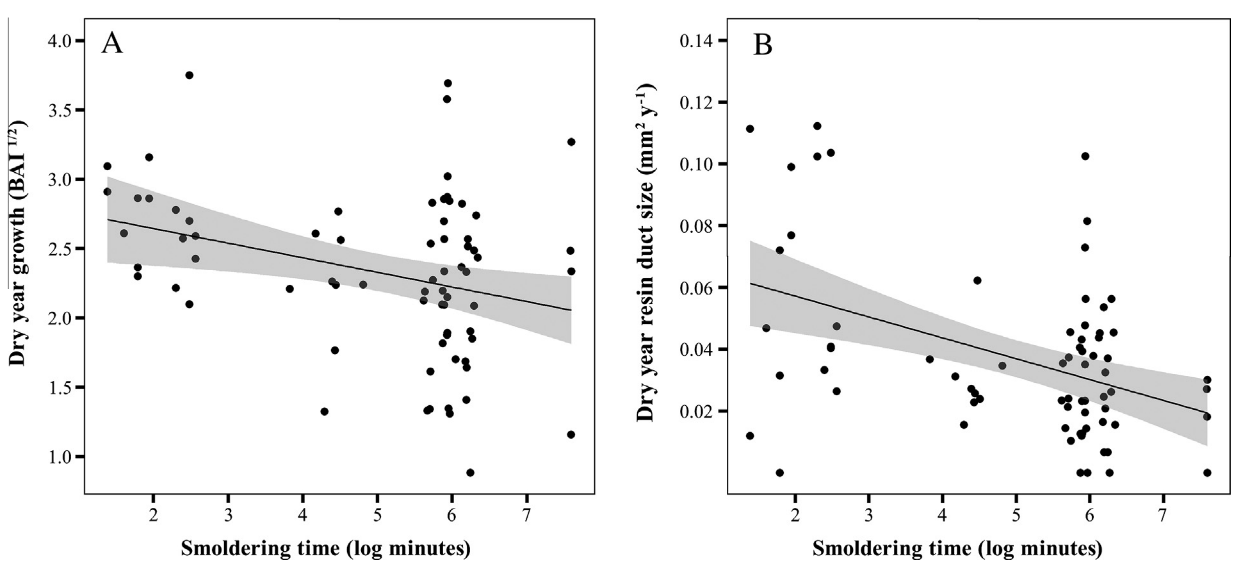

Fig. 6. The relationship between smoldering duration and (A) dry year growth, measured as basal area increment (BAI) and (B) defense, measured as mean resin duct size. A log transformation was applied to the unit of smoldering time and a square root transformation was applied to BAI to meet statistical assumptions of linear regression.

4.2. Treatment and climate effects

Our results indicate that longleaf pine growth was relatively resistant to the effects of smoldering fire ten years following treatment, as previous growth, variability among trees, and climate factors explained greater amounts of variation than treatment when predicting basal area increment in the mixed models. We found these results to be somewhat surprising considering that Varner et al. (2009) found that the duration of smoldering duff temperatures were strongly and negatively related to short-term (*ca.* 4 months post-treatment) root non-structural carbohydrate concentrations, and slightly related to latewood growth one year after treatment. We anticipated that the loss of roots and corresponding declines in root carbohydrates might cause further reductions in radial growth in subsequent years. Although treatment was not informative in predicting post-fire growth, there was a significant relationship between increased smoldering duration and reduced growth during the three driest years following treatment. It is possible that smoldering duration better captures the intensity of each experimental fire more than treatment.

Previous research has shown that long-duration soil heating and duff consumption can increase tree stress and mortality (Swezy and Agee, 1991; Stephens and Finney, 2002; Varner et al., 2007; O'Brien et al., 2010). However, scorching that caused crown and bole damage are also important factors contributing to tree mortality, and our study was specifically interested in the effects of smoldering fire only and intentionally omitted scorching as a part of the treatments. It is important to note that the interaction of different fire effects contributing to tree damage could have stronger influences on tree growth than smoldering fire alone.

Resin duct total area was also generally resistant to the effects of the smoldering fire treatment. However, the results revealed that resin duct size was negatively impacted by the treatment. Furthermore, the interaction of lower precipitation during the previous November with smoldering treatment further reduced the size of longleaf pine resin ducts. This may indicate that smoldering treatments could negatively impact longleaf pine defense capabilities, if proceeded by dry conditions and reduced precipitation.

We anticipated that duff burning treatments could have increased vertical resin duct area due to an induced response following burning as found by Hood et al. (2015) and similar to observations of increased resin flow from other studies (Lombardero et al., 2006; Perrakis and Agee, 2006). Conversely, short-term constitutive resin volume in September has been shown to decrease with higher crown scorching (Wallin et al., 2003). While our results suggest that resin duct size was negatively impacted by the smoldering fire treatments, it is difficult to directly compare our results to other studies because we isolated smoldering fire behavior. Hood et al. (2015) found that a low intensity and high frequency fire regime increased total resin duct area, while Wallin et al. (2003) found that high intensity fire resulting in greater crown scorch reduced resin duct defenses (i.e. resin volume). It is possible that our smoldering fire treatments, which intentionally omitted crown scorch, did not create conditions to independently promote or dampen resin duct development. These studies reflect notable differences in how tree defense responded to fire behavior, highlighting the need for more information on the mechanisms responsible for fire-induced changes in resin duct defenses.

While longleaf pine growth and defense were generally resistant to smoldering treatments, this effect was contingent upon the post-fire climatic conditions. We detected a decrease in both growth and defense measures in the driest years following treatment. In fact, one of the dry years analyzed for both growth and defense was 8 years following treatment (2011); suggesting that the interaction of smoldering fire and dry climate conditions may have longer-term effects on longleaf pine growth and defense. This is congruent with other research that has found strong correlations between abrupt growth declines in the past, typically reflective of drought and climate fluctuations, and increased probability of mortality, warranting the need to examine cumulative growth trends over extended time periods (Das et al., 2007; Kane and Kolb, 2014). As a result, smoldering fire may increase the probability of longleaf pine mortality for many years, especially in drier years following treatment. This extended effect may help explain the delayed mortality phenomenon reported for longleaf pine (Varner et al., 2007) and many western conifers following the reintroduction of fire (Agee, 2003; Thies et al., 2006; Hood, 2010; Nesmith et al., 2015).

4.3. Management implications

Growth and defense in longleaf pine was generally resistant to basal duff smoldering treatments over ten years. The exception to this pattern was during drier years following treatments when growth was negatively impacted by smoldering duration. Resin duct size was negatively impacted by the treatment, and the effects were worsened when precipitation was lower during the previous November. These results indicate that smoldering fire after a prolonged period of fire exclusion will not have substantial longer-term negative impacts to longleaf pine vigor unless climate conditions following treatments are consistently drier. The most recent climate projections for Florida include warmer temperatures with more precipitation (Van Oldenborgh et al., 2013), complicating our ability to speculate how climate change may influence long-term resistance following smoldering fire. However, we also found that the negative impacts of smoldering on growth and defense during dry years was related to the duration of smoldering associated with treatments. Managers may decrease these negative impacts by burning during wetter and cooler conditions to reduce the duration of smoldering and its consequences (Varner et al., 2007). The long-term recovery we observed in longleaf pine holds promise for restoration efforts in the region where concerns over potential post-fire mortality impede the application and use of fire (Hiers et al., 2003). Determining thresholds for fire injury, including the compounding effects of crown scorch, will be important steps toward restoring fire-excluded longleaf pine ecosystems.

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