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RESEARCH

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Crown scorch severity has little impact on foliar N and P concentrations of longleaf pine saplings prior to post-fire needle abscission

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Abstract

Background Limiting nutrient loss is an important component of a conservative life history strategy, with relevance for species in fire-prone ecosystems. Substantial research has focused on plant tissue nutrient dynamics associated with seasonal senescence, but little is known about whether plants mitigate nutrient loss from fire-damaged tissues. To explore this question, we compared foliar, branch, and stem carbon (C), total nitrogen (N), calcium (Ca), magnesium (Mg), total phosphorus (P), and potassium (K) concentrations of unburned longleaf pine (*Pinus palustris*) saplings to completely scorched (100%) and partially scorched (30–80%) saplings at 2 weeks, 4 weeks, and 24 weeks post-fire. We also measured soil nitrate (NO_3^-), ammonium (NH_4^+), Ca, Mg, total P, and K content under the same framework 2 weeks post-fire.

Results Burning created patterns in the longleaf pine saplings that varied over time. Soil P, K, and Mg availability was statistically higher near completely scorched saplings compared to unburned saplings 2 weeks post-fire. At the time of scorched needle abscission (4 weeks post-fire), longleaf pine residual foliage and woody tissue N and P concentrations did not statistically differ between completely and incompletely scorched saplings. At this time, however, incompletely scorched sapling foliar N statistically exceeded that of unburned saplings. After 24 weeks post-fire, completely and incompletely scorched longleaf pine saplings maintained lower foliar C:N, C:P, and N:P than unburned saplings.

Conclusions We found little evidence that crown scorch influences residual foliage N and P concentrations immediately prior to scorched needle abscission. This suggests that post-fire nutrient recovery of longleaf pine saplings is primarily driven by root acquisition or remobilization from surviving tissues.

Keywords Crown injury, Nutrient dynamics, Savannas, Resistance, *Pinus*

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Resumen

Antecedentes La limitación en la pérdida de nutrientes es un importante componente en estrategia conservativa de la historia de vida, con relevancia para las especies en ecosistemas propensos al fuego. Investigaciones importantes se han enfocado en la dinámica de nutrientes en los tejidos de las plantas asociados con la senescencia estacional, aunque poco se sabe sobre cómo las plantas mitigan la pérdida de nutrientes en los tejidos debido al daño ocasionado por el fuego. Para explorar sobre este tema, comparamos las concentraciones tanto en hojas, ramas, y carbono en el tronco (C), como también el nitrógeno total (N), el calcio (Ca), Magnesio (Mg), Fósforo total (P), y Potasio (K) de renovales de pino de hoja larga (*Pinus palustris*) no quemado, con renovales totalmente chamuscados (100%) y parcialmente chamuscados (30–80%), a 2, 4 y 24 semanas posteriores al incendio. También medimos nitratos en el suelo (NO_3^-), amonio (NH_4^+), Ca, Mg, P total, y contenido de K bajo el mismo marco dos semanas luego del fuego.

Resultados El incendio creó patrones en los renovales de pino de hoja larga que fueron variando con el tiempo. La disponibilidad de P, K, y Mg del suelo fue estadísticamente más alto cerca de los renovales completamente chamuscados comparados con los suelos cercanos a los no quemados dos semanas luego del incendio. Al momento de la abscisión de las acículas en los renovales chamuscados (cuatro semanas luego del incendio), la concentración de N y P en los tejidos del follaje remanente y en tejidos leñosos no difirieron estadísticamente entre renovales completamente y parcialmente quemados. En ese momento, sin embargo, el N foliar de renovales parcialmente quemados excedieron estadísticamente al de renovales no quemados. Luego de 24 semanas del incendio, los renovales de pino de hoja larga chamuscados total- o parcialmente, mantuvieron una relación más baja entre C:N; C:P y N:P comparados con los renovales no quemados.

Conclusiones Encontramos muy poca evidencia que el chamuscado de la corona influencia las concentraciones residuales de N y P en el follaje inmediatamente antes de la abscisión de las acículas. Esto sugiere que la recuperación de nutrientes en el post fuego en renovales de pino de hoja larga es debido a la movilización de los mismos desde las raíces o la re movilización desde tejidos sobrevivientes al fuego.

Background

Fire-prone woodlands and savannas are globally recognized as biodiversity hotspots (Timonen et al. 2010; Noss et al. 2015). At the forest floor, recurrent surface fire promotes herbaceous biodiversity by preventing tree and shrub encroachment, reducing litter depth, creating mineral soil substrate, and stimulating the soil seed bank (Livingston et al. 2016; Foster et al. 2018; Maikano et al. 2018; Barefoot et al. 2019). In contrast, frequent burning constrains overstory diversity, as saplings of most tree species are killed or perpetually maintained at a size controlled by surface fire (Bond and Midgley 2001). The select group of tree species capable of proliferating under a frequent fire regime do so with a combination of traits and growth strategies that enable persistence through early life stages (Peterson and Reich 2001; Bond and Midgley 2012; NeSmith et al. 2021).

Longleaf pine (*Pinus palustris*) is an archetype tree species for surviving in frequently burned woodlands (Heyward 1939; Glitzenstein et al. 1995). Seedlings begin life in a "grass stage" with minimal height growth, but with foliage accumulation in a dense, insulating tuft of needles that protects the terminal bud from heat (Wahlenberg 1946). Thereafter, longleaf pine seedlings enter the "bolting stage" where stem elongation occurs rapidly, and risk of surface fire-caused mortality increases (Brockway et al. 2006). Bolting seedlings remain vulnerable to most fire conditions until reaching the sapling stage (~2 m tall), with the combination of terminal bud height and bark thickness providing sufficient fire resistance (Jackson et al. 1999; Schafer et al. 2015). Nevertheless, the crown of longleaf pine saplings can still be consumed directly or scorched by convective heating (Dickinson and Johnson 2001; Hood et al. 2018; Bär et al. 2019; Varner et al. 2021). Tissues scorched by fire may be regrown to restore photosynthetic capacity, but this process requires a combination of photosynthate produced by residual foliage, mobilization of stored non-structural carbohydrates from branch, stem, or woody roots, and mineral nutrient acquisition from the soil (Guo et al. 2004; Sayer et al. 2018, 2020). Longleaf pine ecosystems are frequently characterized by soils that are low in N and P (Peet 2006; Ojha et al. 2019). Consequently, strategies that mobilize carbohydrate and mineral nutrients to repair fire-damaged tissues may provide a competitive advantage in longleaf pine woodlands that burned on average every 1–3 years across dormant and growing seasons (Stambaugh et al. 2011; Rother et al. 2020).

Resorption (the level to which nutrients can be reduced in senescing leaves) is another potential strategy used by plants to recover and conserve mobile mineral nutrients in senescing tissues (Killingbeck 1996; Brant and Chen

2015). Evergreen conifers resorb mineral nutrients from senescing needles prior to fascicle abscission at the end of leaf lifespan (Dalla-Tea and Jokela 1994); Killingbeck 1996; Yuan et al. 2018). Resorbed nutrients are stored over the dormant season primarily in needles with the potential for minor storage in terminal shoots and buds (Brant and Chen 2015; Chapin and Kedrowski 1983). Stored nutrients are mobilized in the spring to support new growth (Chapin and Kedrowski 1983; Helmisaari 1992). The potential for resorption depends on nutrient mobility in the phloem and xylem and varies taxonomically (Brant and Chen 2015; Maillard et al. 2015). In *Pinus*, nitrogen (N), phosphorus (P), and potassium (K) are labile with resorption efficiencies usually greater than 50% (Dalla-Tea and Jokela 1994); Piatek and Allen 2000; Zhang and Allen 1996; Zheng et al. 2020). Magnesium (Mg) and sulfur (S) are moderately labile with resorption rates less than 50%, and calcium (Ca) is recalcitrant (Chen et al. 2021; Marschner 2012; Zhang and Allen 1996). Micronutrients are less labile than N, P, and K with low resorption for boron (B), copper (Cu), and molybdenum (Mo), and no resorption of manganese (Mn) (Chen et al. 2021). Like nutrient conservation prior to fascicle senescence, longleaf pine saplings may use resorption to preemptively recover mineral nutrients from fire-damaged needles (as proposed in Varner et al. 2021). In this situation, proximal tissues such as branches and stems (hereafter referred to as woody tissues), which are less vulnerable to fire than foliage, may serve as temporary storage sites for resorbed foliar nutrients to support subsequent crown refoliation. Indeed, woody plant foliar N and P have been shown to increase following surface fire (Rieske 2002; Dijkstra and Adams 2015). Nevertheless, the relative contribution of post-fire resorption to this pattern remains unknown.

Several factors may interfere with post-fire foliar nutrient recovery in longleaf pine bringing its significance to this species into question. Surface fire combustion of organic material generally increases local soil N, P, and base cation availability which reduces the need for resorption (Schafer and Mack 2010; Scharenbroch et al. 2012; Alcañiz et al. 2018). Post-fire increases in soil P can also indirectly increase soil N availability by stimulating nitrogen fixation among herbaceous legumes (Tierney and Wurzburger 2024). Soil nutrient acquisition is further aided by a reduction in root competition resulting from the death of vegetative competition more susceptible to fire (Haywood 2010; Keyser et al. 2017; Willis et al. 2025). Post-fire resorption may also be contingent on fire intensity with high-intensity fire rapidly killing foliar tissue by elevating temperatures beyond a lethal threshold (>60 °C), thereby preventing resorption (Van Wagner 1973; Hood et al. 2018; Varner et al. 2021). Thus, resorption may only be possible after low-intensity surface fire when tissues are partially damaged or necrosis is delayed.

To determine whether crown scorch damage triggers a shift in foliar and woody tissue nutrient dynamics, we destructively sampled longleaf pine saplings with complete (100%) and incomplete crown scorch (30–80%) and compared their nutrient contents with those of unburned saplings at three-time intervals (2 weeks, 4 weeks, and 24 weeks post-burn) in southern Alabama, USA. While this observational study does not directly measure nutrient resorption, we compared foliar N and P concentrations at the time of scorched needle abscission (4 weeks) to known benchmarks of foliar nutrient concentrations in senesced leaves to interpret how effectively longleaf pine saplings conserve foliar N and P following crown scorch (Killingbeck 1996). Additionally, we measured soil nutrition adjacent to completely and incompletely scorched saplings 2 weeks post-fire and compared these values to those of soil samples obtained near unburned saplings to quantify local differences in mineral nutrient availability. Specifically, we predicted: (1) soil P, N, and base cation availabilities would be higher near scorched saplings compared to unburned saplings; (2) incompletely scorched saplings would have lower foliar N and P than completely scorched saplings at the time of needle abscission; and (3) incompletely scorched saplings would have lower foliar C-to-N and C-to-P ratios 24 weeks post-fire compared to completely scorched saplings. Collectively, these results will contribute to our fundamental understanding of how longleaf pine saplings persist in ecosystems where crown scorching is frequent.

Methods

Study area

Our study was established at the Escambia Experimental Forest in southern Alabama, USA (31°01′N, 87°04′W). Average climatic conditions near the site range from 3 °C (January) to 33 °C (July) with an average growing season of ~250 days. Precipitation (average 1672 mm) is abundant throughout the year and falls almost exclusively in the form of rain. Soils are sandy and loamy sediments classified under the Troup Series (loamy, kaolinitic, and thermic Grossarenic Kandiudults). Longleaf pine is the dominant overstory tree species at the site, with scattered southern red oak (*Quercus falcata*), sand post oak (*Q. margaretiae*), sweetgum (*Liquidambar styraciflua*), and water oak (*Q. nigra*) occurring in the canopy. Site index for longleaf pine is estimated to be 25 m at base age 50 years. The understory is a diverse mix of woody shrubs and herbaceous species dominated by inkberry (*Ilex glabra*), Carolina jessamine (*Gelsemium sempervirens*), golden aster (*Chrysopsis mariana*), slender bluestem (*Schizachyrium tenerum*), gopher-apple (*Geobalanus*

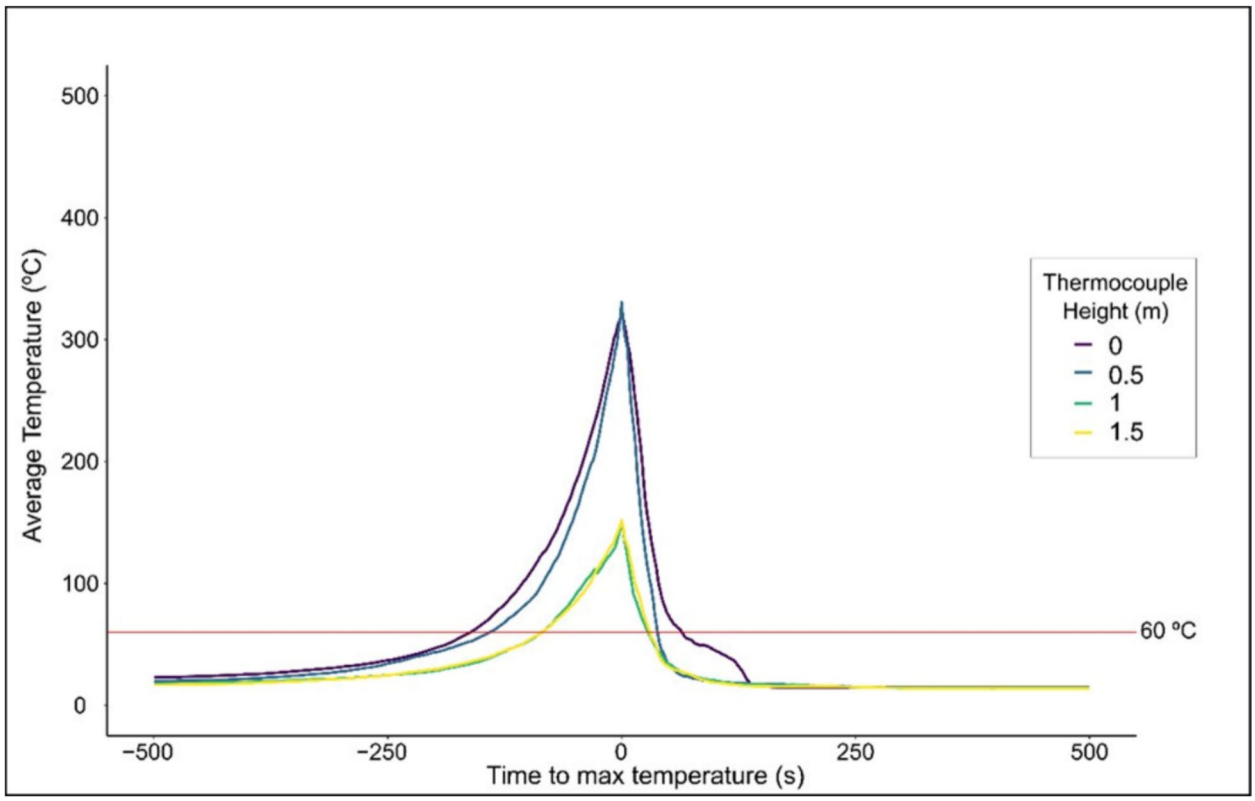


Fig. 1 The average air temperature obtained across all thermocouples 500 s before and after maximum temperature was recorded in a longleaf pine stand in southern Alabama, USA. The 60 °C horizontal line is a standard value for tissue death

oblongifolius), bracken fern (*Pteridium pseudocaudatum*), and greenbriers (*Smilax* spp.).

Experimental design, sample collection, and chemical analysis

Our experiment was designed as an observational study. To produce a range of crown scorch, we selected a 4.8-ha unit with 7 years of fuel accumulation for burning. Adjacent to the burned unit was a 2.5-ha area that served as an unburned control. The burned and unburned units had a similar stand structure (13.8 m^2 ha^{-1} basal area), soil type, and are functionally considered part of the same stand. In February 2023, prescribed fire was applied to the burned unit using a single ring ignition pattern. Prior to ignition, air temperature (10.0 °C), relative humidity (54%), and wind speed (<1 km s^{-1}) were measured with a Kestrel 3000 pocket weather meter (Kestrel Instruments, Nielsen-Kellerman Company, Boothwyn, PA, USA). Fire temperatures were recorded at 12 random locations with 48 thermocouple probes (20 gauge, K-type thermocouples with Nextel ceramic insulation; Omega Engineering, Inc., Stamford, CT, USA) fastened to rebar with aluminum wire at ground-level, 0.5 m, 1.0 m, and 1.5 m height and recorded with a HOBO® datalogger (HOBO UX120 Data Logger, Onset Computer Corporation, Cape Cod, MA, USA) (Fig. 1). The terminal end of each thermocouple was separated from the rebar by approximately 15 cm to reduce its influence on temperature recordings.

Two weeks post-burn, we selected our sapling population using a stratified random sampling procedure. Burned longleaf pine saplings were divided into two scorching groups based on visual estimates (nearest 5%) of crown scorch taken from all sides of the tree by one person. Saplings exhibiting 30–80% scorch were considered incompletely scorched, while those with 100% scorch were considered completely scorched. These ranges were chosen because >70% of the burned saplings displayed complete crown scorch, while most remaining saplings displayed scorching between 30 and 80%. The few saplings displaying 85 to 95% scorch were excluded due to uncertainty on whether their scorching injury was closer to the complete or incomplete scorch group. No saplings were recorded with less than 30% crown scorch. We then randomly selected 60 longleaf pine saplings from each group. Additionally, we selected 60 longleaf pine saplings from the unburned control. All longleaf pine saplings were naturally established, occupied a free-to-grow position, had no visible injury, defect, or

disease, and fell within a 1 to 4 m height range (Appendix 1). Large saplings (>2 m tall) generally had branches, while branches were absent on saplings shorter than 2 m. Selected saplings were separated by at least 10 m. From this initial population of 180 individuals, we randomly partitioned 20 for destructive sampling at intervals of 2 weeks, 4 weeks, and 24 weeks post-burn. Each sapling was sampled one time because extracting stem samples caused mortality. These sampling intervals corresponded with the timing of crown scorch expression, scorched needle abscission, and the seasonal initiation of a new needle cohort (Wade and Johansen 1986; Varner et al. 2021). Unburned saplings were sampled on the same calendar dates as completely and incompletely scorched saplings. During the first two sampling intervals, all longleaf pine saplings had a single needle cohort. However, at the final sampling interval, two needle cohorts existed on saplings in the unburned and incompletely scorched groups. To account for this, we obtained samples from the new cohort of needles when two age classes were present. Samples of needles and woody tissues were obtained at the sapling level. During the first two sampling intervals, we stripped visibly scorched needles from branches throughout all parts of the crown and placed them in sealed polyethylene bags for transport. The same protocol was used during the third sampling interval, but this time with green needles following refoliation. Cross-sections of woody tissue were cut from the stem and branches of the sapling and combined in a separate sealed polyethylene bag. All foliar and woody tissues were transported to the lab in a cooler containing ice, transferred to paper bags, oven-dried at 65 °C for 48 h, mixed thoroughly, and then ground using a Thomas Scientific Wiley mill. The foliar and woody samples were analyzed for total carbon (C), total nitrogen (N), calcium (Ca), magnesium (Mg), phosphorus (P), and potassium (K) concentrations at the United States Forest Service Research Triangle Park Analytical Laboratory. Foliar C and N were determined using standard operating procedures of a CE Elantech Flash EA 1112 analyzer (Milan, Italy). Twenty percent of the samples were duplicated to check instrument repeatability. Three certified standards and a blank were analyzed by sample batch to confirm analysis accuracy. For all other foliar and woody nutrients, samples were ashed in a 450 °C muffle furnace for 6 h, digested in 20 ml of 0.3 N hydrochloric acid for 6 h, decanted into vials, and analyzed with a Horiba Ultimate Expert Inductively Coupled Plasma (ICP) Optical Emission Spectrometer (Palaiseau, France) using standard operating procedures. Analysis accuracy was checked following the procedures described above. Foliar and woody tissue C, N, P, K, Ca, and Mg concentrations were expressed as percentage dry mass.

In addition to sampling longleaf pine foliar and woody tissues, we collected soil samples from the burned and unburned area 2 weeks post-fire. To assess fire effects on surface soil properties, we obtained one soil core (0–10 cm) within 20 cm of five randomly chosen completely scorched and incompletely scorched longleaf pine saplings and near five saplings in the unburned control ($N=15$). We transported soil samples to the lab where they were passed through a 2-mm sieve, ground to powder by a Wiley mill, oven-dried at 65 °C for 24 h, and analyzed for soil inorganic nitrate-N (NO_3^-) and ammonium (NH_4^+), total P, K, Ca, and Mg contents. We determined soil inorganic nitrogen content by digesting samples in potassium chloride. We then quantified NO_3^- and NH_4^+ by sample with an Astoria 2 micro-segmented flow analyzer (Clackamas, OR, USA) using standard operating procedures. All other soil nutrients were determined by ammonium chloride digestion and ICP analysis following standard operating procedures. Analysis accuracy was checked following the methods described above. Soil NO_3^- and NH_4^+ were expressed as mg/kg soil dry mass and soil P, K, Mg, and Ca were expressed as parts per million (ppm) soil dry mass.

Statistical analysis

We assessed longleaf pine foliar and woody tissue nutrient dynamics through a combination of multivariate and univariate analyses across the three sampling intervals (2 weeks, 4 weeks, 24 weeks). First, to visually explore the effects of crown scorch intensity on tissue nutrient concentrations, we assessed foliar and woody tissue nitrogen, phosphorus, potassium, magnesium, calcium, and carbon at each sampling interval using nonmetric multidimensional scaling in R (version 4.5.1, R Core Team 2025). All ordinations were estimated using the *metaMDS* function in the package *vegan* (Oksanen et al. 2025). Nutrient concentrations were scaled by dividing each concentration by its root mean square. Distance matrices were then calculated using a Euclidean distance metric. Data dimensionality was determined using the *dimcheckMDS* function in the package *goeveg* (von Lampe 2025), selecting the lowest number of dimensions with a final stress below 0.2. Differences in foliar and woody tissue nutrient concentrations among fire intensity groups were then quantitatively assessed by a non-parametric multivariate statistical permutation test (PerMANOVA) using function *adonis2* in the package *vegan* when sample sizes were equal (2 and 4 weeks) and a multi-response permutation procedure (MRPP) using the function *mrpp* in the package *vegan* when sample size differed due to the death of five saplings (no green foliar tissue in the crown) in the complete and incomplete scorching groups prior to the 24-week sampling interval ($p=0.05$). No unburned

Table 1 Mean soil nutrition (±1 SE) near unburned, incompletely scorched (30–80%), and completely scorched (100%) longleaf pine saplings 2 weeks post-fire. Rows featuring different letters were statistically different ($\alpha = 0.05$)

Nutrient	Unburned	Incompletely scorched	Completely scorched
Calcium (ppm)	37.7 ± (9.2)	146.3 ± (39.3)	162.8 ± (44.7)
Potassium (ppm)	13.2 ± (1.2)[b]	37.5 ± (2.5)[a]	33.3 ± (3.4)[a]
Magnesium (ppm)	6.1 ± (0.9)[b]	19.1 ± (2.4)[a]	23.4 ± (4.6)[a]
Phosphorus (ppm)	0.3 ± (<0.1)[b]	0.5 ± (0.1)[b]	0.9 ± (0.1)[a]
Nitrate (mg/kg)	3.0 ± (0.5)	3.6 ± (1.6)	2.0 ± (0.1)
Ammonium (mg/kg)	6.2 ± (0.9)	8.0 ± (0.8)	5.4 ± (0.5)

longleaf pine sapling died at any sampling interval. Pairwise comparisons were made when significant differences in the above tests were detected using Bonferroni adjusted p values.

To further explore stoichiometric differences between completely scorched, incompletely scorched, and unburned saplings over time, foliar and woody tissue C:N, C:P, and N:P at each sampling interval were compared by ANOVA ($p < 0.05$) in R Studio version 4.4.1 (R Core Team 2021). The full model contained scorch group (including the unburned control), sampling interval, and their interaction. We then used a one-way ANOVA ($p < 0.05$) to compare foliar and woody N and P concentration among all three groups at the time of needle abscission (4 weeks) for the burned saplings. Mean foliar N and P concentration of the completely and incompletely scorched groups were then further evaluated with established foliar nutrition benchmarks for senesced evergreen leaves to interpret how effectively scorched longleaf pine saplings limited the loss of foliar N and P (Killingbeck 1996). Resorption proficiency (the level to which nutrients can be reduced in senescing leaves; Killingbeck 1996) was used to evaluate this metric instead of resorption efficiency (the percentage of the living tissue nutrient content that is withdrawn prior to senescence; Killingbeck 1996) because: (1) obtaining pre-burn tissue samples from the stem killed the sapling; (2) scorch intensity could not be predicted a priori; and (3) pre-burn sampling timing is eliminated as a source of variability (Killingbeck 1996, 2004). Finally, we used one-way ANOVAs to determine differences in soil Ca, K, P, Mg, NO_3^-, and NH_4^+ in areas near unburned saplings and those completely and incompletely scorched 2 weeks post-burn. In all univariate analyses, the assumptions of homogeneity of variance and normality were checked with Levene's and Shapiro-Wilk tests, respectively, in the package *car* (Fox et al. 2012). Models producing significant differences among groups were further explored with Tukey post hoc tests in the package *emmeans* ($p < 0.05$) (Lenth 2024).

Results

Fire effects on soil nutrition

Two weeks post-fire, soil total P ($F_{(2,12)} = 13.4$; $p = 0.0009$), K ($F_{(2,12)} = 26.7$; $p = 0.0009$), and Mg ($F_{(2,12)} = 8.8$; $p = 0.0045$) statistically differed among completely scorched, incompletely scorched, and unburned saplings (data not shown). Soil total P was nearly three-times more abundant in areas near completely scorched longleaf pine saplings compared to unburned saplings, and nearly twice as abundant relative to areas near incompletely scorched saplings (Table 1). Similarly, soil K was nearly three-times more abundant near completely and incompletely scorched longleaf pine saplings compared to near unburned saplings (Table 1). Trends in soil Mg followed a similar trajectory, as areas burned near completely and incompletely scorched saplings contained at least three-times as much Mg as near unburned saplings (Table 1). Soil Ca was also biologically highest in areas burned near completely scorched saplings; however, statistical differences were not detected among scorched and unburned saplings ($F_{(2,12)} = 3.8$; $p = 0.0521$) (Table 1). Trends in soil NO_3^- ($F = 0.7_{(2,12)}$; $p = 0.5230$) and NH_4^+ ($F = 3.1$; $p = 0.0806$) were variable and not statistically different among scorched and unburned saplings (Table 1).

Scorching effects on foliar nutrition

The ordination of foliar nutrients 2 weeks post-fire showed that unburned longleaf pine saplings' foliar nutrition metrics overlapped near the center of both axes with completely and incompletely scorched saplings (Fig. 2). Nevertheless, completely and incompletely scorched saplings were more widely dispersed along the positive range of axis one while unburned saplings were more dispersed along the positive range of axis two (Fig. 2). Calcium was strongly positively correlated ($r = 0.87$) with axis one, whereas K was strongly negatively correlated ($r = -0.84$) with axis two (Fig. 2). Differences in foliar nutrient concentration among completely scorched, incompletely scorched, and unburned saplings were statistically significant (Pseudo-$F_{(2,57)} = 7.74$, $p = 0.001$). Unburned

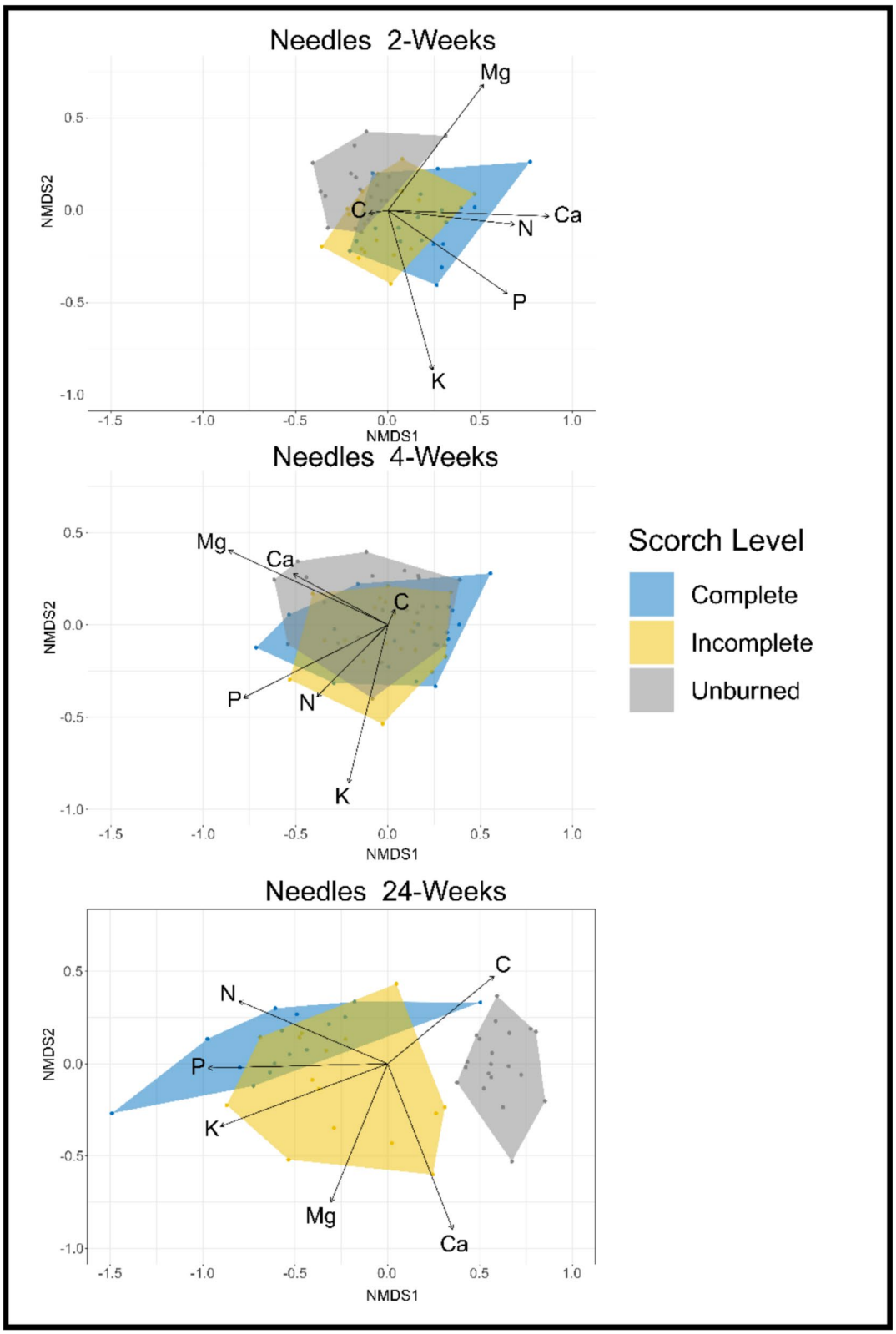


Fig. 2 Nonmetric multidimensional scaling ordination of crown scorching effects on longleaf pine sapling foliar tissue nutrition 2 weeks (final stress = 0.142; nonmetric $r^2 = 0.98$), 4 weeks (final stress = 0.152; nonmetric $r^2 = 0.98$), and 24 weeks (final stress = 0.054; nonmetric $r^2 = 0.99$) post-fire. Blue points represent completely scorched saplings (100%), yellow points represent incompletely scorched saplings (30–80%), and gray points represent unburned saplings (0%). Vectors represent the direction and strength of correlation of nutrient concentrations to ordination axes

saplings' foliar nutrition differed statistically from incompletely ($p_{adj}=0.003$) and completely scorched saplings ($p_{adj}=0.003$). Moreover, statistical differences were detected between completely and incompletely scorched longleaf pine saplings ($p_{adj}=0.009$).

Four weeks post-fire, little separation in foliar nutrition occurred among completely scorched, incompletely scorched, and unburned longleaf pine saplings (Fig. 2). All saplings were similarly oriented along both axes. Magnesium and P were negatively correlated ($r=-0.91$ and -0.83, respectively) with axis one, whereas K ($r=-0.83$) was negatively correlated with axis two (Fig. 2). While significant differences in foliar nutrition were detected among completely scorched, incompletely scorched, or unburned saplings (Pseudo-$F_{(2,57)}=2.54$, $p=0.03$), no differences were found in pairwise comparisons after adjusting for multiple comparisons ($p_{adj}=0.183$, 0.081, and 0.735 for unburned versus low, unburned versus high, and low versus high intensity).

At 24 weeks post-fire, minimal overlap in foliar nutrition occurred among completely scorched, incompletely scorched, and unburned longleaf pine saplings (Fig. 2). Completely and incompletely scorched saplings were primarily concentrated within the negative range of axis one, while unburned saplings were segregated within the positive range of axis one (Fig. 2). Phosphorus ($r=-0.97$), K ($r=-0.96$), and N ($r=-0.86$) were highly negatively correlated with axis one. Conversely, C ($r=0.71$) was positively correlated with axis one (Fig. 2). Calcium ($r=-0.69$) was negatively correlated with axis two. Foliar nutrition statistically differed among completely scorched, incompletely scorched, and unburned saplings ($A=0.364$, $p=0.001$). Completely ($A=0.424$, $p_{adj}=0.003$) and incompletely scorched saplings ($A=0.3415$, $p_{adj}=0.003$) were statistically different from unburned saplings. However, no statistical differences were found between completely and incompletely scorched saplings ($A=0.041$, $p_{adj}=0.255$).

Scorching effects on woody nutrition

Two weeks post-fire, woody tissues nutrition in unburned longleaf pine saplings overlapped with completely and incompletely scorched saplings near the center of both ordination axes (Fig. 3). However, completely scorched and unburned saplings were more dispersed along the positive range of axis one than incompletely scorched saplings (Fig. 3). Additionally, completely scorched saplings were more dispersed along the negative range of axis two while unburned saplings were more dispersed along the positive range of axis two. Phosphorus ($r=0.89$), Mg ($r=0.88$), and K ($r=0.76$) were positively correlated with axis one, while K ($r=-0.59$) had the strongest correlation with axis two (Fig. 3). Woody nutrient concentrations varied statistically among completely scorched, incompletely scorched, and unburned saplings (Pseudo-$F_{(2,57)}=8.55$, $p=0.001$). Incompletely scorched saplings did not differ statistically from completely scorched ($p_{adj}=0.057$) but did differ from unburned saplings ($p_{adj}=0.003$). Completely scorched and unburned saplings were also significantly different ($p_{adj}=0.012$).

Four weeks post-fire, unburned longleaf pine saplings overlapped with completely and incompletely scorched saplings but were located more within the positive range of axis one in ordination space (Fig. 3). In contrast, completely and incompletely scorched saplings were more variable across both axes (Fig. 3). Phosphorus ($r=-0.89$), Mg ($r=-0.84$), Ca ($r=-0.81$), and K (-0.75) were negatively correlated with axis one, while N ($r=-0.58$) and K (0.57) had the strongest correlation with axis two. Woody nutrient concentrations varied statistically among completely scorched, incompletely scorched, and unburned saplings (Pseudo-$F_{(2,57)}=5.928$, $p=0.001$). Completely ($p_{adj}=0.006$) and incompletely scorched saplings ($p_{adj}=0.003$) statistically differed from unburned saplings. However, completely and incompletely scorched saplings did not statistically differ ($p_{adj}=1.00$).

At 24 weeks post-fire, completely and incompletely scorched longleaf pine saplings overlapped in ordination space, whereas unburned saplings clustered separately in the positive ranges of both axes (Fig. 3). Additionally, completely and incompletely scorched saplings were more dispersed across the negative range of axis two than unburned saplings (Fig. 3). Potassium ($r=-0.88$) and P ($r=-0.74$) were negatively correlated with axis one, while N ($r=0.73$) was positively correlated with axis two. Differences in woody tissue nutrient concentrations varied statistically among completely scorched, incompletely scorched, and unburned saplings ($A=0.187$, $p=0.001$). Unburned saplings statistically differed from completely ($A=0.189$, $p_{adj}=0.003$) and incompletely scorched saplings ($A=0.179$, $p_{adj}=0.003$). No statistical differences were detected between completely and incompletely scorched saplings ($A=-0.018$, $p_{adj}=1.00$).

Foliar stoichiometry

Longleaf pine sapling foliar C:N ($F_{(4,161)}=15.84$, $p<0.0001$), C:P ($F_{(4,161)}=55.10$, $p<0.0001$), and N:P ($F_{(4,161)}=26.94$, $p<0.0001$) varied significantly among completely scorched, incompletely scorched, and unburned saplings over time. Two weeks post-fire, completely scorched longleaf pine saplings maintained 10% and 9% lower foliar C:N levels compared to incompletely scorched and unburned saplings, respectively (Fig. 4) (Appendix 2). A statistical difference in foliar C:N between completely and incompletely scorched saplings was not detected (Fig. 4) (Appendix 2). Unburned saplings also maintained 20% and 10% higher foliar C:P

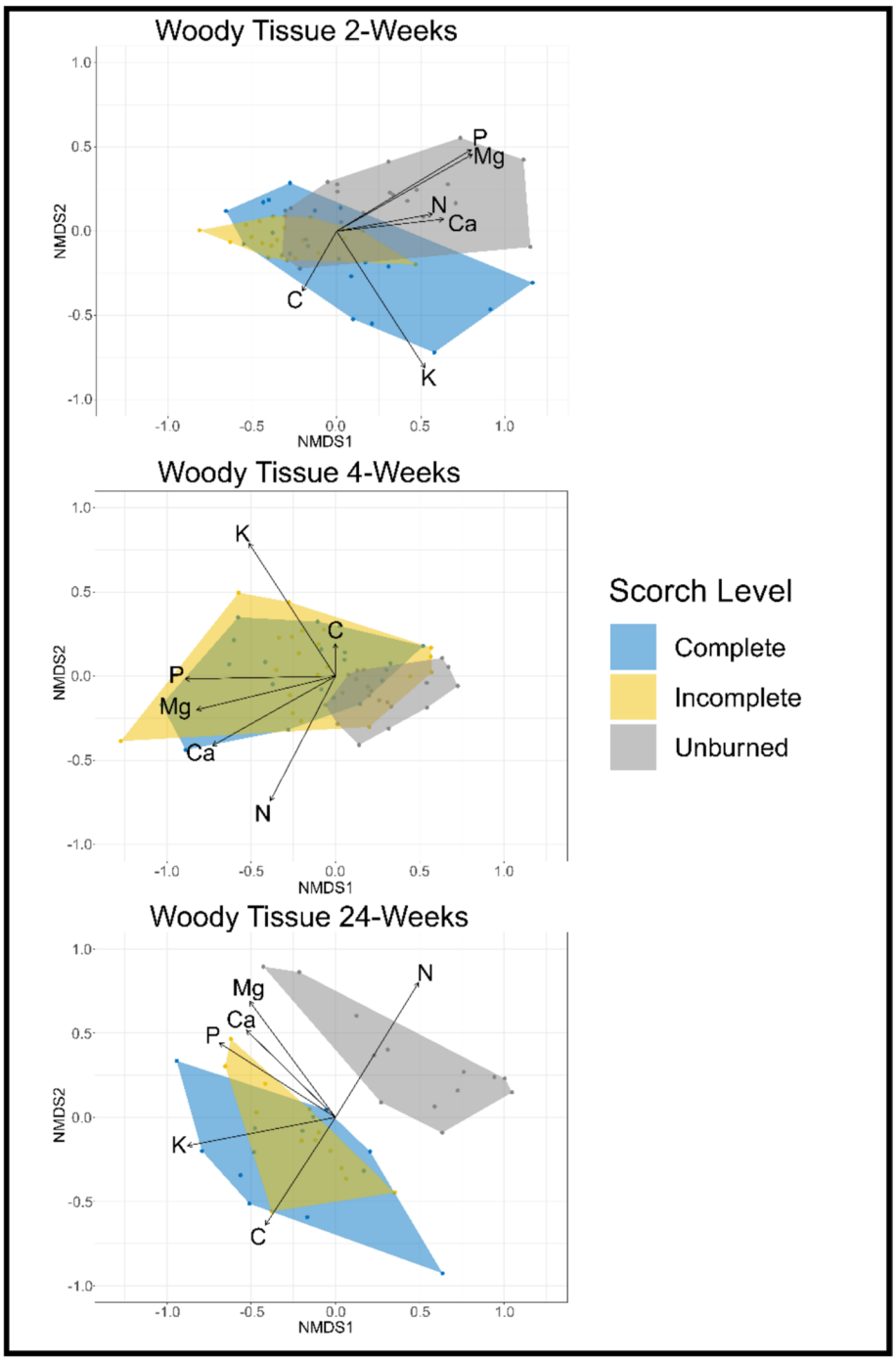
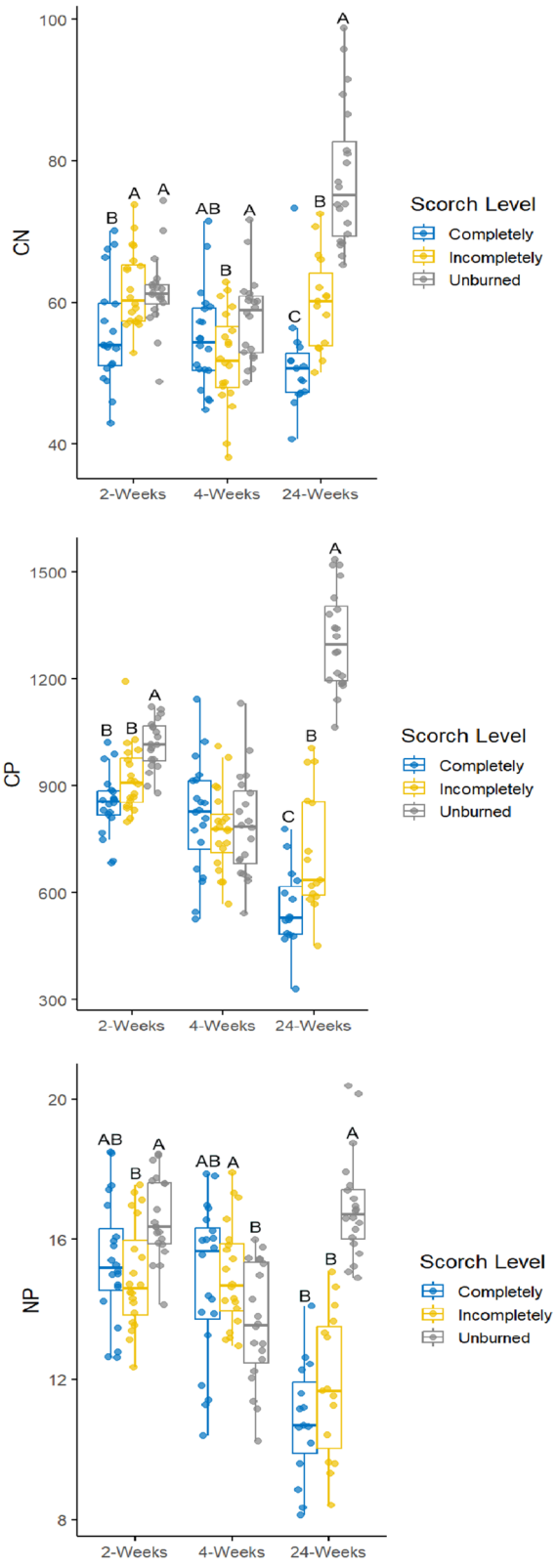


Fig. 3 Nonmetric multidimensional scaling ordination of crown scorching effects on longleaf pine sapling woody tissue nutrition 2 weeks (final stress = 0.108; nonmetric $r^2 = 0.99$), 4 weeks (final stress = 0.108; nonmetric $r^2 = 0.99$), and 24 weeks (final stress = 0.115; nonmetric $r^2 = 0.99$) post-burn. Blue points represent completely scorched saplings (100%), yellow points represent incompletely scorched saplings (30–80%), and gray points represent unburned saplings (0%). Vectors represent the direction and strength of correlation of nutrient concentrations to ordination axes

compared to completely scorched and incompletely scorched saplings, respectively (Fig. 4) (Appendix 2). Foliar C:P did not statistically differ between completely and incompletely scorched saplings (Fig. 4) (Appendix 2). Two weeks post-fire, unburned longleaf pine saplings maintained 11% higher foliar N:P compared to incompletely scorched saplings (Fig. 4) (Appendix 2). Completely scorched longleaf pine sapling foliar N:P did not



◄ **Fig. 4** The effects of crown scorching on longleaf pine sapling foliar tissue C:N, C:P, and N:P 2 weeks, 4 weeks, and 24 weeks post-burn. Boxplots featuring different letters were statistically different ($\alpha = 0.05$). Post hoc comparisons were made within temporal sampling periods

statistically differ from incompletely scorched saplings or unburned saplings (Fig. 4) (Appendix 2).

At 4 weeks post-fire, unburned longleaf pine saplings maintained 11% higher foliar C:N than incompletely scorched saplings (Fig. 4) (Appendix 2). No statistical differences in foliar C:N were detected between completely scorched and incompletely scorched saplings (Fig. 4) (Appendix 2). Foliar C:P was statistically similar among completely scorched, incompletely scorched, and unburned saplings (Fig. 4) (Appendix 2). In contrast to 2-week observations, by 4 weeks post-fire, incompletely scorched longleaf pine saplings maintained 9% higher foliar N:P compared to unburned saplings (Fig. 4) (Appendix 2). At 4 weeks post-burn, completely scorched sapling foliar N:P did not statistically differ from those of incompletely scorched saplings or unburned saplings (Fig. 4).

At 24 weeks post-fire, unburned longleaf pine saplings maintained 52% and 30% higher foliar C:N than completely or incompletely scorched saplings, respectively (Fig. 4) (Appendix 2). Incompletely scorched sapling foliar C:N was also statistically higher than that of completely scorched saplings (Fig. 4) (Appendix 2). Similar trends in foliar C:P were observed, as unburned saplings maintained 136% or 83% higher foliar C:P than completely or incompletely scorched saplings, respectively (Fig. 4) (Appendix 2). Incompletely scorched sapling foliar C:P also statistically exceeded that of completely scorched saplings (Fig. 4) (Appendix 2). Finally, unburned saplings maintained 56% and 43% greater foliar N:P compared to completely scorched and incompletely scorched saplings, respectively (Fig. 4) (Appendix 2). However, incompletely scorched sapling foliar N:P did not statistically differ from that of completely scorched saplings (Fig. 4) (Appendix 2).

Woody tissue stoichiometry

Longleaf pine sapling woody C:N ($F_{(4,161)} = 26.64$, $p < 0.0001$), C:P ($F_{(4,161)} = 12.68$, $p < 0.0001$), and N:P ($F_{(4,161)} = 43.52$, $p < 0.0001$) varied significantly among completely scorched, incompletely scorched, and unburned saplings over time. Two weeks post-fire, incompletely scorched longleaf pine saplings maintained 22% higher woody C:N than unburned saplings (Fig. 5) (Appendix 3). At this time, completely scorched longleaf pine sapling woody C:N did not statistically differ

from that of incompletely scorched or unburned saplings (Fig. 5) (Appendix 3). Also, at 2 weeks post-fire, incompletely and completely scorched longleaf pine sapling wood C:P was 55% and 39% higher than that of unburned saplings, respectively (Fig. 5) (Appendix 3). Similarly, at 2 weeks post-fire, incompletely and completely scorched longleaf pine sapling woody N:P was 25% and 23% greater than that of unburned saplings (Fig. 5) (Appendix 3). No statistical differences in woody C:P or N:P were detected between completely and incompletely scorched longleaf pine saplings 2 weeks post-fire (Fig. 5) (Appendix 3).

Four weeks post-fire, longleaf pine woody C:N, C:P, and N:P were statistically similar across completely scorched, incompletely scorched, and unburned longleaf pine saplings (Fig. 5) (Appendix 3). However, after 24 weeks post-fire, completely scorched longleaf pine sapling woody C:N was 167% and 32% higher than that of unburned and incompletely scorched saplings, respectively (Fig. 5) (Appendix 3). Incompletely scorched longleaf pine sapling woody C:N also statistically exceeded that of unburned saplings (Fig. 5) (Appendix 3). Unburned longleaf pine sapling woody C:P was 29% larger than that of incompletely scorched saplings (Fig. 5) (Appendix 3). Similarly, unburned longleaf pine sapling woody N:P was 193% and 166% larger than values of incompletely and completely scorched saplings, respectively (Fig. 5) (Appendix 3). Completely and incompletely scorched longleaf pine saplings did not significantly differ in woody C:P or N:P (Fig. 5) (Appendix 3).

N and P concentration in senescing scorched needles and living woody tissues

Four weeks post-fire, longleaf pine sapling foliar N concentration ranged from 0.87 to 0.98% and statistically differed among completely scorched, incompletely scorched, and unburned saplings ($F_{(2,57)}=4.18$, $p=0.0203$) (Fig. 6). Incompletely scorched longleaf pine saplings maintained 13% higher foliar N than unburned saplings (Fig. 6). Completely scorched sapling foliar N concentration did not statistically differ from either incompletely scorched or unburned saplings. At the time of needle abscission (4 weeks), the foliar N concentration of incompletely (0.98%) and completely scorched (0.93%) longleaf pine saplings fell within the intermediate range of N resorption proficiency (0.7 to 1.0%). At 4 weeks post-fire, longleaf pine woody tissue N concentration was similar (0.44–0.45%) among completely scorched, incompletely scorched, and unburned longleaf pine saplings and did not statistically differ ($F_{(2,57)}=0.07$, $p=0.9290$) (Fig. 6).

Four weeks post-fire, longleaf pine foliar P concentration was nearly identical among completely scorched, incompletely scorched, and unburned saplings (0.061–0.066%) ($F_{(2,57)}=0.20$, $p=0.8200$) (Fig. 7). At this time, incompletely (0.066%) and completely (0.064%) scorched longleaf pine sapling foliar P concentration fell within the incomplete range of P resorption proficiency for evergreen species (>0.05%).

In contrast, treatment did have a significant ($F_{(2,57)}=4.70$, $p=0.013$) effect on woody P concentration, which ranged from 0.038 to 0.048% (Fig. 7). Completely scorched longleaf pine saplings had significantly (21%) higher woody P concentration at the 4 weeks post-fire timepoint than unburned saplings (Fig. 7). However, there was no statistical difference between incompletely scorched saplings and any other treatment group (Fig. 7).

Discussion

Woody plants are subjected to lethal heating during wildland fires, with consequences for short- and long-term stress and mortality. The capacity of woody plants to recover from fire-caused injuries enables some species to dominate post-fire environments while other species lacking the necessary adaptations are locally extirpated (Hood et al. 2018; Stevens et al. 2020; Reed et al. 2025). How woody plants deal with ubiquitous crown scorch following wildland fires has been a major unknown, as these injuries are the primary correlate of post-fire tree mortality across diverse taxa (Cansler et al. 2020; Varner et al. 2021).

Partially consistent with our initial hypothesis, completely and incompletely scorched longleaf pine saplings possessed significantly lower foliar C:N, C:P, and N:P than unburned saplings 24 weeks post-fire. However, in contrast to our initial hypothesis, foliar N concentrations of completely and incompletely scorched saplings at the time of needle abscission were greater than or equal to that of unburned saplings and fell within the intermediate range of N resorption proficiency (0.7 to 1.0%) (Killingbeck 1996). Moreover, no statistical difference in woody tissue N was found among completely scorched, incompletely scorched, and unburned saplings at the time of post-fire needle abscission. Similar trends occurred with P, as completely and incompletely scorched longleaf pine saplings did not statistically differ in foliar or woody tissue P concentrations at the time of needle abscission and fell within the incomplete range of foliar P resorption proficiency for evergreen species (>0.05%) (Killingbeck 1996). Collectively, these results indicate that crown scorch intensity had no effect on foliar N or P content at the time of scorched needle abscission, and suggest, but do not conclusively confirm, that fire-injured longleaf pine saplings are not effective at conserving N or P from scorched needles. Rather, a substantial increase in soil P 2 weeks post-fire combined with remobilization from surviving residual tissues likely drove post-fire nutrient

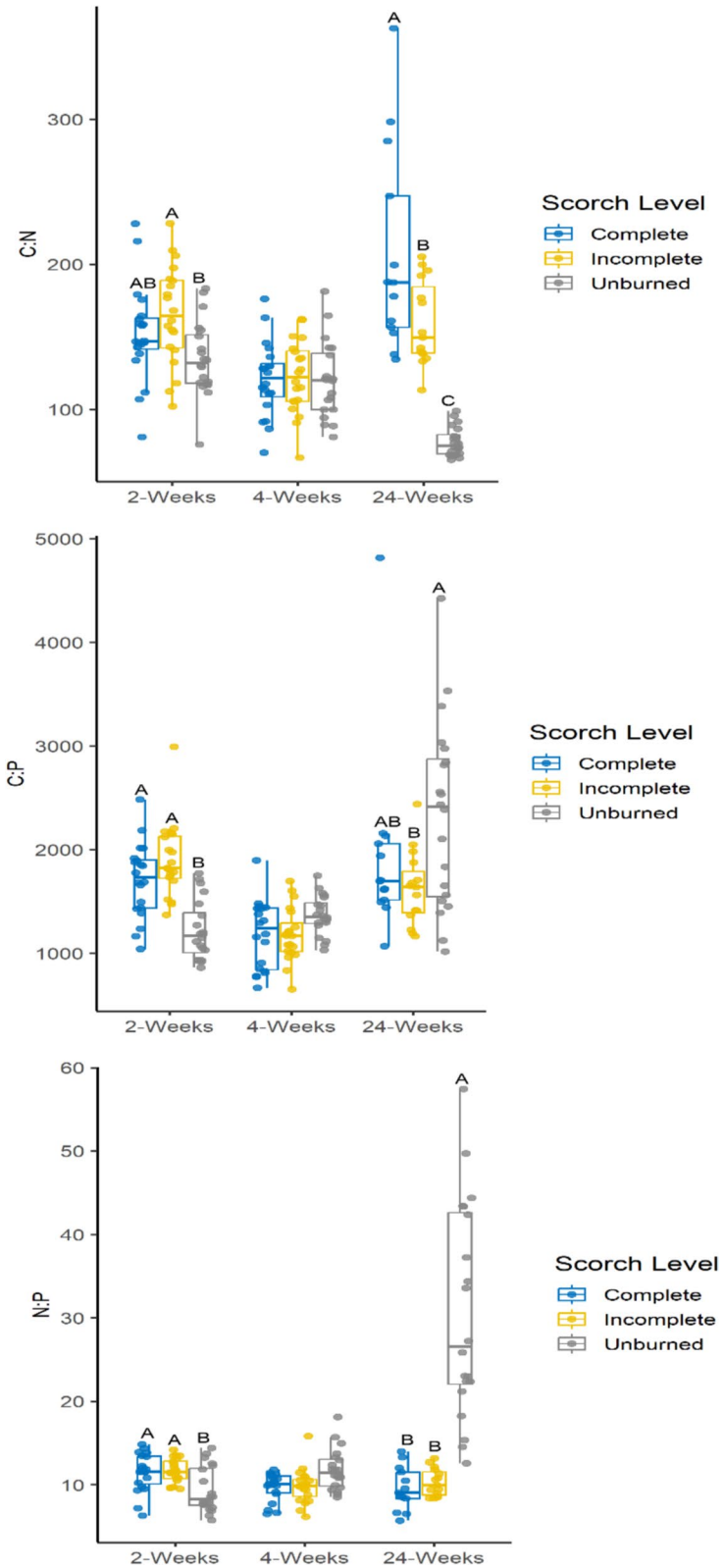


Fig. 5 The effects of crown scorching on longleaf pine sapling woody tissue C:N, C:P, and N:P 2 weeks, 4 weeks, and 24 weeks post-burn. Boxplots featuring different letters were statistically different ($\alpha = 0.05$). Post hoc comparisons were made within temporal sampling periods

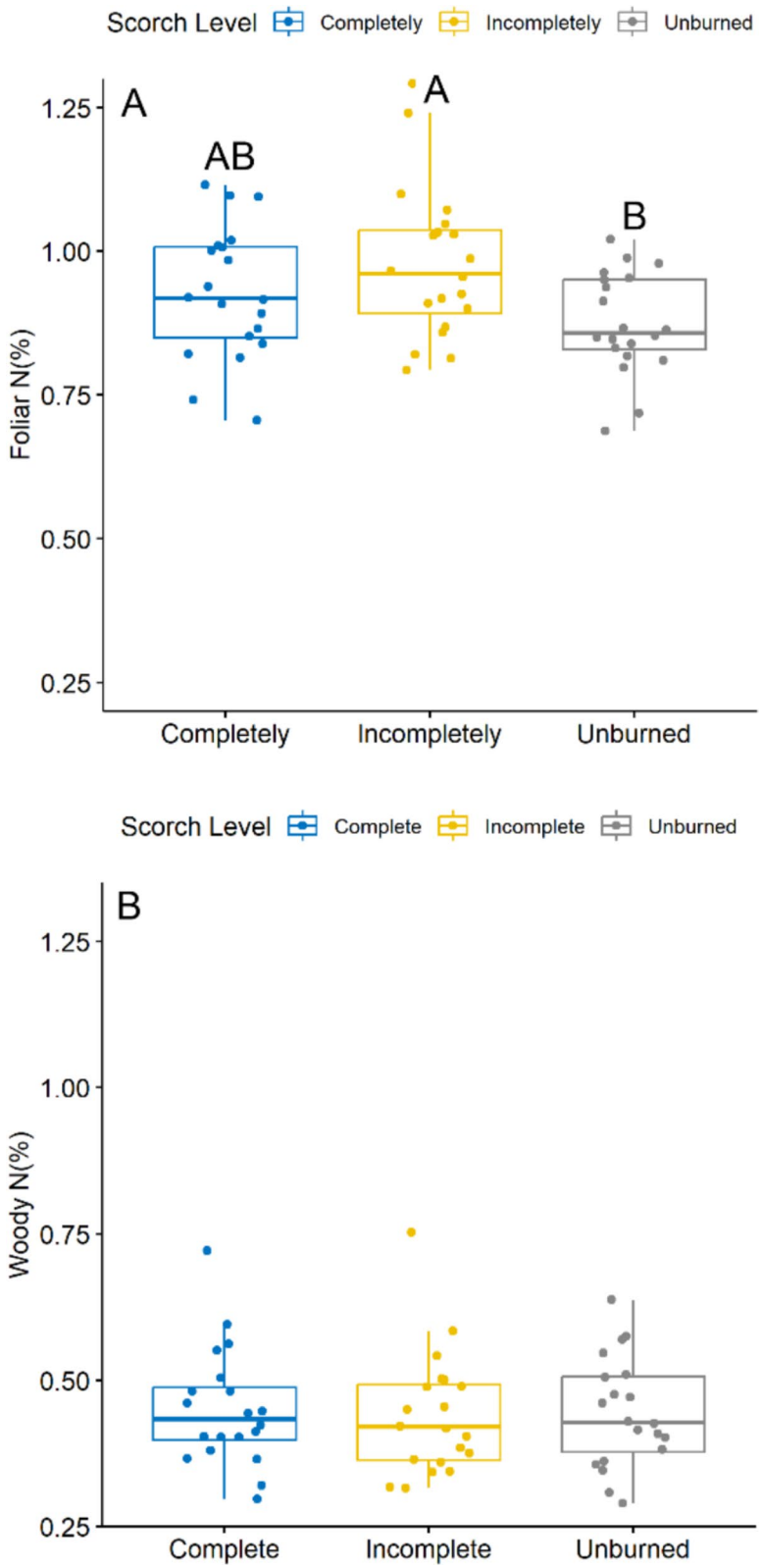


Fig. 6 The effects of fire intensity on longleaf pine sapling foliar (**A**) and woody tissue (**B**) nitrogen concentration 4 weeks post-burn. Boxplots featuring different letters were statistically different ($\alpha = 0.05$)

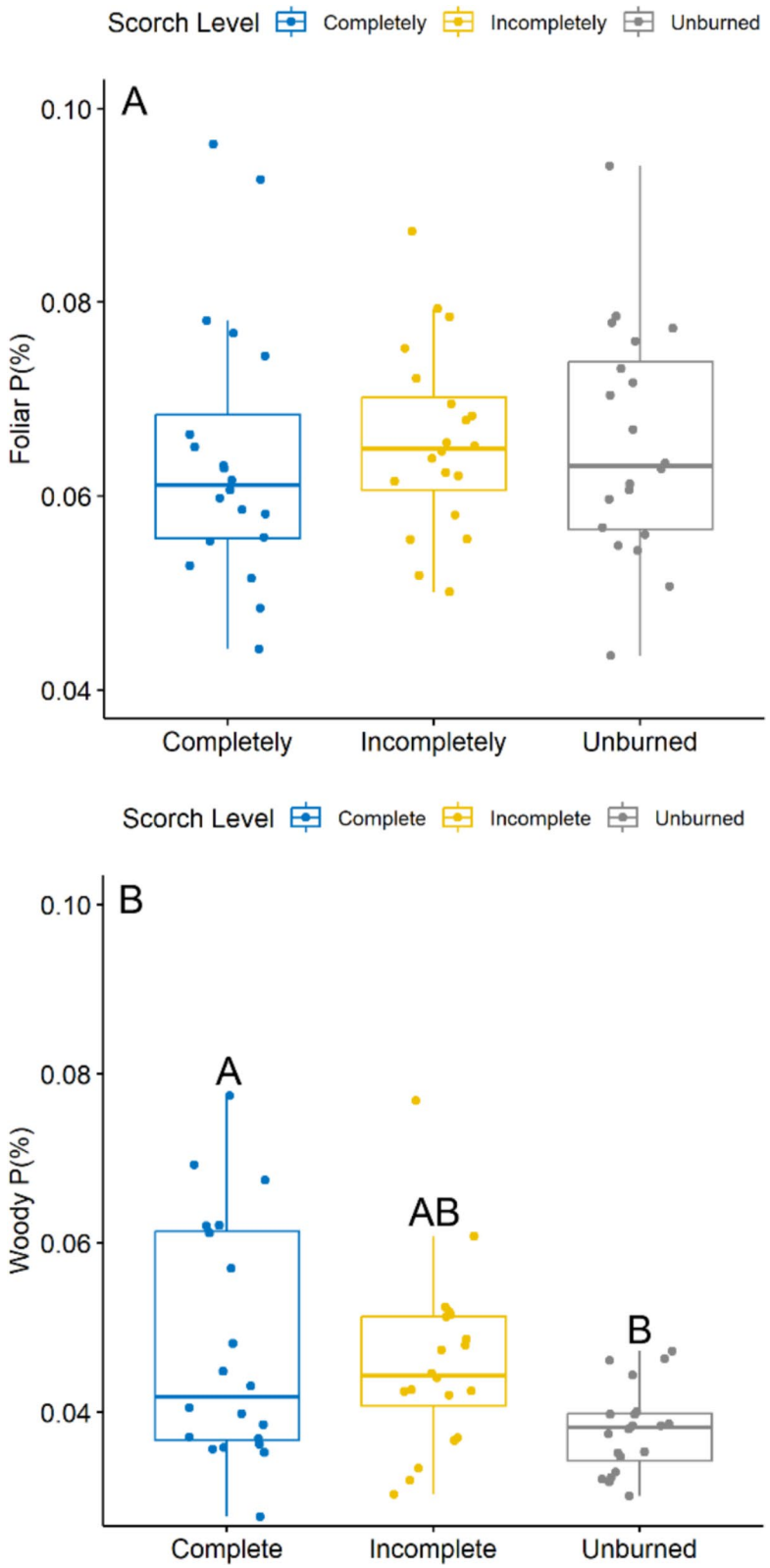


Fig. 7 The effects of fire intensity on longleaf pine sapling foliar (**A**) and woody tissue (**B**) phosphorus concentration 4 weeks post-burn. Boxplots featuring different letters were statistically different ($\alpha = 0.05$)

dynamics. Below, we discuss salient trends and provide potential explanations for our results.

N and P loss from scorched needles

One hypothesis for the loss of foliar N and P from completely scorched longleaf pine saplings is the potential occurrence of rapid, irreparable physiological damage by fire to the foliage. While exposure to heat was not measured at the sapling level, fire temperatures (surface to 1.5 m height) averaged across the entire burned unit surpassed the lethal tissue temperature of 60 °C for 2 to 4 min (Wade and Johansen 1986; Dickinson and Johnson 2001). Longleaf pine saplings were on average exposed to an additional 7 min of sub-lethal temperatures adding to the total heat energy dose (O'Brien et al. 2018). Given that seedling size was largely controlled by our sampling design, it is probable that completely scorched saplings received a higher total energy dose than incompletely scorched saplings and may have experienced rapid needle necrosis. For comparison, exposure to convective heating for 10 min at 55 °C caused yellowing of Scots pine (*P. sylvestris*) needles after 4 days, and near complete abscission of foliage after 4 weeks (Gette and Pakharkova 2020). Thus, if completely scorched saplings indeed experienced rapid, widespread needle xylem and phloem necrosis, any pre-existing foliar N and P would likely become trapped leading to its eventual loss. Rapid needle necrosis may also explain why similar foliar N and P trends were observed in saplings with incomplete crown scorch, but other factors must also be considered.

Although not always statistically detectable in our study, fire generally increases soil NO_3^- and total P availabilities, potentially making post-fire N and P acquisition energetically efficient (Wright and Westoby 2003; Schafer and Mack 2010; Agbeshie et al. 2022). Another plausible explanation for poor conservation of foliar N and P in completely and incompletely scorched longleaf pine saplings could be attributed to the timing of fire relative to seasonal resorption, as conifers seasonally transfer nutrients from old to young needle cohorts before fall senescence (Chapin and Kedrowski 1983; Nambiar and Fife 1991; Yuan et al. 2018). Thus, the saplings sampled in this study may not have been physiologically primed to transport nutrients from scorched needles given that our prescribed burn occurred in February. During the growing season, luxury nutrient stores in conifer foliage may also be remobilized to support the strong nutritional demand of reproductive organs (Wu et al. 2023). However, this too is unlikely to have influenced our results due to the timing of our fire and the lack of conelets and cones observed on saplings prior to burning.

Early post-fire soil P enrichment effects on foliar nutrition

Evidence supporting the role of fire in nutrient enrichment was most apparent with P, which was scarce at our site (<1 ppm). In general, soil P less than 4 to 6 ppm is considered deficient for longleaf pine (Dickens et al. 2017; Dickens et al. 2020). We observed soil enrichment with P near completely scorched saplings 2 weeks post-burn. This result aligns with ash deposition and both chemical and biological soil changes that yield a pulse of available P after fire (Agbeshie et al. 2022; Butnor et al. 2020; Giardina et al. 2000; Lavoie et al. 2010). Increases in soil P 2 weeks post-fire corresponded with lower foliar C:P in completely scorched saplings compared to unburned saplings. Nevertheless, trends in foliar stoichiometry at 2 and 4 weeks post-fire may not be directly related to changes in soil nutrient availability 2 weeks post-fire considering that completely and incompletely scorched saplings may have lost the ability to transport root acquired N and P into fire-damaged needles. Moreover, there is no biological reason to transport soil-acquired nutrients to tissues that are nearing senescence. It is more likely that newly acquired N and P would be stored in undamaged living tissues and remobilized to support crown refoliation (Millard and Grelet 2010a, b). In support, Dunson et al. (2023) reported the temporal dynamics of soil nutrients among mixed pine sites in east Texas that were prescribed burned every 2 to 3 years. They found that some mobile nutrients (e.g., K, Mg, and ammonium-N) increased in the surface mineral soil immediately after prescribed burning but then decreased for the first growing season after prescribed fire. Synchrony between fire deployment and the acquisition, storage, and remobilization of soil resources that are stockpiled and later utilized for rapid growth warrants further investigation as an adaptation of longleaf pine to frequent fire on nutrient-poor sites.

Additional hypotheses related to post-fire P dynamics

At our P-deficient site, the extent of soil P available for sapling use after crown scorch was likely affected by at least two factors. First, the degree of crown scorch may have affected how P was partitioned within saplings. Specifically, the healthy residual needles of incompletely scorched longleaf pine saplings likely shifted from P-deficiency to P-sufficiency following the pulse of soil P 2 weeks post-fire. Subsequently, a fraction of the soil P pulse would be available to both residual foliage and immature needles of emerging shoots in early spring. In contrast, after complete crown scorch, residual foliage was eliminated as a destination for newly acquired P. As such, the greatest opportunity for developing foliage to acquire adequate P on this P-deficient site was afforded to completely scorched saplings. By July which was 24 weeks post-fire, this scenario may have contributed to

completely scorched saplings maintaining higher foliar C:P than incompletely scorched saplings.

Similar to P observations, foliar K concentrations by treatment at 24 weeks post-fire indicate that foliage retained after dormant season fire may hinder the supply of K to new foliage produced in the next growing season. Specifically, foliar K concentrations at 24 weeks post-fire averaged 0.50% for the incompletely and completely scorched saplings but was 0.22% for the unburned saplings (Appendix 2). This trend in K nutrition is likely inconsequential on sites where K is plentiful. However, results of a region-wide loblolly pine (*P. taeda*) nutrition assessment suggest that K limitations to pine growth are possible on highly leached soils formed from weathered sand and marine terrace deposits (Carlson et al. 2014). Poor growth among a subset of loblolly pine stands fertilized with N and P was attributed to K deficiency with surface mineral soil K values of 11.8 ppm and 33.8 ppm, and dormant season foliage K values of 0.30% and 0.47%, respectively, for K-deficient and K-sufficient stands. In our study, unburned sapling soil and foliar K in February were 13.2 ppm and 0.37%, respectively, and were not indicative of K deficiency by available standards (Dickens et al. 2017). However, during the growing season after fire application when bolting was underway for most saplings, we observed foliar K concentrations of unburned and burned seedlings of 0.22% and 0.50%, respectively. The Troup sand at our study site developed from a parent material of unconsolidated sandy and loamy marine deposits like that of the K-poor soils reported by Carlson et al. (2014). These findings suggest that further research is warranted to determine K sufficiency for maximum stem growth during the bolting stage in young stands of longleaf pine on deep sands. A second factor that may have affected post-fire available P is a change in surface soil P-mineralization in response to the accumulation of scorched needles on the forest floor, and subsequent shifts in the soil environment that favor microbial activity. In our study, all scorched foliage was deposited on the forest floor by July (Gette and Pakharkova 2020; Wade and Johansen 1986). Under normal mid-summer conditions, the surface soil in longleaf pine stands is characterized by low moisture content. However, accumulation of longleaf pine litter at the base of saplings provided fresh inputs of decomposable organic material and may have reduced evaporative water loss and increased soil moisture content (Hornsby et al. 1995; Singh et al. 2021). Past research has shown that soil moisture is correlated with P-mineralization and other microbial processes in southern pine forest soils (Grierson et al. 1999; Wilson et al. 1999). Compared to incompletely scorched saplings, perhaps the decrease in foliar C:P observed in completely scorched saplings in July was due, in part, to greater litter accumulation, less evaporative soil water loss, and more P-mineralization in the surface soil.

Conclusions

There remains a perplexing question about woody evergreens and fire injury: what physiological mechanism(s) enable survival following periodic fire damage? In *Pinus-dominated* ecosystems, fire return intervals are often as frequent as several times per decade (Guyette et al. 2012; Varner et al. 2022). Surface fire was particularly important in shaping the longleaf pine ecosystem which burned on average every 1 to 3 years in a combination of dormant and growing seasons (Stambaugh et al. 2011; Rother et al. 2020). These frequent fires injure foliage via crown scorch and consumption, often damage branch and stem vascular tissues, and injure roots near the surface of the soil (Dickinson and Johnson 2001, Hood et al. 2018, O'Brien et al. 2018; Partelli-Feltrin et al. 2023; Bizzarri et al. 2025). Fire-tolerant species like longleaf pine and others have adapted to fire by traits such as crown lift in response to heat-induced lower crown pruning, development of a thick and rugose bark, seasonal availability of ample carbon resources for post-scorch foliage regrowth, and crown and branch architectures that minimize convective heating (Keeley and Zedler 1998; Sayer et al. 2020; Stevens et al. 2020; McGuire et al. 2021). Co-occurring physiological mechanisms that repair injured tissues, retain nutrients and water, and otherwise enable post-fire stress tolerance remain elusive.

Our results indicate that completely and incompletely scorched longleaf pine saplings lose foliar N and P from senesced needles post-fire. The most plausible cause of this is heat-induced impairment of the needle vascular system. At the same time, a possible outcome of needle scorch is a short-lived increase in the availability of essential nutrients creating a window of time when the acquisition and uptake of scarce resources (i.e., P, K) is energetically inefficient. Our results further suggest that coordination may be warranted between the timing of fire and periods of high nutrient demand on infertile sites. Future studies can build upon our results by assessing the physiological function of scorched needles immediately post-burn, incorporating isotopic labeling to track post-fire nutrient dynamics in the soil and stand, and evaluating the value of coordination between fire timing and seasonal peaks in nutrient demand. Researching these unaddressed areas of inquiry will further our understanding of how this iconic tree species persists in a fire-dependent ecosystem.

Appendix 1

Table 2 Mean pre-fire longleaf pine sapling root collar diameter and height ± 1 SE in the completely scorched (100%), incompletely scorched (30–80%), and unburned (0%) groups

Pre-fire sapling size	Unburned	Incompletely scorched	Completely scorched
Root collar diameter (mm)	47.0 (1.4)	47.9 (1.7)	47.8 (1.8)
Height (m)	2.2 (0.2)	2.2 (0.5)	2.3 (0.3)

Appendix 2

Table 3 Mean foliar tissue N, P, K, and C concentration (±1 SE) of completely scorched (100%), incompletely scorched (30–80%), and unburned (0%) longleaf pine saplings at 2 weeks, 4 weeks, and 24 weeks post-fire

Crown damage	Foliar N (%)	Foliar P (%)	Foliar K (%)	Foliar C (%)
2 weeks post-fire				
Completely scorched	0.91 ± (0.03)	0.06 ± (<0.01)	0.46 ± (0.02)	50.04 ± (0.19)
Incompletely scorched	0.82 ± (0.02)	0.05 ± (<0.01)	0.45 ± (0.02)	50.12 ± (0.16)
Unburned	0.82 ± (0.02)	0.05 ± (<0.01)	0.37 ± (0.02)	49.99 ± (0.13)
4 weeks post-fire				
Completely scorched	0.93 ± (0.03)	0.06 ± (<0.01)	0.43 ± (0.02)	50.19 ± (0.15)
Incompletely scorched	0.98 ± (0.03)	0.07 ± (<0.01)	0.44 ± (0.02)	50.03 ± (0.10)
Unburned	0.87 ± (0.02)	0.07 ± (<0.01)	0.42 ± (0.02)	50.09 ± (0.15)
24 weeks post-fire				
Completely scorched	0.98 ± (0.03)	0.09 ± (<0.01)	0.49 ± (0.02)	49.41 ± (0.43)
Incompletely scorched	0.82 ± (0.02)	0.07 ± (<0.01)	0.50 ± (0.02)	48.70 ± (0.20)
Unburned	0.68 ± (0.02)	0.04 ± (<0.01)	0.22 ± (0.02)	51.90 ± (0.16)

Appendix 3

Table 3 Mean woody tissue N, P, K, and C concentration (±1 SE) of completely scorched (100%), incompletely scorched (30–80%), and unburned (0%) longleaf pine saplings 2 weeks, 4 weeks, and 24 weeks post-fire

Crown damage	Woody N (%)	Woody P (%)	Woody K (%)	Woody C (%)
2 weeks post-fire				
Completely scorched	0.37 ± (0.02)	0.03 ± (<0.01)	0.27 ± (0.01)	53.28 ± (0.24)
Incompletely scorched	0.34 ± (0.02)	0.03 ± (<0.01)	0.22 ± (0.01)	54.06 ± (0.23)
Unburned	0.41 ± (0.02)	0.05 ± (<0.01)	0.24 ± (0.01)	52.74 ± (0.30)
4 weeks post-fire				
Completely scorched	0.45 ± (0.02)	0.05 ± (<0.01)	0.31 ± (0.01)	52.13 ± (0.19)
Incompletely scorched	0.44 ± (0.02)	0.05 ± (<0.01)	0.31 ± (0.01)	51.48 ± (0.18)
Unburned	0.44 ± (0.02)	0.04 ± (<0.01)	0.21 ± (0.01)	51.02 ± (0.20)
24 weeks post-fire				
Completely scorched	0.29 ± (0.02)	0.03 ± (<0.01)	0.23 ± (0.02)	55.07 ± (0.21)
Incompletely scorched	0.36 ± (0.02)	0.04 ± (<0.01)	0.24 ± (0.02)	55.13 ± (0.25)
Unburned	0.68 ± (0.02)	0.03 ± (<0.01)	0.13 ± (0.01)	51.77 ± (0.19)

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Code availability
The code used and/or analyzed during the current study is available from the corresponding author on reasonable request.

Authors' contributions
The study was designed by JLW, TMS, MV, and AS. Material preparation, data collection, and analysis were conducted by JLW and AS. The first draft of the manuscript was written by JLW and all authors commented on previous versions of the manuscript. All authors read and approved of the final manuscript.

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Data availability
The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate
This article does not contain any studies with human participants or animals performed by any of the authors.
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare no competing interests.

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